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FRONTIERS IN CONSERVATION SCIENCE – HIGHLIGHTS FROM ITS FIRST YEAR.

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Table of Contents

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A World for Reactive Phenotypes

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Humans currently occupy all continents and by doing so, modify the environment and create novel threats to many species; a phenomenon known as human-induced rapid environmental changes (HIREC). These growing anthropogenic disturbances represent major and relatively new environmental challenges for many animals, and invariably alter selection on traits adapted to previous environments. Those species that survive often have moved from their original habitat or modified their phenotype through plasticity or genetic evolution. Based on the most recent advances in this research area, we predict that wild individuals with highly plastic capacities, relatively high basal stress level, and that are generally shy—in other words, individuals displaying a reactive phenotype—should better cope with sudden and widespread HIREC than their counterparts' proactive phenotypes. If true, this selective response would have profound ecological and evolutionary consequences and can therefore impact conservation strategies, specifically with respect to managing the distribution and abundance of individuals and maintaining evolutionary potential. These insights may help design adaptive management strategies to maintain genetic variation in the context of HIREC.

Keywords: coping style, antipredator behavior, evolution, stress physiology, ecology, predation, urbanization, pollution

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INTRODUCTION

Conservation scientists have long recognized the importance of genetic variation for the management of sustainable populations (Loeschcke et al., 2013), including in the context of global changes (Rice and Emery, 2003). However, much less is known regarding the significance of evolutionarily important phenotypic traits, including physiological and personality traits, on the likelihood of successful management. Emphasizing the role of physiology is relatively recent, as exemplified by the recent launch (2013) of the journal "Conservation Physiology" (see also Cooke et al., 2014). Animal personality has also been recently included in the myriad of factors that could have profound consequences on population management (Réale et al., 2010a).

When within-individual variation of a behavioral trait is less than among-individual variation, this is defined as "personality" (Roche et al., 2016). Sometimes different personality traits co-vary (e.g., boldness is positively correlated with aggressiveness), and this defines a behavioral syndrome (Sih et al., 2004; Bell, 2007). Behavioral syndromes are related to the older notion of "coping styles" (Koolhaas et al., 1999), in that individuals are described on a reactive-proactive continuum based on their physiological and behavioral responses to a challenge. At one end of the continuum, reactive animals are those that are shy, less aggressive and less active compared to their proactive counterparts. But they are also characterized by high hypothalamic-pituitary-interrenal/adrenal (HPI/A) responses to stressors and low sympathetic activity compared to proactive ones

(Koolhaas et al., 2010). In this sense, Koolhaas et al. (2010) specified that "proactive coping is characterized by low flexibility expressed as rather rigid, routine-like behavioral tendencies and reduced impulse control (behavioral inhibition) in operant conditioning paradigms." Many studies have identified a range of behavioral and physiological traits that are linked to being reactive or proactive. **Figure 1** illustrates to what extent proactive and reactive animals differ based on two authoritative reviews on the subject (Koolhaas et al., 1999, 2010).

Coping styles can evolve. Significant heritability in coping styles has been reported multiple times in wild and captive contexts and for various taxa including mammals, birds, reptiles, and fishes (Carere et al., 2003; Drent et al., 2003; Øverli et al., 2007; Ferrari et al., 2016; Øverli and Sørensen, 2016; Navas González et al., 2018; Wong et al., 2019). These studies all provide evidences that coping styles are genetically driven and can be shaped by selective pressures that lead to evolved changes. Additionally, coping styles may have fitness consequences where proactive or reactive individuals are differently favored depending on the environment (Smith and Blumstein, 2008; Réale et al., 2010b; Monestier et al., 2015; Moiron et al., 2020).

Early research on coping styles was carried out on animals selected for aggressiveness, or for HPI response, thus giving the well-known proactive/reactive dichotomy (Koolhaas et al., 1999; Øverli et al., 2007). However, later work in non-selected populations observed a continuum between these two extremes responses rather than a bimodal distribution (Ferrari et al., 2013; Monestier et al., 2015; Bensky et al., 2017; Daniel and Bhat, 2020). It is worth noting that some studies failed to discover consistent coping styles in the wild (Qu et al., 2018), possibly because predation pressure (a major selective force) might constrain the variability of behavioral and physiological traits (Geffroy et al., 2020), by selecting proactive or reactive individuals as a function of predation intensity.

From an ecological perspective, this structure has major implications for ecosystem dynamics since it drives intra-population competition as well as inter-species interactions (Bolnick et al., 2011; Sih et al., 2012). From an evolutionary point of view, variability in coping styles is also of primary importance since it constrains a population's capacity to adapt to environmental changes and determines the response to natural selection (Dingemanse and Réale, 2005). Yet, most of the studies focusing on coping styles in different contexts have been performed in fishes (**Figure 2**) and we suggest that a more comprehensive understanding of coping styles in all taxa must be developed because they may play a vital demographic role and hence influence population persistence and ecosystem dynamics.

Through extensive harvesting, environmental pollution, habitat loss and fragmentation, the introduction of exotic species, urbanization and climate change, humans modify the strength and direction of natural selection. This has profound consequences on the behavior and physiology of many species. These human-induced rapid environmental changes, or HIREC (Sih et al., 2011), have rapidly proliferated across the world, and better understanding the response to these changes is of primary importance for conservation and management Another emerging threat for wild species concerns the increased pressure caused by tourism and eco-tourism on wildlife (Geffroy et al., 2015; Blumstein et al., 2017), so that we suggest here to include mass tourism as a new HIREC. While behavioral responses to HIREC have previously been reviewed (Sih et al., 2011; Tuomainen and Candolin, 2011; Sih, 2013; Wong and Candolin, 2015), the associated underlying physiological mechanisms of the differences in coping style have been relatively ignored (**Figure 2**). We argue that they are essential traits to consider when animals will have to cope with HIREC, since behavioral responses alone do not necessarily map on perfectly with physiological responses and long-term associated costs.

Here, we focus on the multiple physiological and behavioral processes by which HIREC modifies the coping style structure of populations. Based on recent literature, we hypothesize that evolutionary responses to HIREC that resulted in increased selection at the intraspecific level may generally favor reactive individuals. Under this hypothesis, the reactive-proactive continuum of a population influenced by HIREC is assumed to shift toward reactive individuals. We propose that this change is the consequence of three different time-related steps starting with habitat changes (migration or dispersal), where proactive animals would be more likely leave unfavorable situations. Then, we suggest that reactive individuals have enhanced survival due to higher physiological and behavioral plasticity when facing unexpected events. Finally, we propose that long-term exposure to HIREC can result in genetic evolution favoring more reactive phenotypes (**Figure 3**). We provide accumulated evidence for all three described processes, but also note the limits of this perspective by providing relevant counter-examples. We discuss the ecological consequences of this speculative loss of proactive phenotypes and highlight its conservation relevance.

CHALLENGING SITUATIONS MAKE PROACTIVE INDIVIDUALS CHANGE HABITATS

The quickest response for individuals in a wild population to avoid human presence and associated environmental changes is to flee and change habitats. This first step in response to HIREC (**Figure 3.1**), is nevertheless highly dependent upon an individual's personality. Prior work has indeed shown that inter-individual differences in the propensity to disperse are linked to personality traits (Cote and Clobert, 2007; Clobert et al., 2009; Cote et al., 2010a). Bold individuals are generally more active, explore novel areas faster and are more likely to disperse farther (reviewed in Réale and Montiglio, 2020). Harrison et al. (2015) also differentiated "resident" from "mobile" individuals. Mobile individuals tend to explore more, be more active and be less site-specific, and thus, they resemble proactive individuals. In this sense, less socially embedded yearling female marmots (*Marmota flaviventer*) are also more likely to disperse (Blumstein et al., 2009), and in the month preceding dispersal these marmots upregulate a suite of specific genes, many of which are associated with migration (Armenta et al., 2018).

Yet, the fact that bolder individuals are more likely to disperse might not be always true. For example, resident wild

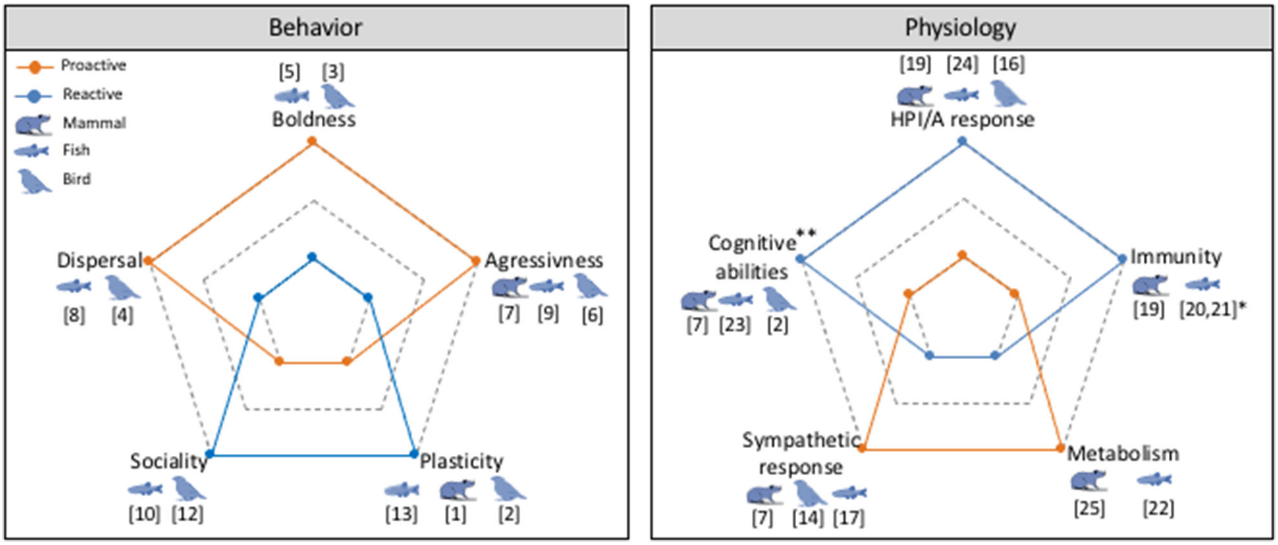

FIGURE 1 | Radar charts describing the behavioral and physiological features of proactive (orange) and reactive (blue) coping style. *Note that concerning immune capacities, fishes exhibit opposite tendency to that described in Koolhaas et al. (2010) and Réale et al. (2010b). **Here, cognitive capacities are referring to cognitive capacities in changing environment context, where reactive animals displayed better performances. A non-exhaustive list of examples is presented in this figure from mammals, fishes and birds. Numbers refer to the studies as follows: Behavior: [1] (Benus et al., 1990); [2] (Verbeek et al., 1994); [3] (Carere and van Oers, 2004); [4] (Mettke-Hofmann et al., 2005); [5] (Øverli et al., 2006); [6] (Kralj-Fišer et al., 2007); [7] (Koolhaas et al., 2010); [8] (Chapman et al., 2011); [9] (Castanheira et al., 2013); [10] (Geffroy et al., 2014); [11] [12] (Kralj-Fišer et al., 2007); [13] (Ruiz-Gomez et al., 2008). Physiology: [2] (Verbeek et al., 1994); [14] (Korte et al., 1998); [15] (Bolhuis et al., 2003); [16] (Carere et al., 2003); [17] (Brelin et al., 2005); [18] (Huntingford et al., 2010); [7] (Koolhaas et al., 2010); [19] (De Miguel et al., 2011); [20] (Kittilsen et al., 2012); [21] (Vargas et al., 2018); [22] (Yuan et al., 2018); [23] (Baker and Wong, 2019); [24] (Wong et al., 2019); [25] (Careau et al., 2011).

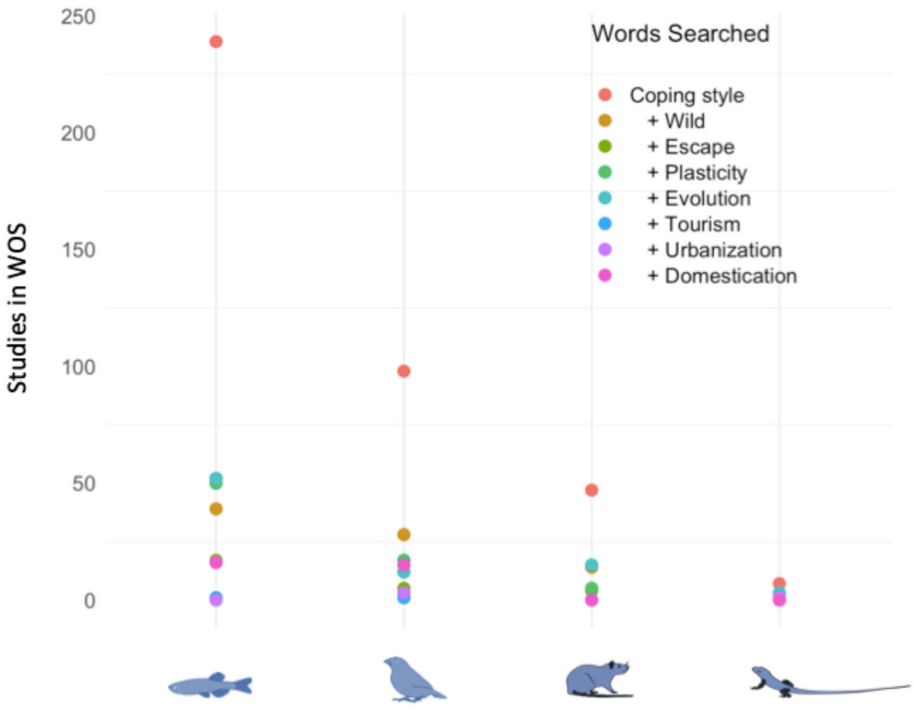

FIGURE 2 | Number of studies in Web of Science investigating coping styles and various HIRECs in 4 taxa: Fish, Birds, Mammals, and Lizards (searched on the 14 September 2020 with Ifremer access).

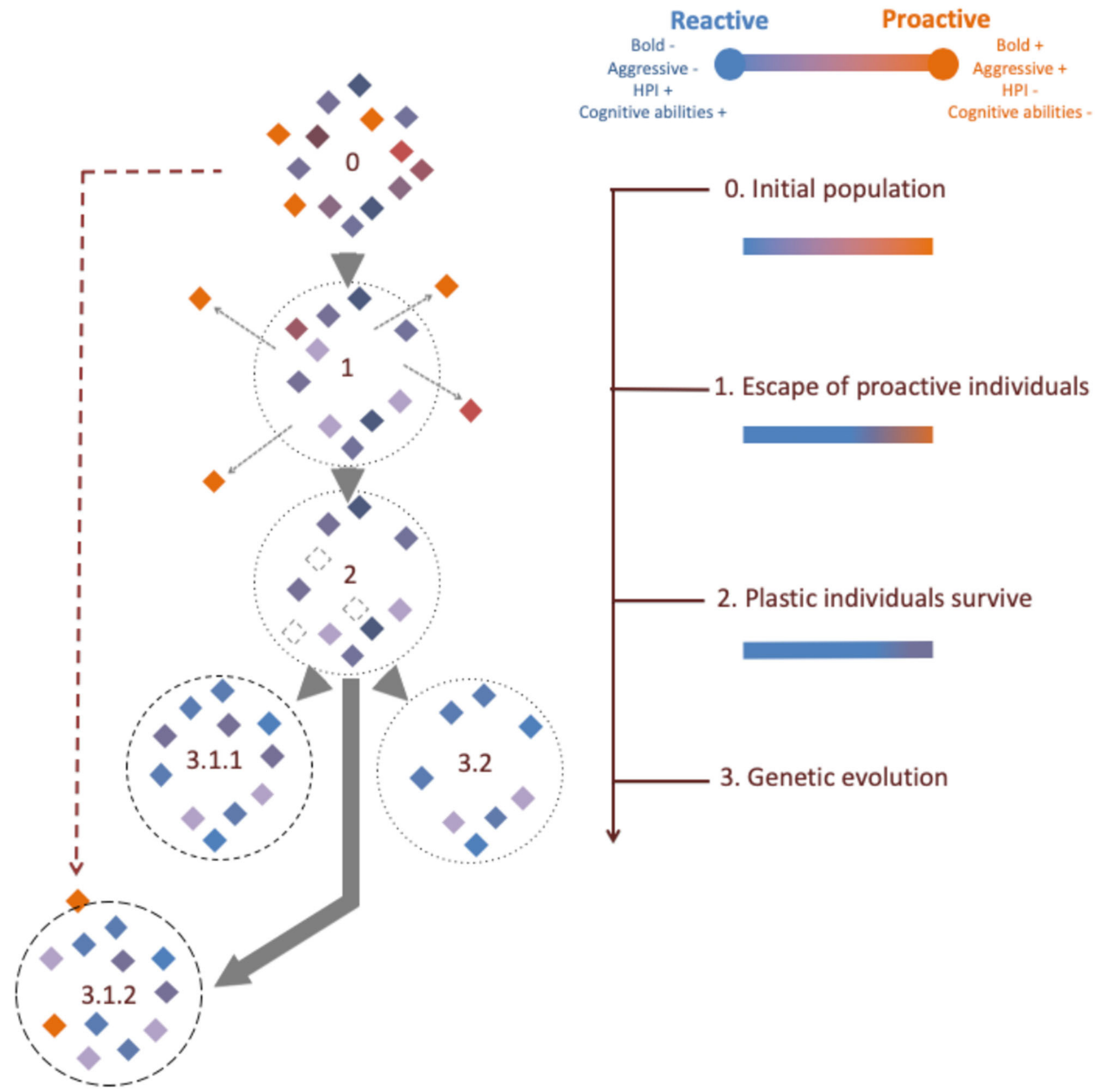

FIGURE 3 | Temporal consequences of Human Induced Rapid Environmental Changes (HIREC) on the reactive-proactive continuum. Animals are from 0. An initial pristine population exposed to HIREC with effects on 1. dispersal, 2. phenotypic plasticity, 3. genetic evolution related to HIREC that produce 3.1. a human predator shield such as 3.1.1. Tourism and 3.1.2. Urbanization or 3.2. that do not produce a human shield (e.g., Climate Change, Pollution, or Harvesting). The dashed purple arrow highlights the fact that some proactive individuals could invade urban areas. The shape of the border of each circle directly correlates to the intensity of human-shield, from no contact (light dashed circle), to high contact (full circle). The diamond color corresponds to individual phenotypic coping style.

elk (*Cervus canadensis*) habituated to human presence in two Canadian national parks (Banff and Jasper) were shown to be bolder and more dominant than migrants elk (Found and St. Clair, 2019). One reason could be that this was because dominant individuals were residents. But this observation could also be the result of high contact with humans in the parks, where some individuals are, or become bold to exploit new food sources or due to habituation (Found and St. Clair, 2019), a case we specifically discuss below (see HIREC relaxing selection pressure section). Interestingly, these individuals also exhibited characteristics of reactive phenotypes (i.e., high cognitive flexibility), which could support the second hypothesis where initially shy individuals become bold following human contact.

Overall, when the outcome of the encounter is positive (e.g., increased access to food or protection from predators), then we might expect that bold individuals remain. However, when HIREC reduces habitat quality or when the situation becomes more challenging, then we expect bold individuals to be better at escaping (**Figure 3.1**). For instance, bold crabs were the first to disperse when habitat quality was reduced (Belgrad and Griffen, 2018). Bolder fish make more attempts to escape laboratory-induced hypoxia (Brelin et al., 2005; Ferrari et al., 2016), salinity challenges (Zeng et al., 2019) or high ammonia concentrations (Gesto et al., 2020). Bold individuals are also better at avoiding or escaping fishing gear (Diaz Pauli and Sih, 2017). And, individual great tits (*Parus major*) that are relatively more exploratory are located further away from polluted sites (Grunst et al., 2019a,b), although we cannot exclude that pollutants directly affects their exploration abilities.

Most studies conducted to date on the subject have investigated behavioral traits, while ignoring physiological ones. With respect to coping styles that associate behavior and physiology, most of our knowledge comes from fishes (**Figure 2**). A recent study conducted on juvenile eels pinpointed that individuals that were more likely to climb dams to accomplish their upstream migration, also had lower levels of transcription of synapse-related genes (which are associated with cognitive abilities) compared to others, and were thus coined as proactive (Podgorniak et al., 2016). In European sea bass and Atlantic salmon, individuals who flee from hypoxic environments also have lower HPI stress response and greater serotonin turnover ratio than individuals who remain in hypoxic environments, which is indicative of proactive coping style (Damsgård et al., 2019; Ferrari et al., 2020). Thus, this suggests that proactive individuals are more prone to leave HIREC-impacted areas. Additional work on distinct taxa is, however, needed to clearly identify the physiological and cognitive features of bold/mobile animals in the context of HIREC. We suggest that in many cases, bold/mobile individuals with lower stress responses (i.e., those that are relatively proactive) are more likely to change habitats in stressful situations related to HIREC (**Figure 3.1**) and this may have evolutionary and ecological consequences (Hebblewhite et al., 2005).

HIREC-DRIVEN ADVANTAGES OF PLASTIC INDIVIDUALS

Phenotypic variations for individuals exposed to HIREC are largely documented in their responses to exposure to contaminants, changes in temperature, acidification, environmental noise, etc. Individuals with the best capacities to respond rapidly via behavioral plasticity (van Baaren and Candolin, 2018) or physiological plasticity (Taff and Vitousek, 2016) are therefore the most likely to survive HIREC, as seen with how some species respond to climate change (Beever et al., 2017). In a wide range of taxa, proactive, and reactive phenotypes diverge in their capacities to respond to environmental changes (**Figure 1**). Overall, case studies highlighted the ability of reactive individuals to be more behaviorally plastic in a wide range of circumstances. In house mice (*Mus musculus*) selected for their aggressive behavior, proactive individuals developed routines; a putatively superior strategy in predictable environments (or situations) but not when the environment frequently changed (Benus et al., 1991).

Plasticity may nevertheless be energetically costly (Moran, 1992; Murren et al., 2015). Consequently, in a stable environment, proactive individuals, which are less plastic than reactive individuals, are expected to better perform because less energy is invested in coping abilities, memory and learning capacities (**Figure 1**). The cost of plasticity has been highlighted in great tits, where fast exploring/proactive individuals performed better in stable environments, while the slow exploring/reactive individuals performed better in a variable and fluctuating environment (Dingemanse and de Goede, 2004). In rainbow trout (*Oncorhynchus mykiss*) moved from the UK to Norway, reactive individuals had greater feeding motivation and started to win dyadic fights against proactive opponents; the opposite outcome that occurred prior to being moved (Ruiz-Gomez et al., 2008). Moreover, reactive rainbow trout are also more efficient at finding food when it is relocated (Ruiz-Gomez et al., 2011). Overall, these examples show that reactive individuals have better coping capacities in modified environments, and this highlights the benefits of plasticity. Similarly, in brook trout (*Salvelinus fontinalis*), reactive fish performed better in cognitively complex foraging tasks, even after environmental modifications (White et al., 2017). Comparable conclusions were drawn in birds (Verbeek et al., 1994) and pigs (*Sus scrofa*; Bolhuis et al., 2004), where proactive individuals were less successful in reversal learning than reactive pigs, suggesting that proactive individuals are less plastic. In monogamous red point cichlids (*Amatitlania siquia*), reactive individuals were better at varying their behavioral profile within the pair (Laubu et al., 2016), a capacity that enhances their reproductive success (Gabriel and Black, 2012; Harris and Siefferman, 2014). A recent study on gray seals (*Halichoerus grypus*) also highlighted that mothers displaying reactive coping style presented a more variable energy expenditure in reproduction and reproductive success compared to their proactive counterparts (Twiss et al., 2020); while mean fitness was equal across coping styles (Twiss et al., 2020). The authors proposed that this high variability was linked to reactive mothers attempting to match pup phenotypes to the local environmental conditions (Twiss et al., 2020). Hence, in case of a sudden extreme event (i.e., HIREC), one might expect higher fitness for reactive mothers.

Altogether, the various studies conducted on the subject showed that reactive individuals have increased behavioral capacities to cope with rapid environmental changes, and this might be essential in the context of HIRECs. This is also seen at the physiological level, with reactive individuals having higher capacities to mount physiological responses required to cope with environmental challenges (**Figure 3.2**), partly due to greater HPI/A axis activation when exposed to stressors.

EVOLUTIONARY SHIFTS OBSERVED IN RESPONSE TO HIREC

In response to persistent HIREC, populations might evolve to adapt to new environmental constraints (**Figure 3.3**). It should however be noted that sometimes, environmental (biotic and abiotic) pressures are so intense and ubiquitous (climate, predation, competition and parasitism) that the population does not have sufficient time to adapt, and may instead collapse (White et al., 2014).

Due to its intrinsic variability, it appears essential to categorize HIREC according to its effect since some are acting as additional new direct selective forces on wild populations (e.g., climate change, harvesting, etc.), while others act by reducing selective forces by, for example, protecting prey from their predators (e.g., urbanization, ecotourism). Below, we will explain why this distinction is essential because the two categories have different evolutionary consequences.

i) HIREC increasing selection pressure

HIREC increasing selective pressures drive both behavioral and physiological changes. For example, fish with bold phenotypes can be preferentially, although unintentionally, harvested, resulting in the selective depletion of bold individuals (Biro and Post, 2008). While intensive fishing selects on life history traits (growth, maturation, reproduction), demonstrations of fishing's effects on behavior remained scarce until the last decade (Uusi-Heikkilä et al., 2008). Fishing methods are diverse, and lead to different selection pressures on behavior (Diaz Pauli et al., 2015; Arlinghaus et al., 2017). Passive fishing (e.g., using long-lines, angling, trapping or gill nets) preferentially catch proactive individuals (Biro and Post, 2008; Arlinghaus et al., 2017), while active gear (e.g., trawls or purse seines) unintentionally targets reactive individuals (Heino and Godø, 2002; Diaz Pauli et al., 2015).

Hunting may have weaker effects on wild populations than fishing, yet it too selects for specific behavioral traits. Shyer captive-reared and released pheasants (*Phasianus colchicus*) were more likely to survive to the hunting season than bolder ones (Madden and Whiteside, 2014). In wild reindeer (*Rangifer tarandus*), a long-term study showed that hunting pressure was correlated with increased flight distance over time, suggesting that populations become shyer under consistent hunting pressure (Reimers et al., 2009). Importantly, those elk (*Cervus elaphus*) that were successfully hunted were bolder (Ciuti et al., 2012). Thus, hunting leads to the same result as passive fishing because it selects against bolder individuals and therefore favors reactive phenotypes. Notably, fewer active animals die from active hunting techniques, such as when dogs are used to chase animals, as seen in bear-hunting (Leclerc et al., 2019). As a consequence, the HIREC linked to fishing and hunting seems to favor one coping style over another depending on whether the harvesting technique is active or passive.

We have long known that populations evolve in response to exposure to pollutants and, with the toxification of Earth, chemical pollution has become a common new direct selective force. Empirical studies in the lab monitoring the evolution of behavioral and physiological traits over many generations following exposure to pollutants are rare, despite abundant evidence of rapid evolutionary responses (Whitehead et al., 2017; Saaristo et al., 2018). If the exposure to only one pollutant selected one behavioral response (e.g., boldness or activity), it could be attenuated by a plastic behavioral response (Saaristo et al., 2018). However, there are many pollutants, each with different properties, and the possible interactions between them (Peterson et al., 2017; Saaristo et al., 2018). Additionally, the method of exposure varies and together these pollutants may act as multiple environmental stressors for organisms which must continuously respond to new threats and stressors. This makes it difficult to make concrete predictions about the precise selective forces that may act on a specific coping style.

Nevertheless, pollution is known to generally alter various behavioral traits–such as boldness, activity, dispersal and sociability–as well as physiological traits–such as cognitive abilities or metabolic rate (reviewed in Jacquin et al., 2020). Pollutants can disrupt the syndrome linking physiology and behavior (Jacquin et al., 2020) and could even increase plasticity of physiological and behavioral traits (Tan et al., 2020). Such a variety of responses to the different stressors are likely context-dependent and species-specific, so that it is difficult to anticipate the direction of changes over generations (toward reactive or proactive). In agreement with other authors (Jacquin et al., 2020), we suggest that plasticity, a characteristic more often seen in individuals that tend to be reactive, will be essential to cope with the diversity of stressors created by pollution, as recently highlighted in fishes (Tan et al., 2020).

In the context of climate change, both progressive changes (e.g., increased temperature) as well as an increase in the frequency of extreme events are expected, leading to new direct selective forces. This combinations of threats may also lead to evolutionary changes in the physiology and behavior of wild population by selecting highly plastic individuals who can respond to increased variability (Nussey et al., 2005). Following this reasoning we may thus infer that climate change is driving the evolution of reactive phenotypes (**Figure 3.3.2**). It is nevertheless worth noting that in some very specific cases, opposite results were observed with, for example, tropical cyclones that select for aggressive phenotypes (Little et al., 2019). This suggests that, sometimes, proactive individuals may be better equipped to survive environmental alterations related to climate change.

ii) HIREC relaxing selection pressure

Contrary to previous examples, urbanization and ecotourism are known to relax selective pressure related to predation for species inhabiting these areas, due to the well-described "human shield" they create (Berger, 2007). Studies of the consequences of urbanization and ecotourism have proposed that boldness increases in populations subjected to these HIRECs (Geffroy et al., 2015) in response to the "human shield." A recent phylogenetic meta-analysis showed that antipredator traits of urbanized animals decreased to a similar manner to that of domesticated animals, though at a rate 3 times slower (Geffroy et al., 2020). Throughout the process of urbanization, individuals are becoming bolder and less stressed over generations (Geffroy et al., 2020), and in that sense, more proactive.

This increase in boldness has been seen many times. Birds from urban areas have reduced flight initiation distances (Samia et al., 2015), and engage in more risk-taking behaviors than rural individuals (Miranda et al., 2013). With respect to physiological responses, urban birds facing humans have reduced stress reactivity (Partecke et al., 2006; Atwell et al., 2012). However, increased stress reactivity was observed in urban lizards compared to rural ones in the context of inter-individual social interactions (Batabyal and Thaker, 2019). These results suggest that the response might be tightly associated with the intensity of human-animal interactions, since lizards might be less likely to interact with humans compared to birds, which may view humans as a source of food. Being able to live in urban environments requires substantial individual plasticity. For instance, in response to urban noise, great tits increase their pitch during mating calls to increase the likelihood that potential mates receive the signal (Slabbekoorn and Peet, 2003).

It's important to consider that we still do not really know whether some individuals in urbanized areas become bolder due to consistent interactions with humans or that bold individuals are the one who invade towns (Sol et al., 2013, 2018) (**Figure 3.3.1.2**; dashed arrow). For tourism and ecotourism, biological consequences directly depends on the intensity of human contact, with strong negative interactions triggering avoidance, not habituation (Geffroy et al., 2017) (**Figure 3.3.1.1**). For instance, increased stress reactivity was found in fish interacting closely with tourists (so that they were bold toward humans), but this also came with increased production of neurogenesis markers, suggesting higher plasticity (Geffroy et al., 2018).

Hence, to identify the better coping style under HIREC, two essential parameters must be considered: (1) Does HIREC trigger relaxed selection in the wild? (Lahti et al., 2009), and (2) Does HIREC trigger an ecological trap depending on the scale of the impact? (Hale and Swearer, 2016). For the first parameter, if a HIREC protects animals (i.e., through a human shield), then some proactive phenotypes would thrive in these impacted areas (e.g., an urbanized area). By contrast, if HIREC are increasing selection (by being, for example, consumptive through hunting or fishing), then we expect that reactive individuals will perform better. Note that in both cases, we expect that plastic individuals will do better coping with human presence. For the second parameter, if HIREC are relatively local, then we expect that proactive individuals would perform better due to their higher propensity to escape (reactive individuals will face ecological traps: e.g., localized pollution). However, if HIREC are widespread (which many are), then reactive individuals would likely benefit, due to their greater plasticity. To summarize, we predict that more reactive phenotypes would thrive in most HIREC contexts (note however that urbanized individuals are likely a mixture of proactive and reactive phenotypes).

POSSIBLE ECOLOGICAL CONSEQUENCES OF THE VANISHING OF ONE PHENOTYPE: EXTRAPOLATING THE POTENTIAL LOSS OF PROACTIVE

Intra-species variation is a powerful driver of ecological success (Forsman and Wennersten, 2016). Removing proactive phenotypes might lead to a reduction in intra-species variability with consequences on the population to cope with environmental variation. We know that behavioral variation is an index of genetic variation (Smith and Blumstein, 2013). If we selectively reduce phenotypic variation, we likely reduce genotypic variation. Such a reduction may be ultimately costly if it reduces a population's adaptive potential to what may ultimately be a more variable environment. This loss of behavioral diversity may be particularly acute in conservation management when animals are brought into captivity for breeding with subsequently planned translocations and reintroductions (e.g., Smith and Blumstein, 2012; White et al., 2014; Merrick and Koprowski, 2017). We expect captivity to reduce genetic variation and also to eliminate the very variation that may be essential for maintaining sustainable populations.

Many studies have noted the essential role of keystone species that warrant specific conservation efforts due to their central position in their ecological network (Mills et al., 1993; Paine, 1995; Betts et al., 2015), and whose extinction or population decline could have drastic consequences on community structure (Cortés-Avizanda et al., 2015). Recent work has focused on the essential role played by some individuals in a group and coined the term keystone individuals (Pruitt and Keiser, 2014). Modlmeier et al. (2014, p. 55) defined these individuals as having "a disproportionally large, irreplaceable effect on other group members and/or the overall group dynamics relative to its abundance."

The systematic loss of proactive phenotypes could initially influence group composition and population dynamics because these individuals are likely to be keystone individuals. As noted above, proactive individuals tend to disperse more, while reactive individuals are more likely to join newly colonized areas (Cote et al., 2010a). If new populations are mostly composed of reactive individuals, this may constrain dispersal and space use. For instance, average group personality scores (boldness, activity, and sociability) of some feral guppy (*Poecilia reticulata*) populations were not associated with exploratory propensity. Rather, group exploratory propensity was driven by the personality of key individuals, whereby slow individuals tended to slow down the shoal's exploration rates (Brown and Irving, 2014). In mosquitofish (*Gambusia affinis*) average group personality appeared to also drive group dispersion in the expected pattern; groups with many asocial individuals dispersed further. However, this study failed to identify keystone individuals (Cote et al., 2010b). Because exploration is likely associated with resource harvesting, we can envision that HIREC may modify these patterns and have consequences on other trophic levels. Thus, if a system evolved with a mix of shy and bold individuals, and HIREC systematically eliminated one type, we should expect changes in species composition.

The potential disappearance of one phenotype could have substantial consequences on prey-predator relationships. A recent review noted that whether a prey has a proactive or a reactive response depends on the predictability of an encounter with a predator (Creel, 2018). The former response will have an energetic cost (fleeing) while the latter would have a stress-mediated cost, by activating the HPI/A axis (Creel, 2018). However, this previous analysis largely ignored potential intra-individual differences in coping abilities by assuming that all individuals can mount a similar response according to the situation.

We suggest here that the type of response would also depend on the coping style of each individual, although the ecological consequences may be the same. If a population loses all proactive individuals, then responses to a predator consisting of displaying aggressive behaviors, modifying activity periods, or engaging in particular patterns of vigilance (Creel, 2018) may likely be quite different. Specifically, without proactive responses, we will only see reactive responses, driving a variety of associated stress-related costs. For instance, in the snowshoe hare-lynx system, predation risk increased glucocorticoid production with direct consequences in the decline of offspring production (Krebs et al., 1995). Hence, we can expect that if prey mount a reactive response to predatory encounters, prey will become chronically stressed and this will have a cascading effect on reproductive success (Krebs et al., 1995).

For predators too, the ecological consequences of losing proactive individuals could be dramatic. For instance, when comparing the behavior of predatory fishes living in relatively unprotected areas (recreational fishing permitted) to old no-take kelp forests (that have been protected for 40 years), some species are 6.5 times less bold toward prey (as quantified by the number of attacks) and consequentially consume nearly half the prey compared to those in fully protected areas (Rhoades et al., 2019). Spotted hyenas (*Crocuta crocuta*) inhabiting highly disturbed areas (close to humans) are less bold toward a mock intruder, compared to those living in undisturbed areas (Turner et al., 2020). As a consequence, shyer hyaenas had higher survival rates (Turner et al., 2020). Taken together, these examples illustrate how the vanishing of proactive phenotypes due to human presence or harvesting could have profound impacts on predatory-prey dynamics. In addition to predator-prey interactions, it is worth noting that physiological and behavioral changes induced by HIRECs on wild populations may also affect the host-parasite/pathogen dynamics and beneficial partnerships between species, causing cascading impacts on ecosystem functioning (Hammond et al., 2020).

CONCLUSIONS AND CONSERVATION RELEVANCE

Taken together, human-induced rapid environmental changes (HIREC) have profound and potentially cascading effects on the behavior and physiology of wild animals that may impact the proportion of proactive and reactive individuals in a population. These alterations may lead to modifications in species' distribution and abundance. If this occurs, this would be the result of three distinct time-related steps: (1) the loss of proactive individuals because they move away, (2) the enhanced survival of reactive individuals, and (3) genetic evolution. Based on our current knowledge, we suggest that HIREC that do not systematically relax predation pressure—such as seen with climate change, pollution or harvesting—would lead to genetic evolution toward reactive individuals. This, of course, assumes that individuals are able to initially survive these widespread changes, which of course is not a given. Knowledge of this systematic selection is essential to inform conservation actions to maintain genetic diversity, and hence evolutionary potential, in natural populations. Importantly, these insights may help design adaptive management strategies to maintain genetic variation within populations in the context of HIREC.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

BG: conceptualization, writing—review, and editing. SA and BS: writing—review and editing. DTB: supervision, writing–review, and editing. All authors contributed to the article and approved the submitted version.

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Underestimating the Challenges of Avoiding a Ghastly Future

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We report three major and confronting environmental issues that have received little attention and require urgent action. First, we review the evidence that future environmental conditions will be far more dangerous than currently believed. The scale of the threats to the biosphere and all its lifeforms—including humanity—is in fact so great that it is difficult to grasp for even well-informed experts. Second, we ask what political or economic system, or leadership, is prepared to handle the predicted disasters, or even capable of such action. Third, this dire situation places an extraordinary responsibility on scientists to speak out candidly and accurately when engaging with government, business, and the public. We especially draw attention to the lack of appreciation of the enormous challenges to creating a sustainable future. The added stresses to human health, wealth, and well-being will perversely diminish our political capacity to mitigate the erosion of ecosystem services on which society depends. The science underlying these issues is strong, but awareness is weak. Without fully appreciating and broadcasting the scale of the problems and the enormity of the solutions required, society will fail to achieve even modest sustainability goals.

Keywords: sustainability, extinction, climate change, political will, human population, consumption

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INTRODUCTION

Humanity is causing a rapid loss of biodiversity and, with it, Earth's ability to support complex life. But the mainstream is having difficulty grasping the magnitude of this loss, despite the steady erosion of the fabric of human civilization (Ceballos et al., 2015; IPBES, 2019; Convention on Biological Diversity, 2020; WWF, 2020). While suggested solutions abound (Díaz et al., 2019), the current scale of their implementation does not match the relentless progression of biodiversity loss (Cumming et al., 2006) and other existential threats tied to the continuous expansion of the human enterprise (Rees, 2020). Time delays between ecological deterioration and socio-economic penalties, as with climate disruption for example (IPCC, 2014), impede recognition of the magnitude of the challenge and timely counteraction needed. In addition, disciplinary specialization and insularity encourage unfamiliarity with the complex adaptive systems (Levin, 1999) in which problems and their potential solutions are embedded (Selby, 2006; Brand and Karvonen, 2007). Widespread ignorance of human behavior (Van Bavel et al., 2020) and the incremental nature of socio-political processes that plan and implement solutions further delay effective action (Shanley and López, 2009; King, 2016).

We summarize the state of the natural world in stark form here to help clarify the gravity of the human predicament. We also outline likely future trends in biodiversity decline (Díaz et al., 2019), climate disruption (Ripple et al., 2020), and human consumption and population growth to demonstrate the near certainty that these problems will worsen over the coming decades, with negative impacts for centuries to come. Finally, we discuss the ineffectiveness of current and planned actions that are attempting to address the ominous erosion of Earth's life-support system. Ours is not a call to surrender—we aim to provide leaders with a realistic "cold shower" of the state of the planet that is essential for planning to avoid a ghastly future.

BIODIVERSITY LOSS

Major changes in the biosphere are directly linked to the growth of human systems (summarized in **Figure 1**). While the rapid loss of species and populations differs regionally in intensity (Ceballos et al., 2015, 2017, 2020; Díaz et al., 2019), and most species have not been adequately assessed for extinction risk (Webb and Mindel, 2015), certain global trends are obvious. Since the start of agriculture around 11,000 years ago, the biomass of terrestrial vegetation has been halved (Erb et al., 2018), with a corresponding loss of >20% of its original biodiversity (Díaz et al., 2019), together denoting that >70% of the Earth's land surface has been altered by *Homo sapiens* (IPBES, 2019). There have been >700 documented vertebrate (Díaz et al., 2019) and ∼600 plant (Humphreys et al., 2019) species extinctions over the past 500 years, with many more species clearly having gone extinct unrecorded (Tedesco et al., 2014). Population sizes of vertebrate species that have been monitored across years have declined by an average of 68% over the last five decades (WWF, 2020), with certain population clusters in extreme decline (Leung et al., 2020), thus presaging the imminent extinction of their species (Ceballos et al., 2020). Overall, perhaps 1 million species are threatened with extinction in the near future out of an estimated 7–10 million eukaryotic species on the planet (Mora et al., 2011), with around 40% of plants alone considered endangered (Antonelli et al., 2020). Today, the global biomass of wild mammals is <25% of that estimated for the Late Pleistocene (Bar-On et al., 2018), while insects are also disappearing rapidly in many regions (Wagner, 2020; reviews in van Klink et al., 2020).

Freshwater and marine environments have also been severely damaged. Today there is <15% of the original wetland area globally than was present 300 years ago (Davidson, 2014), and >75% of rivers >1,000 km long no longer flow freely along their entire course (Grill et al., 2019). More than two-thirds of the oceans have been compromised to some extent by human activities (Halpern et al., 2015), live coral cover on reefs has halved in <200 years (Frieler et al., 2013), seagrass extent has been decreasing by 10% per decade over the last century (Waycott et al., 2009; Díaz et al., 2019), kelp forests have declined by ∼40% (Krumhansl et al., 2016), and the biomass of large predatory fishes is now <33% of what it was last century (Christensen et al., 2014).

With such a rapid, catastrophic loss of biodiversity, the ecosystem services it provides have also declined. These include *inter alia* reduced carbon sequestration (Heath et al., 2005; Lal, 2008), reduced pollination (Potts et al., 2016), soil degradation (Lal, 2015), poorer water and air quality (Smith et al., 2013), more frequent and intense flooding (Bradshaw et al., 2007; Hinkel et al., 2014) and fires (Boer et al., 2020; Bowman et al., 2020), and compromised human health (Díaz et al., 2006; Bradshaw et al., 2019). As telling indicators of how much biomass humanity has transferred from natural ecosystems to our own use, of the estimated 0.17 Gt of living biomass of terrestrial vertebrates on Earth today, most is represented by livestock (59%) and human beings (36%)—only ∼5% of this total biomass is made up by wild mammals, birds, reptiles, and amphibians (Bar-On et al., 2018). As of 2020, the overall material output of human endeavor exceeds the sum of all living biomass on Earth (Elhacham et al., 2020).

SIXTH MASS EXTINCTION

A mass extinction is defined as a loss of ∼75% of all species on the planet over a geologically short interval—generally anything <3 million years (Jablonski et al., 1994; Barnosky et al., 2011). At least five major extinction events have occurred since the Cambrian (Sodhi et al., 2009), the most recent of them 66 million years ago at the close of the Cretaceous period. The background rate of extinction since then has been 0.1 extinctions million species^{-1} year^{-1} (Ceballos et al., 2015), while estimates of today's extinction rate are orders of magnitude greater (Lamkin and Miller, 2016). Recorded vertebrate extinctions since the 16th century—the mere tip of the true extinction iceberg—give a rate of extinction of 1.3 species year^{-1}, which is conservatively >15 times the background rate (Ceballos et al., 2015). The IUCN estimates that some 20% of all species are in danger of extinction over the next few decades, which greatly exceeds the background rate. That we are already on the path of a sixth major extinction is now scientifically undeniable (Barnosky et al., 2011; Ceballos et al., 2015, 2017).

ECOLOGICAL OVERSHOOT: POPULATION SIZE AND OVERCONSUMPTION

The global human population has approximately doubled since 1970, reaching nearly 7.8 billion people today (prb.org). While some countries have stopped growing and even declined in size,

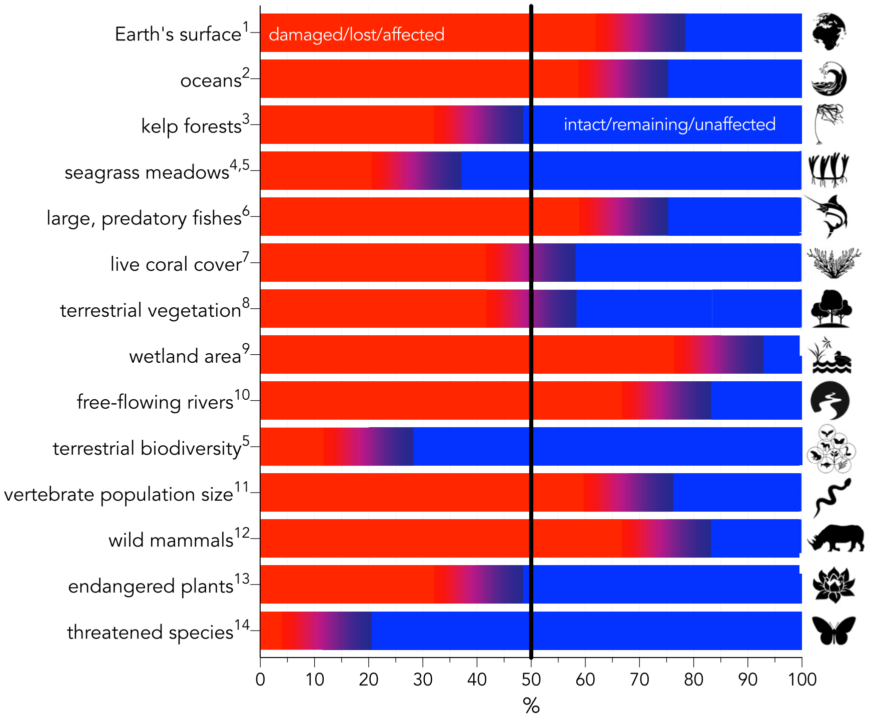

FIGURE 1 | Summary of major environmental-change categories expressed as a percentage change relative to the baseline given in the text. Red indicates the percentage of the category that is damaged, lost, or otherwise affected, whereas blue indicates the percentage that is intact, remaining, or otherwise unaffected. Superscript numbers indicate the following references: [1]IPBES, 2019; [2]Halpern et al., 2015; [3]Krumhansl et al., 2016; [4]Waycott et al., 2009; [5]Díaz et al., 2019; [6]Christensen et al., 2014; [7]Frieler et al., 2013; [8]Erb et al., 2018; [9]Davidson, 2014; [10]Grill et al., 2019; [11]WWF, 2020; [12]Bar-On et al., 2018; [13]Antonelli et al., 2020; [14]Mora et al., 2011.

world average fertility continues to be above replacement (2.3 children woman^{-1}), with an average of 4.8 children woman^{-1} in Sub-Saharan Africa and fertilities >4 children woman^{-1} in many other countries (e.g., Afghanistan, Yemen, Timor-Leste). The 1.1 billion people today in Sub-Saharan Africa—a region expected to experience particularly harsh repercussions from climate change (Serdeczny et al., 2017)—is projected to double over the next 30 years. By 2050, the world population will likely grow to ∼9.9 billion (prb.org), with growth projected by many to continue until well into the next century (Bradshaw and Brook, 2014; Gerland et al., 2014), although more recent estimates predict a peak toward the end of this century (Vollset et al., 2020).

Large population size and continued growth are implicated in many societal problems. The impact of population growth, combined with an imperfect distribution of resources, leads to massive food insecurity. By some estimates, 700–800 million people are starving and 1–2 billion are micronutrient-malnourished and unable to function fully, with prospects of many more food problems in the near future (Ehrlich and Harte, 2015a,b). Large populations and their continued growth are also drivers of soil degradation and biodiversity loss (Pimm et al., 2014). More people means that more synthetic compounds and dangerous throw-away plastics (Vethaak and Leslie, 2016) are manufactured, many of which add to the growing toxification of the Earth (Cribb, 2014). It also increases chances of pandemics (Daily and Ehrlich, 1996b) that fuel ever-more desperate hunts for scarce resources (Klare, 2012). Population growth is also a factor in many social ills, from crowding and joblessness, to deteriorating infrastructure and bad governance (Harte, 2007). There is mounting evidence that when populations are large and growing fast, they can be the sparks for both internal and international conflicts that lead to war (Klare, 2001; Toon et al., 2007). The multiple, interacting causes of civil war in particular are varied, including poverty, inequality, weak institutions, political grievance, ethnic divisions, and environmental stressors such as drought, deforestation, and land degradation (Homer-Dixon, 1991, 1999; Collier and Hoeer, 1998; Hauge and llingsen, 1998; Fearon and Laitin, 2003; Brückner, 2010; Acemoglu et al., 2017). Population growth itself can even increase the probability of military involvement in conflicts (Tir and Diehl, 1998). Countries with higher population growth rates experienced more social conflict since the Second World War (Acemoglu et al., 2017). In that study, an approximate doubling of a country's population caused about four additional years of full-blown civil war or low-intensity conflict in the 1980s relative to the 1940–1950s, even after controlling for a country's income-level, independence, and age structure.

Simultaneous with population growth, humanity's consumption as a fraction of Earth's regenerative capacity has grown from ∼ 73% in 1960 to 170% in 2016 (Lin et al., 2018), with substantially greater per-person consumption in countries with highest income. With COVID-19, this overshoot dropped to 56% above Earth's regenerative capacity, which means that between January and August 2020, humanity consumed as much as Earth can renew in the entire year (overshootday.org). While inequality among people and countries remains staggering, the global middle class has grown rapidly and exceeded half the human population by 2018 (Kharas and Hamel, 2018). Over 70% of all people currently live in countries that run a biocapacity deficit while also having less than world-average income, excluding them from compensating their biocapacity deficit through purchases (Wackernagel et al., 2019) and eroding future resilience via reduced food security (Ehrlich and Harte, 2015b). The consumption rates of high-income countries continue to be substantially higher than low-income countries, with many of the latter even experiencing declines in per-capita footprint (Dasgupta and Ehrlich, 2013; Wackernagel et al., 2019).

This massive ecological overshoot is largely enabled by the increasing use of fossil fuels. These convenient fuels have allowed us to decouple human demand from biological regeneration: 85% of commercial energy, 65% of fibers, and most plastics are now produced from fossil fuels. Also, food production depends on fossil-fuel input, with every unit of food energy produced requiring a multiple in fossil-fuel energy (e.g., 3× for high-consuming countries like Canada, Australia, USA, and China; overshootday.org). This, coupled with increasing consumption of carbon-intensive meat (Ripple et al., 2014) congruent with the rising middle class, has exploded the global carbon footprint of agriculture. While climate change demands a full exit from fossil-fuel use well before 2050, pressures on the biosphere are likely to mount prior to decarbonization as humanity brings energy alternatives online. Consumption and biodiversity challenges will also be amplified by the enormous physical inertia of all large "stocks" that shape current trends: built infrastructure, energy systems, and human populations.

It is therefore also inevitable that aggregate consumption will increase at least into the near future, especially as affluence and population continue to grow in tandem (Wiedmann et al., 2020). Even if major catastrophes occur during this interval, they would unlikely affect the population trajectory until well into the 22nd Century (Bradshaw and Brook, 2014). Although population-connected climate change (Wynes and Nicholas, 2017) will worsen human mortality (Mora et al., 2017; Parks et al., 2020), morbidity (Patz et al., 2005; Díaz et al., 2006; Peng et al., 2011), development (Barreca and Schaller, 2020), cognition (Jacobson et al., 2019), agricultural yields (Verdin et al., 2005; Schmidhuber and Tubiello, 2007; Brown and Funk, 2008; Gaupp et al., 2020), and conflicts (Boas, 2015), there is no way—ethically or otherwise (barring extreme and unprecedented increases in human mortality)—to avoid rising human numbers and the accompanying overconsumption. That said, instituting human-rights policies to lower fertility and reining in consumption patterns could diminish the impacts of these phenomena (Rees, 2020).

FAILED INTERNATIONAL GOALS AND PROSPECTS FOR THE FUTURE

Stopping biodiversity loss is nowhere close to the top of any country's priorities, trailing far behind other concerns such as employment, healthcare, economic growth, or currency stability. It is therefore no surprise that none of the Aichi Biodiversity Targets for 2020 set at the Convention on Biological Diversity's (CBD.int) 2010 conference was met (Secretariat of the Convention on Biological Diversity, 2020). Even had they been met, they would have still fallen short of realizing any substantive reductions in extinction rate. More broadly, most of the nature-related United Nations Sustainable Development Goals (SDGs) (e.g., SDGs 6, 13–15) are also on track for failure (Wackernagel et al., 2017; Díaz et al., 2019; Messerli et al., 2019), largely because most SDGs have not adequately incorporated their interdependencies with other socio-economic factors (Bradshaw and Di Minin, 2019; Bradshaw et al., 2019; Messerli et al., 2019). Therefore, the apparent paradox of high and rising average standard of living despite a mounting environmental toll has come at a great cost to the stability of humanity's medium- and long-term life-support system. In other words, humanity is running an ecological Ponzi scheme in which society robs nature and future generations to pay for boosting incomes in the short term (Ehrlich et al., 2012). Even the World Economic Forum, which is captive of dangerous greenwashing propaganda (Bakan, 2020), now recognizes biodiversity loss as one of the top threats to the global economy (World Economic Forum, 2020).

The emergence of a long-predicted pandemic (Daily and Ehrlich, 1996a), likely related to biodiversity loss, poignantly exemplifies how that imbalance is degrading both human health and wealth (Austin, 2020; Dobson et al., 2020; Roe et al., 2020). With three-quarters of new infectious diseases resulting from human-animal interactions, environmental degradation via climate change, deforestation, intensive farming, bushmeat hunting, and an exploding wildlife trade mean that the opportunities for pathogen-transferring interactions are high (Austin, 2020; Daszak et al., 2020). That much of this degradation is occurring in Biodiversity Hotspots where pathogen diversity is also highest (Keesing et al., 2010), but where institutional capacity is weakest, further increases the risk of pathogen release and spread (Austin, 2020; Schmeller et al., 2020).

CLIMATE DISRUPTION

The dangerous effects of climate change are much more evident to people than those of biodiversity loss (Legagneux et al., 2018), but society is still finding it difficult to deal with them effectively. Civilization has already exceeded a global warming of $\sim 1.0°C$ above pre-industrial conditions, and is on track to cause at least a 1.5°C warming between 2030 and 2052 (IPCC, 2018). In fact, today's greenhouse-gas concentration is >500 ppm CO_2-e (Butler and Montzka, 2020), while according to the IPCC, 450 ppm CO_2-e would give Earth a mere 66% chance of not exceeding a 2°C warming (IPCC, 2014). Greenhouse-gas concentration will continue to increase (via positive feedbacks such as melting permafrost and the release of stored methane) (Burke et al., 2018), resulting in further delay of temperature-reducing responses even if humanity stops using fossil fuels entirely well before 2030 (Steffen et al., 2018).

Human alteration of the climate has become globally detectable in any single day's weather (Sippel et al., 2020). In fact, the world's climate has matched or exceeded previous predictions (Brysse et al., 2013), possibly because of the IPCC's reliance on averages from several models (Herger et al., 2018) and the language of political conservativeness inherent in policy recommendations seeking multinational consensus (Herrando-Pérez et al., 2019). However, the latest climate models (CMIP6) show greater future warming than previously predicted (Forster et al., 2020), even if society tracks the needed lower-emissions pathway over the coming decades. Nations have in general not met the goals of the 5 year-old Paris Agreement (United Nations, 2016), and while global awareness and concern have risen, and scientists have proposed major transformative change (in energy production, pollution reduction, custodianship of nature, food production, economics, population policies, etc.), an effective international response has yet to emerge (Ripple et al., 2020). Even assuming that all signatories do, in fact, manage to ratify their commitments (a doubtful prospect), expected warming would still reach 2.6–3.1°C by 2100 (Rogelj et al., 2016) unless large, additional commitments are made and fulfilled. Without such commitments, the projected rise of Earth's temperature will be catastrophic for biodiversity (Urban, 2015; Steffen et al., 2018; Strona and Bradshaw, 2018) and humanity (Smith et al., 2016).

Regarding international climate-change accords, the Paris Agreement (United Nations, 2016) set the 1.5–2°C target unanimously. But since then, progress to propose, let alone follow, (voluntary) "intended national determined contributions" for post-2020 climate action have been utterly inadequate.

POLITICAL IMPOTENCE

If most of the world's population truly understood and appreciated the magnitude of the crises we summarize here, and the inevitability of worsening conditions, one could logically expect positive changes in politics and policies to match the gravity of the existential threats. But the opposite is unfolding. The rise of right-wing populist leaders is associated with anti-environment agendas as seen recently for example in Brazil (Nature, 2018), the USA (Hejny, 2018), and Australia (Burck et al., 2019). Large differences in income, wealth, and consumption among people and even among countries render it difficult to make any policy global in its execution or effect.

A central concept in ecology is *density feedback* (Herrando-Pérez et al., 2012)—as a population approaches its environmental carrying capacity, average individual fitness declines (Brook and Bradshaw, 2006). This tends to push populations toward an instantaneous expression of carrying capacity that slows or reverses population growth. But for most of history, human ingenuity has inflated the natural environment's carrying capacity for us by developing new ways to increase food production (Hopfenberg, 2003), expand wildlife exploitation, and enhance the availability of other resources. This inflation has involved modifying temperature via shelter, clothing, and microclimate control, transporting goods from remote locations, and generally reducing the probability of death or injury through community infrastructure and services (Cohen, 1995). But with the availability of fossil fuels, our species has pushed its consumption of nature's goods and services much farther beyond long-term carrying capacity (or more precisely, the planet's biocapacity), making the readjustment from overshoot that is inevitable far more catastrophic if not managed carefully (Nyström et al., 2019). A growing human population will only exacerbate this, leading to greater competition for an ever-dwindling resource pool. The corollaries are many: continued reduction of environmental intactness (Bradshaw et al., 2010; Bradshaw and Di Minin, 2019), reduced child health (especially in low-income nations) (Bradshaw et al., 2019), increased food demand exacerbating environmental degradation via agro-intensification (Crist et al., 2017), vaster and possibly catastrophic effects of global toxification (Cribb, 2014; Swan and Colino, 2021), greater expression of social pathologies (Levy and Herzog, 1974) including violence exacerbated by climate change and environmental degradation itself (Agnew, 2013; White, 2017, 2019), more terrorism (Coccia, 2018), and an economic system even more prone to sequester the remaining wealth among fewer individuals (Kus, 2016; Piketty, 2020) much like how cropland expansion since the early 1990s has disproportionately concentrated wealth among the super-rich (Ceddia, 2020). The predominant paradigm is still one of pegging "environment" against "economy"; yet in reality, the choice is between exiting overshoot by design or disaster—because exiting overshoot is inevitable one way or another.

Given these misconceptions and entrenched interests, the continued rise of extreme ideologies is likely, which in turn limits the capacity of making prudent, long-term decisions, thus potentially accelerating a vicious cycle of global ecological deterioration and its penalties. Even the USA's much-touted New Green Deal (U. S. House of Representatives, 2019) has in fact exacerbated the country's political polarization (Gustafson et al., 2019), mainly because of the weaponization of 'environmentalism' as a political ideology rather than being viewed as a universal mode of self-preservation and planetary protection that ought to transcend political tribalism. Indeed, environmental protest groups are being labeled as "terrorists" in many countries (Hudson, 2020). Further, the severity of the commitments required for any country to achieve meaningful reductions in consumption and emissions will inevitably lead to public backlash and further ideological entrenchments, mainly because the threat of potential short-term sacrifices is seen as politically inopportune. Even though climate change alone will incur a vast economic burden (Burke et al., 2015; Carleton and Hsiang, 2016; Auffhammer, 2018) possibly leading to war (nuclear, or otherwise) at a global scale (Klare, 2020), most of the world's economies are predicated on the political idea that meaningful counteraction now is too costly to be politically palatable. Combined with financed disinformation campaigns in a bid to protect short-term profits (Oreskes and Conway, 2010;

Mayer, 2016; Bakan, 2020), it is doubtful that any needed shift in economic investments of sufficient scale will be made in time.

While uncertain and prone to fluctuate according to unpredictable social and policy trends (Boas et al., 2019; McLeman, 2019; Nature Climate Change, 2019), climate change and other environmental pressures will trigger more mass migration over the coming decades (McLeman, 2019), with an estimated 25 million to 1 billion environmental migrants expected by 2050 (Brown, 2008). Because international law does not yet legally recognize such "environmental migrants" as refugees (United Nations University, 2015) (although this is likely to change) (Lyons, 2020), we fear that a rising tide of refugees will reduce, not increase, international cooperation in ways that will further weaken our capacity to mitigate the crisis.

CHANGING THE RULES OF THE GAME

While it is neither our intention nor capacity in this short *Perspective* to delve into the complexities and details of possible solutions to the human predicament, there is no shortage of evidence-based literature proposing ways to change human behavior for the benefit of all extant life. The remaining questions are less about *what* to do, and more about *how*, stimulating the genesis of many organizations devoted to these pursuits (e.g., ipbes.org, goodanthropocenes.net, overshootday.org, mahb.stanford.edu, populationmatters.org, clubofrome.org, steadystate.org, to name a few). The gravity of the situation requires fundamental changes to global capitalism, education, and equality, which include *inter alia* the abolition of perpetual economic growth, properly pricing externalities, a rapid exit from fossil-fuel use, strict regulation of markets and property acquisition, reigning in corporate lobbying, and the empowerment of women. These choices will necessarily entail difficult conversations about population growth and the necessity of dwindling but more equitable standards of living.

CONCLUSIONS

We have summarized predictions of a ghastly future of mass extinction, declining health, and climate-disruption upheavals (including looming massive migrations) and resource conflicts this century. Yet, our goal is not to present a fatalist perspective, because there are many examples of successful interventions to prevent extinctions, restore ecosystems, and encourage more sustainable economic activity at both local and regional scales. Instead, we contend that only a realistic appreciation of the colossal challenges facing the international community might allow it to chart a less-ravaged future. While there have been more recent calls for the scientific community in particular to be more vocal about their warnings to humanity (Ripple et al., 2017; Cavicchioli et al., 2019; Gardner and Wordley, 2019), these have been insufficiently foreboding to match the scale of the crisis. Given the existence of a human "optimism bias" that triggers some to underestimate the severity of a crisis and ignore expert warnings, a good communication strategy must ideally undercut this bias without inducing disproportionate feelings of fear and despair (Pyke, 2017; Van Bavel et al., 2020). It is therefore incumbent on experts in any discipline that deals with the future of the biosphere and human well-being to eschew reticence, avoid sugar-coating the overwhelming challenges ahead and "tell it like it is." Anything else is misleading at best, or negligent and potentially lethal for the human enterprise at worst.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

CJAB, DTB, and PRE designed the concept and wrote the article, with contributions from AB, GC, EC, JD, RD, AHE, JH, MEH, GP, PHR, WJR, FS, CT, and MW. CJAB prepared the figure. All authors contributed to the article and approved the submitted version.

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frontiers in Conservation Science

REVIEW
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Genetic Rescue and the Plight of Ponui Hybrids

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Long-term sustainable and resilient populations is a key goal of conservation. How to best achieve this is controversial. There are, for instance, polarized views concerning the fitness and conservation value of hybrid populations founded through multi-origin translocations. A classic example concerns *Apteryx* (kiwi) in New Zealand. The *A. mantelli* of Ponui Island constitute a hybrid population where the birds are highly successful in their island habitat. A key dilemma for managers is understanding the reason for this success. Are the hybrid birds of Ponui Island of "no future conservation value" as recently asserted, or do they represent an outstanding example of genetic rescue and an important resource for future translocations? There has been a paradigm shift in scientific thinking concerning hybrids, but the ecological significance of admixed genomes remains difficult to assess. This limits what we can currently predict in conservation science. New understanding from genome science challenges the sufficiency of population genetic models to inform decision making and suggests instead that the contrasting outcomes of hybridization, "outbreeding depression" and "heterosis," require understanding additional factors that modulate gene and protein expression and how these factors are influenced by the environment. We discuss these findings and the investigations that might help us to better understand the birds of Ponui, inform conservation management of kiwi and provide insight relevant for the future survival of *Apteryx*.

Keywords: hybridization, outbreeding depression, heterosis, translocation, conservation management, evolutionary potential, epigenetics, *Apteryx*

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INTRODUCTION

The arrival of humans to New Zealand and the accompanying deforestation and predation by introduced mammals have decimated many native and endemic species (Holdaway, 1989; Robertson et al., 2016). In responding to this catastrophic development, New Zealand conservation efforts have attracted international recognition for their bold and pioneering methods aimed at rescuing species from the brink of extinction. Most notably, strategies for translocation have influenced practices worldwide (Armstrong and McLean, 1995; Armstrong and Seddon, 2008). Despite this, controversy remains in New Zealand and elsewhere for how to best achieve long-term sustainable and resilient populations (Love Stowell et al., 2017; Ralls et al., 2018, 2020; Von Holdt et al., 2018). Specifically, the outcome of translocations involving the mixing of individuals from genetically distinct populations remains difficult to predict and questions have been raised about the future fate and conservation value of admixed populations originating from such historic translocations.

An iconic example concerns the flightless, nocturnal genus *Apteryx*, or kiwi birds, which once were common and widespread throughout New Zealand but now are confined mainly to isolated and/or small populations relying on active management to achieve net growth (Innes et al., 2015; Germano et al., 2018). *Apteryx* face many threats such as habitat degradation, fragmentation, disrupted gene flow, and small population sizes (McLennan and Potter, 1992; McLennan and McCann, 2002; Germano et al., 2018). However, depredation by invasive mammals, in particular stoats (*Mustela erminea*), ferrets (*M. furo*), and dogs (*Canis lupus familiaris*), have been identified as the main cause of their decline (Taborsky, 1988; McLennan et al., 1996; Innes et al., 2010; Germano et al., 2018). For example, in unmanaged populations, about 95% of *Apteryx* chicks are predated by stoats (McLennan et al., 1996; Innes et al., 2010). Consequently, *Apteryx* management focuses on trapping and poisoning mammalian predators and on artificial rearing of eggs and chicks collected from the wild under a program referred to as Operation Nest Egg (ONE; Colbourne et al., 2005). In addition, a program called "kohanga kiwi" involves sites where *Apteryx* pairs are held and allowed to breed in predator-free areas and a proportion of the chicks are "harvested" and used to supplement existing or establish new populations (Innes et al., 2016; Kiwis for Kiwi, 2016). A principle of kohanga kiwi sites is that they are founded by 40 unrelated birds. However, relatedness is inferred based on geographic origin rather than genetic testing (Innes et al., 2016; Kiwis for Kiwi, 2016).

Apteryx genetics have received extensive research attention (Ramstad and Dunning, 2020; Undin et al., in press). Based on findings from these studies, *Apteryx* is currently split into five extant species (Tennyson et al., 2003) and further into 14 management units based on observed or inferred barriers to gene flow (Powlesland, 1988; Burbidge et al., 2003; Weir et al., 2016; Germano et al., 2018). The exploration of *Apteryx* diversity has so far focused on describing observations from a taxonomic perspective. Hence, parameters based on population genetic models have not been estimated and there is little understanding of migration between populations, inbreeding within populations, and local adaptation (Shepherd and Lambert, 2008; Germano et al., 2018). Consequently, lack of studies of genetic variation within management units, the nature of the genetic difference between taxa, and the prevalence of in- and outbreeding, means that far-reaching *Apteryx* conservation decisions and policy are currently being implemented despite a lack of crucial information (McLennan and McCann, 2002; Dussex et al., 2018).

One policy linked to the demarcation of 14 management units is that *Apteryx* translocations are strictly limited to movement within units (Pierce et al., 2006; Innes et al., 2016; Germano et al., 2018). Another is that several *Apteryx* populations, regarded as hybrid populations because they originated from translocations involving two or more units, are considered unsuitable sources as well as targets for future translocations (Herbert and Daugherty, 2002; Colbourne, 2005; Shepherd et al., 2012; Germano et al., 2018). One such hybrid population is present on Ponui Island. Concerned for the rapid decline of kiwi on the North Island, in 1964 the landowner Peter Chamberlin on Ponui (Chamberlin's) Island in the Hauraki Gulf had 14 North Island brown kiwi (*Apteryx mantelli*) translocated to the island (Colbourne, 2005). Six of these birds came from Hauturu-o-Toi (also known as Little Barrier Island; Colbourne, 2005; **Figure 1**). The remaining eight birds came from the Waipoua Forest in the northernmost part of the North Island mainland (Colbourne, 2005). In turn, the origin of the population on Hauturu-o-Toi was a translocation from Taranaki in the early 1900's, but anecdotal evidence suggests that additional birds of unknown sources may have been present on Hauturu-o-Toi prior to this translocation (Baker et al., 1995; Burbidge et al., 2003; Colbourne, 2005; **Figure 1**). Because the parental populations belong to different management units, the Ponui birds are classified as hybrids. The initial success of the translocated birds and their Ponui hatched offspring is unknown, but the current high density is evidence for rapid and extensive population growth within a small number of generations. *Apteryx* typically reach sexual maturity around 4 years of age and live to be over 40 years old (Sales, 2005; Robertson and de Monchy, 2012). Consequently, in the 56 years that have passed since their introduction, the current population on Ponui is likely best described as a hybrid swarm where some individuals birds will be of pure Waipoua or Hauturu-o-Toi origin, others will be F1 hybrids or offspring from crossing and backcrossing between parental types and/or F1 individuals (Hwang et al., 2011; Hamilton and Miller, 2016). While Ponui Island lacks stoats, about one third of the *A. mantelli* chicks on the island are preyed upon by feral cats (*Felis catus*) every year and ship rats (*Rattus rattus*) likely compete with chicks for food (Shapiro, 2005; Dixon, 2015; Strang, 2018). Despite this presence of invasive mammals, the population density on Ponui is suggestive of a population growth rate otherwise only seen in populations in predator-free sanctuaries and/or sites where juvenile mortality is reduced through Operation Nest Egg (Colbourne et al., 2005; Robertson and de Monchy, 2012). The Ponui *Apteryx* population has been extensively studied over the past 17 years, providing ground-breaking data on habitat utilization, diet, parasite impact, disease, anatomy, social interactions, and causes of chick and egg mortality (e.g., Cunningham and Castro, 2011; Ziesemann, 2011; Hiscox, 2014; Wilson, 2014; Dixon, 2015; Reynolds et al., 2017; Abourachid et al., 2019; Bansal, 2020; Vieco-Galvez et al., 2020). No studies have so far investigated the impact of their mixed heritage on the success of the birds on Ponui.

Despite the lack of studies, the mixed provenance and the untested assumption that the birds introduced to Ponui Island had limited genetic diversity, it was concluded that the Ponui birds "have no genetic value whatsoever for use in restoration" (Letter to Department of Conservation and the Kiwi Recovery Group shared with Ponui landowners and Ponui Kiwi Research Team, 2016). The suggestion is that the Ponui birds suffer from (1) inbreeding depression resulting from the small number of founding birds and (2) outbreeding depression resulting from anthropogenically-mediated hybridization of birds deemed likely to be adapted to different local conditions (Allendorf et al., 2001). These potential problems have not impacted policymaking around translocations and admixture of geographically adjacent populations. On the contrary, translocations of birds within management units to boost population numbers and attempt to

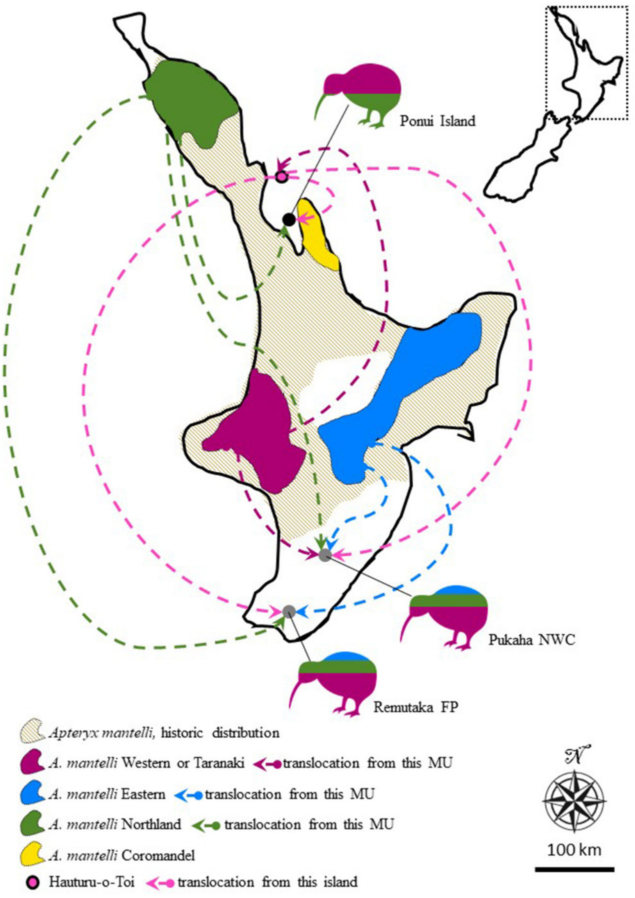

FIGURE 1 | Map of the North Island of New Zealand illustrating the historic, as well as, current distribution of *Apteryx mantelli*, North Island brown kiwi, and how this species is further split into four geographically disjunct and genetically distinct management units (MU, or taxa Burbidge et al., 2003; Weir et al., 2016; Germano et al., 2018). Arrows and kiwi silhouettes represent three separate cases where multi-origin translocations over the last 100 years have resulted in hybrid populations. Silhouette coloring roughly illustrates the proportional representation of different taxa in the founding population at each site. Translocations from Hauturu-o-Toi (also known as Little Barrier Island) are colored in a different shade of pink for clarity and to highlight the somewhat disputed MU identity of this island. FP, Forest park; NWC, National Wildlife Centre. Inset show the location of the zoomed in map in New Zealand.

maintain genetic diversity remains a paramount part of ongoing *Apteryx* conservation (Kiwis for Kiwi, 2016; Germano et al., 2018).

The plight of the Ponui kiwi illustrates the importance of improving our understanding of inbreeding, outbreeding depression, and the sometimes contrasting outcomes of hybridization. This understanding is also needed to realize the full potential of genetic rescue and other forms of translocation involving endangered species. In our contribution, we highlight why study of the Ponui birds will be informative for (1) illuminating the ecological and evolutionary significance of hybrids, (2) establishing evidence-based principles for identifying and matching source and target populations for translocations involving admixture, (3) proposing the most appropriate source(s) of individuals for repopulating areas after locally extinctions, and (4) evaluating the biological relevance of *Apteryx* management units in New Zealand. We emphasize that addressing these four questions is key for the long-term successful conservation of *Apteryx* whose populations are highly fragmented and are arguably in need of augmented gene flow given their insular New Zealand habitat. We think that if these questions could be answered for *Apteryx* in New Zealand, they may be informative for conservation practices elsewhere. We see an important role for integrating genome science in ecological studies of *Apteryx* that will help us to better understand the evolutionary significance of hybrids and their conservation value.

One reason discussion of hybridization in conservation can be problematic, and often fruitless, stems from a lack of agreement concerning the many criteria for delimiting species (Mallet, 2013). The prevalence of hybridization in plant evolution and the challenges of delimiting plant species has recently led to emphasis being placed on what occurs when taxa from distinct evolutionary lines are brought together, rather than on whether or not these taxa are named as distinct species (Winkworth et al., 2005; Abbott et al., 2013; Hoffmann et al., 2015; Canestrelli et al., 2016; Chan et al., 2019). We adopt this approach, and this review accepts the definition of hybridization used by Canestrelli et al. (2016) as "mating between individuals from genetically distinct populations that produces offspring." We also adopt the perspective that it may not be helpful to distinguish hybridization that results from human intervention or otherwise since, for philosophical as well as practical reasons, the causes of some hybridization events are almost impossible to disentangle (Allendorf et al., 2001).

POPULATION GENETIC MODELS AND PREDICTING HYBRID SUCCESS

Hybridization will impact genetic diversity and plasticity, however, predicting the success of managed gene flow requires understanding not only the genetic diversity and plasticity of species, but also of the extent and directionality of the gene flow and how admixture between genetically diverged populations and lineages affect reproductive success (Abbott et al., 2013). Models for the accumulative effects of particular alleles (gene variants) and overall allelic diversity in the genomes of organisms have been used since the early 1900's to help explain the relative fitness (reproductive success) of offspring when the parents are genetically similar (inbreeding) as well as genetically dissimilar (outbreeding or hybridization; Roff, 2002; Wright et al., 2008; Hochholdinger and Baldauf, 2018). The Partial Dominance hypothesis (Davenport, 1908) predicts that mating between close relatives increases the number of genes in offspring where the same sub-optimal (deleterious) variant of a gene is inherited from both parents. This is said to decrease the fitness of the offspring. The Overdominance hypothesis (East, 1908) proposes that it is not deleterious genes *per se,* but that an increased number of genes with the same variant inherited from both parents reduces the fitness of the offspring. These alternative explanations for inbreeding depression – reduced fitness of offspring relative to parents – are still largely unresolved (e.g., Roff, 2002; Wright et al., 2008). While there is good reason that population genetic models based on inheritance of gene variants remain a leading explanation for heterosis and genetic rescue, as well as inbreeding and outbreeding depression, after a 100 years of empirical testing, there is now a chorus of voices questioning the sufficiency of these models (Groszmann et al., 2013; O'Dea et al., 2016; Hochholdinger and Baldauf, 2018; Bell et al., 2019; Rey et al., 2020).

Heterosis or hybrid vigor is expressed as a release from inbreeding depression inferred from relatively higher fitness of offspring compared to its genetically distinct parents (Whitlock et al., 2000; Hochholdinger and Baldauf, 2018; Bell et al., 2019). The superior performance of first-generation (F_1) hybrids is a well-documented phenomenon of ecological and agricultural advantage. It has evolutionary significance for adaptation of populations and generation of novel species (Johansen-Morris and Latta, 2006; Janes and Hamilton, 2017; Hochholdinger and Baldauf, 2018; Junaid et al., 2018; Koide et al., 2019; Miryeganeh and Saze, 2019; Taylor and Larson, 2019). When differences in phenotype and underlying gene expression are much greater or much less between progeny and parents than the additive difference between the parents, it is sometimes referred to as transgressive segregation (Stelkens et al., 2014; Koide et al., 2019). However, whether the mechanisms of heterosis and transgressive segregation are different, the same, or whether one is a subset of the other remains unclear. According to some definitions, the difference lies in that while transgressive segregation results in individuals that "express trait values that fall outside the range of both parent species" in either direction (Stelkens et al., 2014), heterosis only refers to an "increased fitness relative to more 'pure-bred' individuals" (Whitlock et al., 2000). Others suggest that the difference lies in having a population vs. an individual perspective, for instance, heterosis is "usually ascribed to the average fitness of the hybrid offspring" while transgressive segregation refers to "the presence of extreme phenotypes (in either a negative or a positive direction) relative to the parental phenotypes" that make particular individuals "more fit [...] than either of the parents" (Johansen-Morris and Latta, 2006). Another perspective is that the difference concerns at what point in time the positive fitness following hybridization is observed. Heterosis is said to be evident in the "observation that cross-pollinated hybrids are more vigorous than their parents [....] calculated as the difference in the phenotypic performance of a trait between a hybrid and the average of its two distinct parents" (Hochholdinger and Baldauf, 2018) or the "elevated fitness of F1 hybrids relative to their parents" (Bell et al., 2019). In contrast transgressive segregation produces "hybrid progeny phenotypes that exceed the parental phenotypes [...which are] heritably stable" (Koide et al., 2019).

Outbreeding depression, on the other hand, is the reduced fitness of admixed offspring compared to their genetically distinct parents (Marr et al., 2002; Goldberg et al., 2005; Frankham et al., 2011; Barmentlo et al., 2018). Population genetic models have also been used to explain this phenomenon (Lynch, 1991; Marr et al., 2002; Goldberg et al., 2005; Frankham et al., 2011; Whitlock et al., 2013; Kardos et al., 2016). Hybrid offspring will be heterozygous for many genes, and it is suggested this could cause an averaging or intermediate effect that makes the progeny adapted to neither parental habitat (Edmands and Timmerman, 2003). In subsequent generations of interbreeding it has been suggested that the depression could worsen, because particular combinations of gene variants which have been of adaptive value to parental lineages in their environments may no longer co-occur in the genomes of the hybrid offspring (Lynch, 1991; Allendorf et al., 2001; Edmands, 2007). In the worst cases, where parental species have evolved differences in their chromosome karyotypes (the packaged form of their DNA sequences) it is possible that the chromosomes will not pair properly during meiosis and this will affect the fertility of the hybrid offspring (e.g., the famous case of donkeys and horses producing sterile mules; Rieseberg, 2001).

A growing number of studies support the view that outbreeding depression is more likely to occur when genetic differences are linked with local adaptation to specific environments. In contrast, isolation *per se* even for many generations, under similar selection pressure rarely leads to symptoms of outbreeding depression upon admixture (Barton, 1996; Orr and Smith, 1998; Hendry et al., 2000; Rundle et al., 2000; Nosil et al., 2002; Rundle, 2003; Frankham et al., 2011). However, disruption of adapted phenotypes cannot explain some reported instances of outbreeding depression. For example, adaptive differences between parental linages fail to explain why several crosses between the same lineages can generate very different outcomes for offspring fitness and phenotypes (Johansen-Morris and Latta, 2006; Escobar et al., 2008; Barmentlo et al., 2018). The importance of local adaptation in *Apteryx* evolution remains untested. However, there are examples of both within and between species hybrids in kiwi that are vital, reproducing, and even very successful (Herbert and Daugherty, 2002; Cunningham and Castro, 2011; Shepherd et al., 2012). There are also cases of long-distance translocations of *Apteryx* that are reported to be successful (Colbourne, 2005; Robertson et al., 2019). While more rigorous investigations need to be conducted, these observations may suggest a limited role of local adaptation in the disjunct management units.

Despite considerable effort, finding the so-called "sweet spot" of genetic and/or phenotypic distance between taxa that will produce heterosis and not outbreeding depression has not been possible, raising the question of whether the concept of a sweet spot is useful at all (Tallmon et al., 2004; Edmands, 2007; Escobar et al., 2008; Stelkens et al., 2014; Kardos et al., 2016; Barmentlo et al., 2018; Bell et al., 2019; Koide et al., 2019). Further complicating the picture, several studies have found that crossing of different lineages within the same species has sometimes resulted in outbreeding depression and sometimes in heterosis (Edmands, 1999; Rundle et al., 2000; Marr et al., 2002; Escobar et al., 2008; Whitlock et al., 2013). Occasionally, these outcomes have differed depending on which lineage was maternal and which was paternal (Escobar et al., 2008; Barmentlo et al., 2018). While at other times, hybridization has produced some traits with both negative and positive consequences for fitness (Johansen-Morris and Latta, 2006; Escobar et al., 2008). Similarly, Whitlock et al. (2013), have also reported that the frequency and magnitude of outbreeding depression have differed depending on what trait was the subject of study. A further anomaly not explained by population genetic models is the resilience toward inbreeding in some species (Jamieson, 2015). This is perhaps most striking in recovery success following population bottlenecks (Heber et al., 2013; Ramstad et al., 2013; Frankham, 2015; Jamieson, 2015). This success has been attributed to the purging of deleterious gene variants, but empirical evidence for this speculation of losing the worst alleles due to homozygous expression has not yet been forthcoming, and an alternative explanation might be needed (Crnokrak and Barrett, 2002; Kennedy et al., 2014; López-Cortegano et al., 2018). Also anomalous is the observation that inbreeding depression can manifest differently between environments, suggesting that understanding genetic variation alone is insufficient to predict fitness outcomes (Keller et al., 2002; Cheptou and Donohue, 2013). These examples suggest that critical information is missing, and an improved conceptual framework is needed to understand the fitness of populations that we wish to manage (Escobar et al., 2008; Hochholdinger and Baldauf, 2018; Rey et al., 2020). With this increasing realization, attention has recently turned to the phenomenon of epigenetics and the extent to which chemical modification of the DNA in response to environmental signals also contributes to an organism's fitness.

Gene variants (alleles), specifically for transcription factors and in regulatory regions, are thought to play a major role in altering the dynamics of an organism's transcriptome, with consequences for the dynamics of its proteome, morphology, physiology, and behavior (Johnston et al., 2019; Lai et al., 2019). However, the expression of genes is also modulated through chemical modification of DNA, RNA, and proteins in processes linked to environmental signals - a phenomenon known as epigenetics (Donohue, 2014; Junaid et al., 2018). Mechanisms of epigenetic regulation are thought to have a role in the plastic (varied) expression of genes and phenotypes (Bonduriansky et al., 2012; Groszmann et al., 2013; Li et al., 2018; Thiebaut et al., 2019). Such regulation has been linked to the phenotypic divergence of populations and can affect the width of a niche and the capacity to fulfill roles in an ecosystem (Miryeganeh and Saze, 2019; Thiebaut et al., 2019; Rey et al., 2020). Epigenetic change has also been linked to altered patterns of gene expression associated with transgressive segregation and heterosis in hybrid offspring (Groszmann et al., 2013; Junaid et al., 2018; Botet and Keurentjes, 2020). Recent work in plants suggests that epigenetic regulation plays a crucial role in hybrid vigor and that non-additive and yet not random differences in the patterns of chemical DNA modification (methylation of Cytosine bases) between parents and hybrid offspring contributes to phenotypic differences (Kawanabe et al., 2016; Junaid et al., 2018; Lauss et al., 2018; Miryeganeh and Saze, 2019; Sinha et al., 2020). Other studies have also found that inbred and outbred lines exhibit different epigenetic profiles and that manipulating these profiles can revert symptoms of inbreeding depression (Vergeer et al., 2012). Taken together, these findings strongly suggest that accounting for both allelic and epigenetic variation is likely to be necessary to predict fitness outcomes for hybrid populations (Rey et al., 2020). While most studies to date involve plants, common mechanisms of eukaryotic gene expression suggest similar studies in animals will reveal similar results.

GENETIC RESCUE

Prolonged periods of low (effective) population size and/or restricted gene flow are a growing concern among conservationists and there is increasing interest to utilize genetically motivated management to address the loss of genetic diversity and its negative effects (IUCN/SSC, 2013; Frankham, 2015; Hoffmann et al., 2015; Whiteley et al., 2015; Frankham et al., 2017; Ralls et al., 2018; Bell et al., 2019; Chan et al., 2019; Taylor and Larson, 2019). In practice, management interventions to increase genetic diversity usually entail translocation of individuals from a source to a genetically distinct target population with the aim of intentionally generating intermixed (hybrid) populations of the same species (Armstrong and McLean, 1995; Weeks et al., 2011; IUCN/SSC, 2013; Pierson et al., 2016; Wennerström et al., 2017; Flanagan et al., 2018). Efforts to increase genetic diversity have also entailed management of connectivity between distinct populations or different forms of guided mate choice (Soulé, 1985; Pierson et al., 2016; Wennerström et al., 2017; Flanagan et al., 2018). These translocations involving genetically distinct populations differ from more classic supplementary translocations (also referred to as reinforcement translocations) which have the goal to increase population size directly by adding more individuals, and differ from reintroduction translocations where the purpose and focus are to re-establish populations with genetic stock obtained from within its historical range (IUCN/SSC, 2013; Armstrong et al., 2019). All the above-mentioned types of interventions have been suggested for *Apteryx*. However, these proposals have been made without studies having been conducted to quantify inbreeding and/or inbreeding depression in neither source nor target populations (Innes et al., 2015; Kiwis for Kiwi, 2016; Germano et al., 2018).

The interbreeding of individuals from populations with the aim of increasing fitness is now commonly referred to as genetic rescue (Hedrick, 1995; Johnson et al., 2010; Frankham, 2015; Bell et al., 2019; Ochoa et al., 2019). "Rescue," in this case, refers to decreasing the extinction risk in the target population and is commonly evaluated by an observed population growth rate increase after genetic admixture (Ingvarsson, 2001; Hedrick et al., 2011; Frankham, 2015; Whiteley et al., 2015; Bell et al., 2019). A growing number of authors argue that this prospect of alleviating extinction risk by augmented gene flow is underutilized (Frankham et al., 2011; Frankham, 2015; Whiteley et al., 2015; Love Stowell et al., 2017; Ralls et al., 2018, 2020; Bell et al., 2019). Since 1964, the 14 birds released on Ponui Island have produced an estimated population of over 1,700 birds, or one bird per hectare, which makes the Ponui Island brown kiwi population one of the densest in the world having experienced an equivalent of on average 9% annual population growth (Potter, 1990; McLennan and Potter, 1992). Thus, even though this was not an intention of the original translocations, the Ponui population might be one of New Zealand's best examples of genetic rescue.

Conceptually, genetic rescue and hybrid vigor likely describe the same biological phenomenon resulting from hybridization. However, in conservation, genetic rescue is rarely or never promoted as hybridization due to the negative connotations of this word (Allendorf et al., 2001; Wayne and Shaffer, 2016; Love Stowell et al., 2017; Bell et al., 2019; Chan et al., 2019; Taylor and Larson, 2019). Hitherto, most attempts of genetic rescue have focused on utilizing source populations with smallest possible genetic difference to the target population (Edmands, 2007; Frankham et al., 2017; Ralls et al., 2018, 2020). However, discussion about the trade-off between increasing genetic diversity and maintaining genetic integrity is becoming increasingly relevant. Recently, several authors have discussed the ambiguity and sometimes mismatch in genetically motivated conservation interventions. For instance, Von Holdt et al. (2018) highlighted that there is a need for debate around our understanding of the evolutionary significance of hybridization and its implications for conservation management, and Ralls et al. (2018) called for a "paradigm shift in the genetic management of fragmented populations."

As for hybrid vigor, the allele centered modeling of genetic rescue (Davenport, 1908) is still the commonly suggested explanation for successful population growth, leading to the prediction that the magnitude of genetic rescue is a function of the severity of the genetic load in the target population (Bell et al., 2019). A variation on this model, while still having an allele focus, acknowledges the role of the size of the source population (the bigger the better) and the amount of adaptive genetic difference between target and source population (the less the better, Whiteley et al., 2015; Bell et al., 2019). In reviewing 156 published cases, Frankham (2015) identified that in practice the two most important conditions for successful genetic rescue were (1) that the source population was not inbred, and (2) that the target population experienced some level of environmental stress. Interestingly, the review of Frankham (2015) found that severe inbreeding in both target and source population did not have to exclude observed genetic rescue, such as in the case of Mexican wolves (*Canis lupus baileyi*, Fredrickson et al., 2007), however, the magnitude of rescue was larger when outbred sources were used. The noticeable discrepancy between theory and empirical finding highlights the need to identify what is missing from our understanding of inbreeding depression, outbreeding depression and heterosis. Quantification of these phenomena requires a baseline for comparison, and in cases where species are confined to small isolated populations and have been so for a long time, what can be learnt from comparing these populations may be limited (Hedrick and Fredrickson, 2010; Heber et al., 2013; Ramstad et al., 2013; Taylor, 2014). An exemplary case concerns *A. owenii*. This is the only *Apteryx* species in which inbreeding has been thoroughly studied. Results show evidence of several bottlenecks and extremely low variation in the MHC genes (Ramstad et al., 2010; Miller et al., 2011; Shepherd et al., 2012; Taylor, 2014). However, the fact that extant members of this species originate from as few as five founders, means that findings might not be applicable to other *Apteryx* species (Ramstad et al., 2013).

While debate remains surrounding the degree to which genetic load contributes to extinction risk, there will remain debate as to the magnitude of threat aversion or loss of extinction risk that can be expected from genetic rescue (Bell et al., 2019). One challenge for evaluating the success of translocations involving birds from multiple sources is that long term outcomes might not be immediately apparent. While some studies have suggested that the effect of genetic rescue is greatest in the first- and/or second-generation (Johansen-Morris and Latta, 2006; Bell et al., 2019), other studies have shown that initial generations can suffer reduced fitness as a consequence of outbreeding depression. In such cases, crossing, backcrossing, and genomic recombination can later generate a hybrid swarm with higher average fitness than the parental populations (Hwang et al., 2011). While these findings are somewhat contradictory, they caution against drawing conclusions too soon after translocations involving interpopulation crosses. The Ponui island birds, resulting from a mixed translocation that occurred more than 50 years ago, offer the opportunity to investigate the longer-term fitness consequences of admixture.

The successful introduction of diversity resulting in phenotypic diversity on which selection can act and adaptations evolve in response to environmental conditions is said to diffusely depend on the genomic makeup of the introduced individuals (Bell et al., 2019). It will also depend on how the genome is packaged and expressed in individuals, and how this affects the fitness of individuals (Hochholdinger and Baldauf, 2018; Li et al., 2018; Botet and Keurentjes, 2020). This is an area of research where there are many outstanding questions, but where knowledge is increasing rapidly (Hochholdinger and Baldauf, 2018; Rey et al., 2020). Genome Science that links genetic variation, genome expression and local adaptation will be key, and this may require rethinking our measures of biodiversity.

ASSESSING BIODIVERSITY

Since the ratification of the Convention on Biological Diversity (CBD) in 1992, the world has agreed to acknowledge and preserve three levels of biodiversity: ecosystem diversity, species diversity and genetic diversity (UN, 1992). The latter is mainly justified because standing genetic diversity – allelic variation – is thought to contribute most to evolutionary potential of species and thus to their capacity to adapt to a rapidly changing environment (e.g., Haenel et al., 2019; Lai et al., 2019). In practice, this has led to genetic differences being used as an objective criterion to measure diversity, delimit and identify species, subspecies, taxa, lineages, evolutionary significant units (ESUs), or management units, often driven by improving opportunity for legal protection, funding and/or threat acknowledgment (Rojas, 1992; Godfray et al., 2004; Palsbøll et al., 2007; Lohman et al., 2010; Wayne and Shaffer, 2016; Cobley, 2017; Groves et al., 2017; Taylor et al., 2017a,b). The prevailing standpoint in such cases has been that preserving genetic diversity means maintaining the observed differences (see for example Palsbøll et al., 2007; Weir et al., 2016; Richmond et al., 2017; Taylor et al., 2017c; Germano et al., 2018). As mentioned above, the *Apteryx* genus serves as a typical example of both these tendencies (Tennyson et al., 2003; Weir et al., 2016; Germano et al., 2018).

Numerous genetic studies that have identified populations or other groups within species and genera, such as *Apteryx*, as genetically distinct have been based on markers such as microsatellites, allozymes, mitochondrial DNA sequence, or sequence fragments of a small number of selected genes (Baker et al., 1995; Cooper et al., 2001; Haddrath and Baker, 2001, 2012; Burbidge et al., 2003; Shepherd et al., 2013). These traditional markers have successfully been used to provide measures of genetic diversity and infer evolutionary relationships (Mitchell et al., 2014; Weir et al., 2016). However, this approach can be limiting when only a small number of gene loci are investigated and/or when loci evolve at different rates of evolutionary change within and between taxa (Allendorf et al., 2010; Funk et al., 2012; Steiner et al., 2013; Putman and Carbone, 2014). Low resolution can lead to underestimation and/or miss interpretation of the complex history of species and populations (Goldstein et al., 1996; Hudson and Turelli, 2003; Zink and Barrowclough, 2008; Funk et al., 2012; Steiner et al., 2013; Jeffries et al., 2016; Kardos et al., 2016; Hodel et al., 2017; Richmond et al., 2017; Galla et al., 2020). Another limitation of the most commonly used genetic markers is that they are not linked to traits of functional adaptive significance and have restricted ability for determining the cause and nature of ecological distinctiveness of taxa (Allendorf et al., 2010; Funk et al., 2012; Wennerström et al., 2017; Leroy et al., 2018). Hence, there are limitations to the ability of such markers to inform and evaluate the consequences of hybridization and translocation success based on possible outbreeding and inbreeding effects (Funk et al., 2012; Hess et al., 2013; Frankham, 2015; Whiteley et al., 2015; Flanagan et al., 2018; Bell et al., 2019; Taylor and Larson, 2019).

Newer molecular tools allow researchers to reduce these limitations. For example, genomic methods, such as reduced-representation-sequencing (for instance through protocols like genotyping-by-sequencing) (1) provide information from thousands of loci spread throughout the entire genome, and (2) cover both neutral, non-coding sequences and genes under selection (Elshire et al., 2011; Funk et al., 2012; Hess et al., 2013; Narum et al., 2013; Reitzel et al., 2013; Hunter et al., 2018; Leroy et al., 2018; Picq et al., 2018). This resolution allows for much more detailed genetic characterization of closely related taxa, and thus also of historic as well as recent hybridization and introgression between them and the population growth effects over time such admixture has had (Elshire et al., 2011; Weeks et al., 2011; Narum et al., 2013; Escudero et al., 2014; Leaché et al., 2014; Gaughran et al., 2017; Schmickl et al., 2017; Zhen et al., 2017; Picq et al., 2018; Taylor and Larson, 2019). In addition, genome-wide association studies (GWAS), provide insight into the nature of the physiological and behavioral differences of populations (Hess et al., 2013; Flanagan et al., 2018; Hunter et al., 2018). Methodological advances mean that genomics is likely to take on a larger role in conservation biology, in delimiting management units, in identifying suitable source populations and in evaluating translocation outcomes (Funk et al., 2012; Flanagan et al., 2018; Von Holdt et al., 2018; Galla et al., 2019; Ramstad and Dunning, 2020; Russello et al., 2020). Even so, the potential for genomics to contribute to conservation science may not be fully realized while focus remains on genetic variation alone which in many cases will be insufficient to make reliable predictions for managing biodiversity.

While our understanding of diversity, resilience and the contrasting outcomes of hybridization is informed by genetic variation, the importance of epigenetic variation is increasingly being recognized (Cheptou and Donohue, 2013; Groszmann et al., 2013; Biémont and Vieira, 2014). Epigenetic changes accompanying environmental change play a key role in plastic responses that occur at a faster rate than mutational change and the sorting of allelic variation (Hochholdinger and Baldauf, 2018; Miryeganeh and Saze, 2019; Rey et al., 2020). Epigenetic factors could explain why some natural populations are more fit than others, and also why some species that have crashed to very low levels of genetic diversity and adaptive potential can still rebound successfully (Heber et al., 2013; Ramstad et al., 2013; Frankham, 2015; Jamieson, 2015). The contribution of epigenetic processes to evolutionary and ecological success requires more study and understanding, but the potential of "conservation epigenetics" is both exciting and promising (Rey et al., 2020). Differences in epigenetic markers between populations could help us to identify and categorize evolutionary significant units (ESUs) and whether species with low genetic variation might nevertheless be resilient to environmental change. This in turn will help us to better predict the viability and differences between populations – information that could be crucial for identifying suitable source- and target populations for translocations. Epigenetic monitoring, as a complement to genetic investigations, could provide more ecologically significant information than studies of genetic variation alone and improve prediction of what interventions are likely to be most successful (Hochholdinger and Baldauf, 2018; Miryeganeh and Saze, 2019; Rey et al., 2020).

Investigation of epigenetic processes will involve studies of DNA, RNA, and proteins. However, a place to start at the population level is with DNA methylation profiles (Sepers et al., 2019; Rey et al., 2020). Of interest for conservation planning would be understanding variation among individuals and between populations, and whether ESUs are categorized appropriately, determining whether source populations show differences from translocated and admixed populations and whether there is evidence of population fragmentation sooner than is appreciated from studies of genetic variation (Rey et al., 2020). Variant protocols of reduced-representation-sequencing, such as DREAM, EpiGBS and bsRADseq offer the potential to characterize partial methylation profiles (Jelinek and Madzo, 2016; Trucchi et al., 2016; van Gurp et al., 2016). However, these protocols have limitations since they capture only a small subset of the entire epigenome. A more complete methylome profile is possible using whole-genome bisulfite sequencing (Lister et al., 2009; Hansen et al., 2012). Locus specific bisulfite sequencing is also possible (Hernández et al., 2013; Lam et al., 2020). Another alternative is the so-called assay for transposase-accessible chromatin using sequencing (ATAC-seq) which maps genome-wide chromatin accessibility, which is tightly linked to gene expression (Miskimen et al., 2017). However, both the latter methods introduce the cost of whole-genome sequencing. Whatever might be the methodological developments to come in the fast-developing field of high throughput sequencing technologies, a focus on both genomics and epigenetics is likely to provide the insight that is needed to understand hybridization, and its contribution to biological diversity and successful conservation strategies (Goulet et al., 2017; Von Holdt et al., 2018; Chan et al., 2019; Taylor and Larson, 2019; Rey et al., 2020).

THE HYBRID BIRDS OF PONUI

In 2016, the hybrid birds of Ponui were said to be of no value for kiwi conservation other than as specimens for public display. However, this conclusion needs to be reconsidered in light of recent findings and modern tools of genome science. There is no doubt that allelic diversity and the genetic background of individuals is important for individual fitness, population sustainability and genetic rescue. However, knowledge of genetic variation alone appears insufficient to fully understand the link between genotype, transcriptome, phenotype, and fitness. Focusing solely on allelic variation makes for attractive and accessible models. However, the poor performance of these models to predict outcomes has the potential to damage the relationship between researchers and practitioners. This motivates the need for research investigating the interactions and relative contributions of genotype, epigenetics, and the environment for understanding phenotypic diversity, reproductive success, and adaptive potential.

The Ponui birds, which are highly successful in their island habitat, provide an exciting model system to investigate ecological success and potentially the evolutionary and ecological significance of hybridization. In addition, this system could help to inform how conservation translocations can effectively utilize genome-level data to achieve their goals. Ecological factors might help explain the success of this population relative to the mainland and other island populations. For instance, compared to unmanaged populations the juvenile kiwi on Ponui experience much lower mortality from predation (Shapiro, 2005; Dixon, 2015; Strang, 2018). However, this mortality is still higher than observed in the most extensively managed populations (Colbourne et al., 2005; Robertson and de Monchy, 2012). Thus, even if juvenile mortality contributes to population success it may still be important to determine other significant factors. Is the secret to their success the loss of recessive deleterious effects? Is it phenotypic diversity – and if so, how did that come about? Mainly through allelic admixture? Or via epigenetics and thus transcriptome variation? To gain understanding, the next step will be to compare the genomic diversity of Ponui birds with their parent populations and with other mainland populations whose history has not involved extreme genetic bottlenecks associated with the founding of island populations by a small number of translocated birds. Epigenetic studies might initially focus on methylation profiles and their density (Rey et al., 2020). A study could seek to answer questions such as: Is there epigenetic variation within and between populations of *A. mantelli*? How do the epigenetic profiles of Ponui birds compare with other populations? How do the methylation profiles change over generations on Ponui? How do they compare between parents and offspring? Does the genetic distance between parents influence the non-additivity of the epigenetic profile of offspring? What are the methylation patterns for genes of potential adaptive value? Following this investigation, important studies would compare genomic and epigenetic diversity in relation to transcriptome variation, and to how the resulting phenotypic variation relates to fitness, and measures of inbreeding-, outbreeding depression and/or hybrid vigor. A key for meaningful interpretation of transcriptome analyses will be detailed knowledge of individual birds (including information on generation, age, health, and sex) and here again, Ponui could prove suitable after 17 years of extensive studies on this population.

The questions that could be addressed by investigations of the Ponui birds are not only relevant to *Apteryx*, improved understanding of genomics and epigenetics and thus of the nature of population differences is key for conservation of all fragmented populations in need of augmented genetic influx (Tallmon et al., 2004; Edmands, 2007; Escobar et al., 2008; Stelkens et al., 2014; Barmentlo et al., 2018; Von Holdt et al., 2018; Bell et al., 2019; Koide et al., 2019; Rey et al., 2020). Worldwide, habitat and population fragmentation has rendered a situation where focusing solely on species-level conservation may lead to either inbreeding or homogenization, both of which results in loss of genetic diversity. Retaining evolutionary potential is arguably one of the main challenges for conservationists across the globe, not only because of the intrinsic value of diversity but also for providing populations with the ability to adapt to our changing environment. Because of this challenge, we support the call for a paradigm shift in conservation that includes redefining admixture and hybridization (Canestrelli et al., 2016; Ralls et al., 2018; Von Holdt et al., 2018; Taylor and Larson, 2019). We believe that it is wrong to dismiss a prolific population of a threatened species as unimportant in an unsubstantiated way when there remains uncertainty as to the best way of managing the species. This is even more so when these populations have the potential to serve as sources for ongoing, translocation focused interventions – a literal source for individuals and a source of increased knowledge. Lastly, we recognize the importance of multidisciplinary studies that are needed to help better understand and predict hybridization outcomes.

The questions that could be addressed with genetic and epigenetic investigations of the Ponui birds are not only relevant for *Apteryx*. Making meaningful measurements of population differences is important for determining what interventions are appropriate to ensure the sustainability of fragmented populations (Tallmon et al., 2004; Edmands, 2007; Escobar et al., 2008; Stelkens et al., 2014; Barmentlo et al., 2018; Von Holdt et al., 2018; Bell et al., 2019; Koide et al., 2019; Rey et al., 2020). These measurements require embracing the complexity of epigenetic phenomena and understanding how it interacts with genetic variation in affecting the fitness of individuals in different environments. Improved understanding will in turn help us to better understand the adaptive potential and resilience of species to environmental stresses and change. We support the call being made by others for a paradigm shift in conservation to rethink the negative connotations of admixture and hybridization (Canestrelli et al., 2016; Ralls et al., 2018; Von Holdt et al., 2018; Taylor and Larson, 2019). Measures of fitness of individuals and populations need to consider both temporal and environmental factors. Furthermore, until interactions between the environment of Ponui island and the epigenomes of its kiwi are better understood, we believe that it would be wrong to dismiss a prolific population of a threatened species. This is even more important when this population has the potential to serve as a source for ongoing, translocation focused interventions – a literal source of individuals and a source of increased knowledge to be drawn upon in decision making. Lastly, we acknowledge the importance of integrating contributions from other disciplines when using novel tools from genome science to improve understanding and better predict intervention outcomes. An important goal is to inform and develop practices that meet conservation aspirations.

AUTHOR CONTRIBUTIONS

MU and PL performed the literature search. MU wrote the first draft of the manuscript. All authors commented on previous versions of the manuscript, read, approved the final manuscript, and jointly developed the concept for the article.

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Benchmark for the ESA: Having a Backbone Is Good for Recovery

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To forestall the current rate of global extinction, we need to identify strategies that successfully recover species. In the last decade, the recovery record for the United States Endangered Species Act (ESA) has improved. Our aim was to review federal delisting documents for recovered species and quantify patterns in taxonomy, history of threats, policy, funding and actions that are associated with species recovery. In comparison to species still listed, the average recovered species was a vertebrate, had been listed longer under the ESA, was exposed to a lower number of threats at the time of listing, and received relatively higher levels of funding. Based on our review, we suggest the following strategies to improve species recovery: provide more time for ESA protection, allocate more funding for recovery, maintain environmental regulations that facilitate recovery, establish more private landowner agreements, and increase the area of protected lands.

Keywords: ESA, delisting, recovered, endangered, policy

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INTRODUCTION

The current rate of global extinction is 10 to 1,000 times higher than the planet's baseline average (De Vos et al., 2015; Díaz et al., 2019). This is a byproduct of intense human activity causing habitat conversion, overexploitation of species, growing impacts of climate change, pollution, and spread of invasive species (Wilcove et al., 1998; Pimm et al., 2014; Ceballos et al., 2015; Díaz et al., 2019; Leu et al., 2019). There is broad agreement that transformative change, including increased investment in conservation (Malcom et al., 2019), is needed to protect, maintain, and restore biodiversity and curb the extinction crisis (Díaz et al., 2019). To help direct such change, it is important to understand which factors predispose conservation efforts toward successful species recovery from the brink of extinction (Luther et al., 2016). For example, the International Union of the Conservation of Nature (IUCN) is currently in the process of creating metrics to define species recovery and identify a "green list" of species that were once vulnerable and are now recovered (Akçakaya et al., 2018). The purpose of this list is to learn from species conservation success stories and develop an optimistic vision of species conservation. Lessons learned could provide a road map on how to achieve species recovery to incentivize positive recovery actions and programs ([IUCN] International Union for the Conservation of Nature., 2020).

Many countries have laws and regulations to protect and recover native species and populations, such as Canada's Species at Risk Act of 2002, United Kingdom's Wildlife and Countryside Act of 1981, Australia's Endangered Species Protection Act of 1992, and New Zealand's Conservation Act of 1987. In the United States (US), the strongest law for preventing species extinction is the Endangered Species Act (ESA) (Taylor et al., 2005; Malcom and Li, 2015; Evans et al., 2016; Gerber et al., 2018). The ESA has been associated with recovering iconic species such as the peregrine falcon (*Falco peregrinus*) and bald eagle (*Haliaeetus leucocephalus*), as well as lesser-known species including the Magazine Mountain shagreen snail (*Inflectarius magazinensis*) and the Johnston's frankenia flowering plant (*Frankenia johnstonii*).

As of January 2020, 46 US native species have been removed from the ESA list due to their recovery ([USFWS] US Fish Wildlife Service, 2020a). A species listed under the ESA is *recovered* when it is no longer "in danger of extinction throughout all or a significant portion of its range" [ESA sec. 3(6), an endangered species] nor likely to become so "within the foreseeable future" [ESA sec. 3(20), a threatened species]. The United States Fish and Wildlife Service (USFWS) and the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (collectively, the Services) use species recovery plans to guide recovery on a species-by-species basis (Neel et al., 2012). A species recovery plan identifies measurable recovery criteria that, when achieved, would justify a species to be categorized as recovered. However, these recovery criteria are not legally binding [Ginsburg, 2012, ESA sec. 4(f)(1)], and many recommendations have been provided to improve recovery criteria outlined in recovery plans (Neel et al., 2012; Evans et al., 2016; Li et al., 2020). Delisting documents provide the Services' official decision and rationale for delisting a species from the ESA (Neel et al., 2012).

Foin et al. (1998) strongly advocated for continuing analysis of species recovery under the ESA to identify the patterns and histories of recovery success, but there have been, to our knowledge, no analyses since then. Thus, much like the proposed IUCN "green list," our goal was to review and quantify the record of species recovery within the ESA and identify laws, practices and recovery actions that are associated with species recovery. Based on previous literature, we predicted that recovered species would consist of more charismatic taxa with higher rates of funding, longer listing periods under the ESA and fewer threats at time of listing compared to non-recovered species (Taylor et al., 2005; Gibbs and Currie, 2012; Evans et al., 2016; Leu et al., 2019). The only government data available on the progress of listed species toward recovery were biennial reports that the Services (i.e., USFWS and National Oceanic and Atmospheric Administration) submitted to Congress. These reports provided a 2-year status update on each species; however, these reports were terminated in 2012. By looking at the record of recovery as of January 2020, our analysis serves as a benchmark to ESA recovery and can provide insight on what has enabled successful recovery of native species and how recovered species differ from currently listed species.

MATERIALS AND METHODS

A species can be delisted from the ESA because it has become extinct, undergone a taxonomic revision, been revaluated due to new information suggesting that protection is no longer warranted, or has recovered ([USFWS] US Fish Wildlife Service, 2020a). In our analysis, we focused on the record for species recovery for US native species (i.e., species that occur in the US and its territories; note Palau became an independent nation in 1994) because the detail of recovery efforts for these species are well documented. In addition, foreign listed species do not have recovery plans, and legal protections of the ESA are unenforceable outside US jurisdiction (Foley et al., 2017). We reviewed species delisting documents, obtained from the Environmental Conservation Online System website (ECOS, ecos.fws.gov; [USFWS] US Fish Wildlife Service, 2020a) and the US Federal Register website (www.federalregister.gov/) to identify recovery actions that aided in species recovery including international, federal, state, and local polices that provided protection assurances to species post-delisting. We also reviewed delisting documents to determine if justification for species recovery followed specific recovery criteria as laid out in species recovery plans.

To identify factors that differed between recovered and currently listed species, we compared time listed under the ESA (i.e., for recovered species this was the number of years between listing and delisting), taxonomic composition, and threats at time of listing (i.e., habitat modification, pollution, overutilization, environmental stochasticity, demographic stochasticity and/or species-species interactions; Leu et al., 2019) between the two groups. We also compared the number of threats at time of listing (Leu et al., 2019) and the proportion of budget received for ESA species recovery (Gerber, 2016). Proportion of budget received was based on the estimated cost needed for species recovery, as specified in a species recovery plan, compared to a species actual reported government expenditure provided for recovery between 1984 and 2014 (Gerber, 2016). Because Leu et al. (2019) showed that the number of threats at time of listing increased between 1975 and 2017, we controlled for year effects by regressing year to the number of threats for listed and recovered species combined, and then comparing residual values between currently listed and recovered species. We used the same approach for proportion of budget received. For both analyses, we used generalized linear mixed-effect models (lme4 package, Bates et al., 2015; glmmTMB package, Magnusson et al., 2020) with taxa included as a random effect (see Leu et al., 2019). We evaluated appropriate model structure (e.g., Poisson, negative binomial, or Gaussian) by evaluating qq-plots or histograms. We log-transformed response variables if necessary. We evaluated three model forms for year: linear, quadratic ($y = \beta0 + \beta1\ [\Delta \text{ year}] + \beta2\ [\Delta \text{ year }^2]$), and log-based pseudo-threshold ($y = \beta0 + \beta1 \log_e [\Delta \text{ year } +1]$, Scherer et al., 2012). We used package DHARMa (Hartig, 2020) to assess whether a given mixed model structure was appropriate for our data. Based on the top model with lowest AICc value (Akaike Information Criterion adjusted for small sample sizes; Burnham and Anderson, 2002), we estimated number of threats and proportion of funding received by subtracting observed values from fitted line values (i.e., residuals). We determined no year effect if the null model (i.e., intercept model) had the lowest AICc value.

Due to highly unequal sample sizes between recovered and listed species, and because sample sizes also differed between data sets for each factor listed above, we randomly sub-sampled each listed-species data set, including the residual data set, in two ways. One random data set consisted of 1,000 random draws from currently listed species equal to the number of recovered species in a given listed species data set (all-listed species). The other random data set consisted of 1,000 random draws of currently listed species equal to the number of recovered species as represented by their taxa in a given listed species data set (stratified-listed species). This allowed us to investigate whether factors associated with recovered species apply to all listed species or only to those species in taxa represented in recovered species. We used a similar approach to evaluate the number of federal and international policies, as well as state and local policies protecting species once recovered. We subsampled the policy data of recovered vertebrates based on number of recovered plant species because recovery is biased toward vertebrates. Because the recovered species data sets represent the population sample rather than a random sample, we only employed descriptive statistics when comparing factors between groups. We completed all analyses in R version 4.0.2 (R Core Team, 2020). Unless otherwise stated, we report means (± SE). The datasets and R code for this study can be found on our Open Science Framework (OSF) website (*OSF | Benchmark for the ESA: Having a Backbone is Good for Recovery. Data and R code*.

RESULTS

We collected data on 1,757 native species listed under the ESA through 2019. We excluded 20 species that were deemed not "a listable entity" by the USFWS due to errors in original data that were used to list the species, and we excluded 7 species because they were listed due to "similarity of appearance" to an already listed species, which would have inflated the sample size due to duplication. In total, our analyses included 1,730 species, of which 46 were recovered (see **Supplementary Table 1** for list of recovered species). For sample sizes in each analysis, see **Supplementary Table 2**.

Over time, the number of recovered and listed species has increased, with the difference between listed and recovered species declining (**Figure 1**). The first four species delisted from the ESA in 1985 were all birds, which were listed as endangered in 1970. These included a species with a broad distribution, the brown pelican (*Pelecanus occidentalis*), and three island species from Palau: the Palau owl (*Pyrroglaux podargina*), Palau ground-dove (*Gallicolumba canifrons*), and Palau fantail flycatcher (*Rhipidura lepida*). On average 1.3 ± 0.3 (SE) species were delisted annually between 1985 and 2019. Most (65.2%) species were delisted since 2011.

Time listed and taxonomic composition differed between listed and recovered species. Recovered species were listed ∼13 years longer (37.5 ± 1.8) compared to all-listed species (24.4 ± 0.06), and seven years longer compared to stratified-listed species (30.6 ± 0.06). Taxonomy composition for recovered species was biased high for mammals, birds and reptiles, and biased low for fish, flowering plants and snails compared to the taxonomic composition for all-listed species (**Figure 2**).

On average, a recovered species required 2 ± 0.2 (SD) recovery actions, with the number of actions ranging from zero to six. The most frequent recovery action cited in delisting documents to recover species was direct population management ($n = 18$), followed by private landowner agreements ($n = 17$) and take regulations ($n = 15$; **Table 1**, **Supplementary Table 3**). Other recovery actions included biological control of other species ($n = 13$), habitat restoration efforts ($n = 10$), pollution regulation ($n = 9$), development management ($n = 6$), and off-road vehicle management ($n = 5$; **Table 1**, **Supplementary Table 3**). Five species did not require specific recovery actions (Palau ground-dove, Palau owl, Palau fantail flycatcher, Eastern North Pacific gray whale [*Eschrichtius robustus*] and Deseret milkvetch [*Astragalus desereticus*]). These species were recovered because of their increased demographics in combination with them already occurring on protected government land, or the species was protected by an already established policy (e.g., Marine Mammal Protection Act).

The number of federal and international policies as well as state and local policies assuring protection post-delisting was higher for vertebrates than plants. On average, plant species had 0.9 ± 0.4 federal or international policies and 1.5 ± 0.3 state and local policies assuring protection post delisting compared to 3.9 ± 0.04 federal or international policies and 1.9 ± 0.02 state and local policies for vertebrates. A large number of federal and international policies ($n = 60$) mentioned in delisting documents provided assurances for species protection post delisting, with 40 of the 46 recovered species requiring these policies for recovery (**Supplementary Table 1**). Top international and federal US environmental regulatory policies cited in delisting documents for recovered species included the Clean Water Act (24%), Convention on International Trade of Endangered Species (CITES; 17%), Migratory Bird Treaty Act (17%), revoking the registration of DDT in 1972 (13%), and Federal Land Policy and Management Act (11% of species). In total, we found 77 state and local policies that provided recovery assurances (**Supplementary Table 1**), with a mean of 1.8 (SE = 0.4) of these policies per species. Of the recovered species, 37 had completed recovery plans, of which 73% (27) achieved all recovery criteria based on recovery plans, 27% (10) partially achieved recovery criteria (i.e., due to recovery criteria no longer being relevant or a single criteria was not met but the services decided that the species had recovered adequately), while nine recovered species did not have a completed recovery plan.

The percent of species listed for a given threat differed between currently listed and recovered species (**Figure 3**; for sample sizes see **Supplementary Table 2**). Recovered species were less likely to be impacted by five of the six threats – habitat modification, pollution, species-species interactions, environmental stochasticity, and demographic stochasticity – at time of listing. That is, a greater percentage of currently listed species were listed with one of these threats, regardless of whether averages were aggregated across all listed species or species stratified by recovered taxa. Overutilization was the only threat more likely to impact a recovered species at listing compared to averages aggregated between all-listed and stratified-listed species; however, this difference was minimal for the stratified-listed species (**Figure 3**). Last, our analyses showed that averages derived from stratified-listed species cannot be extrapolated to all listed species. Averages for all listed species were higher for pollution, species-species interactions, and demographic stochasticity, but lower for

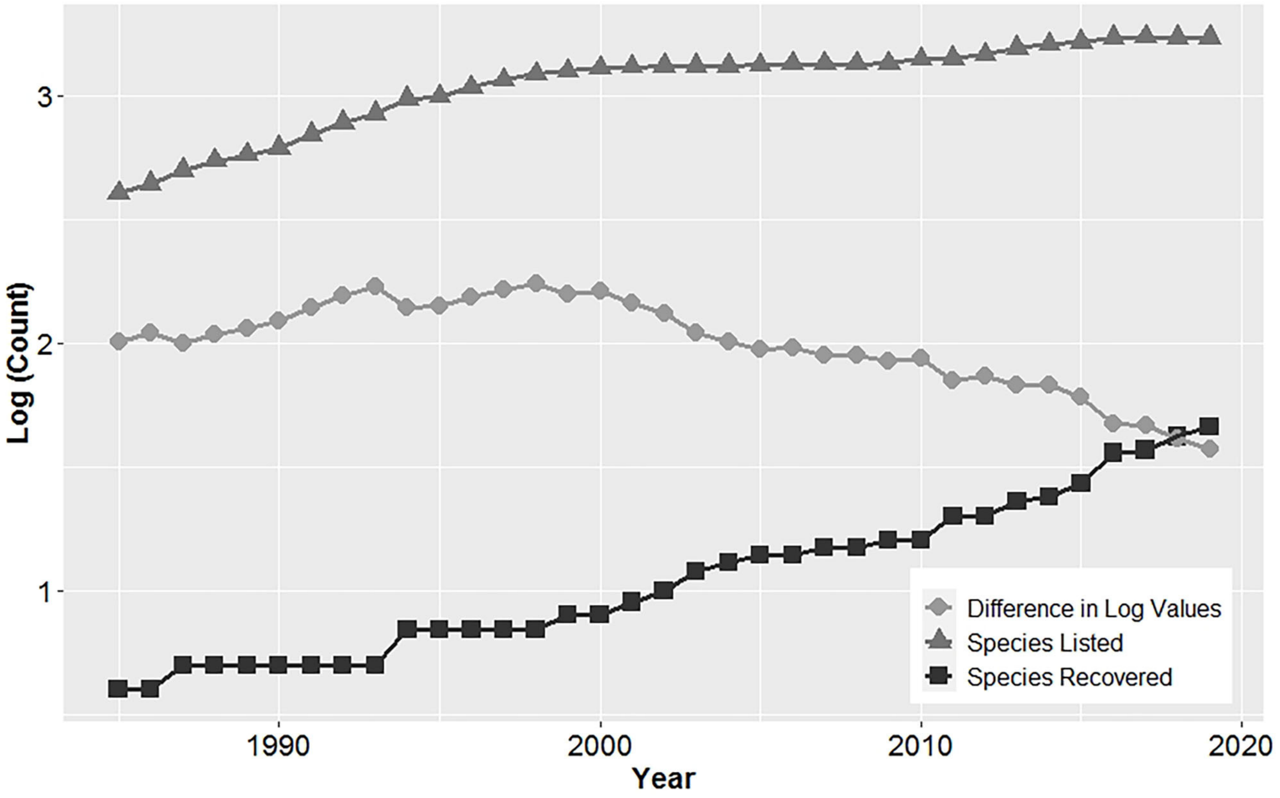

FIGURE 1 | Cumulative log of the number of species listed and recovered under the United States Endangered Species Act showing a declining difference in these values over time, indicating an improvement in recovery.

overutilization compared to stratified-listed species. Averages were similar only for habitat modification and environmental stochasticity between all-listed and stratified-listed species (**Figure 3**).

Our analysis suggests that recovered species were listed with fewer threats at time of listing (**Figure 4A**; for sample sizes see **Supplementary Table 2**). Average number of threats adjusted for year (residual number of threats) was over 30-fold lower compared to the average of all-listed species and stratified-listed species. However, note the large variation associated with the residual number of threats for recovered species. For this analysis we excluded lichens ($n = 2$ species) and cephalopods ($n = 1$) due to small sample sizes, leaving 1,561 species, including the 28 recovered species for which threat data were available (**Supplementary Table 2**). Number of threats was best related to the squared term of year (**Supplementary Table 4**), but it also may relate to the log term of year, the second-best model (**Supplementary Table 4**). The average number of threats adjusted for year in the log form for all-listed and stratified-listed species estimated from the second-best model was very close to the ones estimated from the best model, thereby supporting findings from the best model.

We found that the mean proportion of budget received for recovery actions (Gerber, 2016) was higher for recovered species than for listed species (**Figure 4B**, for sample sizes see **Supplementary Table 2**). Average residuals for recovered species were 60-fold higher compared to listed species, and the log of proportion of budget model related best to the squared term of year when budget was allocated (**Supplementary Table 5**). We found large variations in funding received for both listed and recovered species. For example, funding received for the Florida Scrub-Jay (*Aphelocoma coerulescens*) was 52 times higher than what the recovery plan proposed, whereas 51 listed species have not received any funding as of 2016. The high variation in recovered species funding was due to an outlier for the Louisiana black bear (*Ursus americanus luteolus*), which was allocated 10 times the amount of recovery funding than what was suggested in the recovery plan.

DISCUSSION

Understanding what has worked in the past for the recovery of imperiled species offers important lessons on how to improve the effectiveness and efficiency of recovering still imperiled species. Compared to listed species, we found that the average recovered species was more likely to be a vertebrate, was exposed to a relatively lower number of threats at the time of listing, and received relatively more funding. Other characteristics of recovered species included having been listed for nearly three decades, having been recently recovered (i.e., during

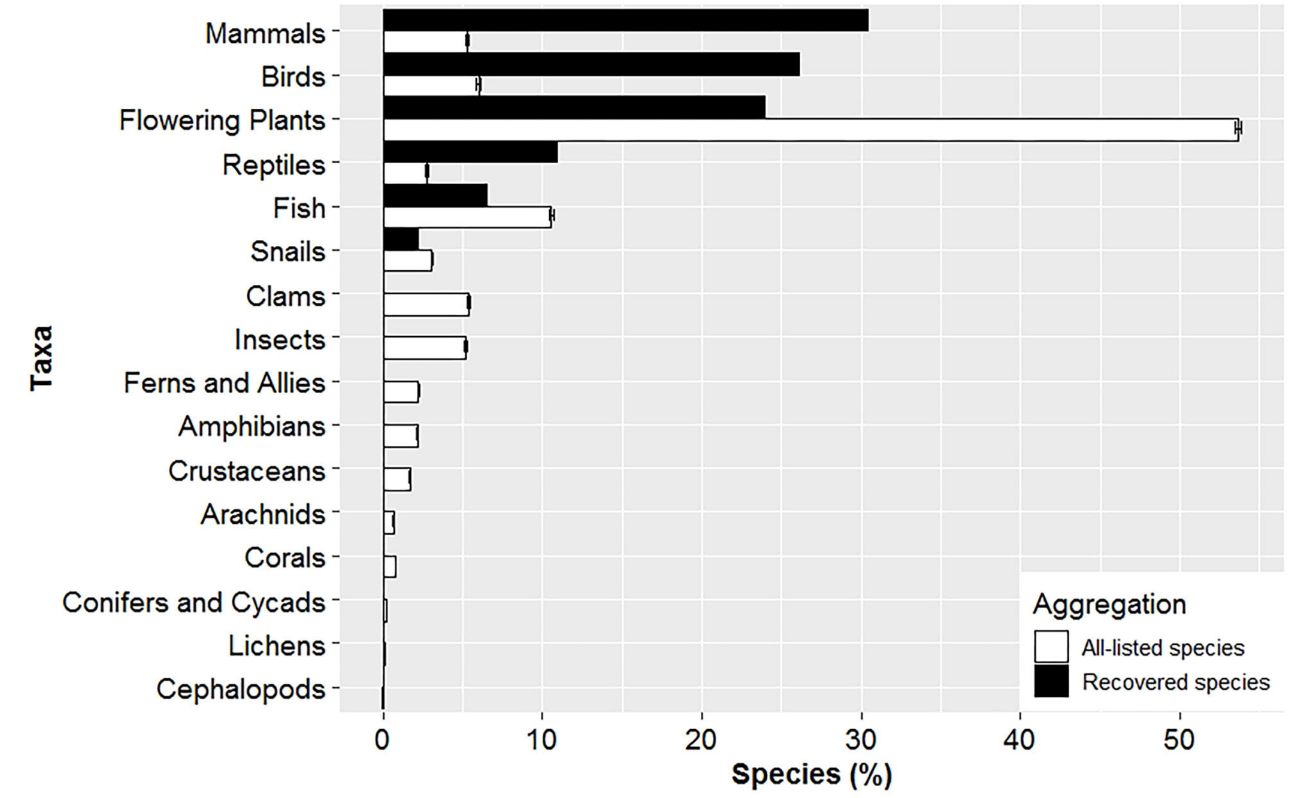

FIGURE 2 | Taxonomic composition differs between recovered and listed species. Mean (± SE) composition of listed species in a given taxa was derived from 1,000 random data sets consisting of 46 species to match the total number of recovered species for comparison. No species are currently recovered for all taxa between clams and cephalopods.

the last six-seven years), requiring approximately two recovery actions, and having numerous policies to help assure recovery post delisting.

As of January 2020, most taxa that have recovered were vertebrates (**Figure 2**). In contrast, 72% of species listed consisted of invertebrates and plants, but represented only 26% of recovered species. Vertebrate species are charismatic (Andelman and Fagan, 2000) and consequently there are established laws that specifically protect them (e.g., Migratory Bird Treaty Act and Marine Mammal Protection Act). Also, from 1967 until 1976, only vertebrates were listed under the ESA. It was not until 1976 and 1977 when the first invertebrates and plant species, respectively, were listed. Therefore, many vertebrates had nearly a decade head start in the recovery process. The longer a species has been listed under the ESA, the greater its improvement in population status and expansion of geographic range (Taylor et al., 2005; Evans et al., 2016; Valdivia et al., 2019). The ability of the ESA to recover species in large numbers is constrained by the ESA only having been implemented in the last several decades, while human activity in the US has negatively been impacting native species since the industrial age (Martin and Szuter, 1999). When species are eventually listed under the ESA, they suffer from complex and large-scale threats likely due to the prolonged listing process. In addition, many species do not obtain critical habitat designations and most only receive a fraction of the funding required for their recovery (Wilcove et al., 1993, 1998; Doremus and Pagel, 2001; Miller et al., 2002; Restani and Marzluff, 2002; Scott et al., 2005; Gerber, 2016). Hence, many species require long periods of time to reach recovery goals and become delisted (Wilcove et al., 1993; Gerber and Hatch, 2002; Neel et al., 2012; Evans et al., 2016; Valdivia et al., 2019).

The proportion of recovery funding allocated to the Services was higher for recovered species compared to listed species (**Figure 4B**), which is consistent with the findings of Male and Bean (2005). This may be the result of the majority of recovered taxa being vertebrates. Restani and Marzluff (2002) found that mammals and birds listed under the ESA were allocated more money for recovery and the amount of funding that goes toward a species' recovery was unrelated to its assigned priority for recovery. Since 1976, federal funding for the endangered species program of the USFWS (in constant, inflation-adjusted dollars) has increased greatly, but the total number of listed species has grown faster such that per-species funding has declined (Evans et al., 2016). Yet, our results indicate that a certain level of funding – certainly higher than the average funding per species – is necessary to achieve recovery. With growing threats such as species-species interactions and climate change (Evans et al., 2016; Leu et al., 2019), even more funding may be required to improve recovery efforts in the future.

TABLE 1 | Recovery actions cited in recovered species delisting documents.

Recovery actions & examples	Number of recovered species
Direct population management	18
Translocations	8
Captive Breeding	7
Reintroductions	6
Nesting habitat closures	3
Seed banks	3
Landowner agreements	17
Educational & technical assistance	7
Conservation easements	5
Habitat conservation plans	4
Memoranda of understanding	3
Voluntary conservation agreement	2
Cost-share program	1
Safe harbor agreement	1
Take regulation	15
Hunting regulations	9
State monitoring	6
Biological control	13
Invasive species control	7
Predator control	6
Competitor control	3
Habitat restoration	10
Land purchases	4
Fire management	4
Artificial habitat	3
Erosion control	1
Pollution regulation	9
Contamination regulation	5
Oil & gas regulation	5
Development management	6
Road closures	3
Zoning ordinances	3
Off-road closure	5
Outreach and public awareness	5

There was no correlation between number of recovery actions and number of threats at listing.
Multiple recovery actions can be cited in one species' delisting document.

We found a higher diversity of threats impacted currently listed species at their time of listing, apart from overutilization (**Figure 3**). The reduction in overutilization may be associated with how the US has developed a governance that establishes sustainable harvest regimes for terrestrial and freshwater animals, regulates inter-state trade of biodiversity (e.g., Game and Wild Birds Preservation and Disposition Act of 1900; Lacey Act of 1900), and provides enforcement and public education for hunting regulations and protection of natural resources (Decker et al., 2015). Abbitt and Scott (2001) also found that recovered and recovering species suffered from easy-to-manage threats that can be dealt with more directly like overexploitation/collecting, while declining species were affected by dams/drainage/diversions, non-indigenous predators and development; threats more difficult to manage against.

Several environmental regulations outside of the ESA, such as the Migratory Bird Treaty Act, National Environmental Policy Act, and Clean Water Act, provide species protection as well as assurances for species recovery. However, recent changes to several of these laws potentially means that they may no longer be able to protect migratory birds from incidental take ([USFWS] US Fish Wildlife Service, 2020b), may shortcut critical environmental reviews (Council on Environmental Quality, 2020), or may no longer provide protections to ephemeral streams and wetlands not directly connected or adjacent to large bodies of water (Department of the Army, 2020). Such changes to environmental policy reduce the suite of tools available to recover and assure the long-term conservation of federally listed species. Further, the reliance on these now weakened regulatory tools in delisting decisions for many species may call into question whether assurances for recovery have truly been achieved and whether ESA protections may again be required.

We found that the most cited recovery actions in delisting documents that aided species recovery included direct population management and working with private landowners (**Table 1**). Successful population management recovery actions have included the translocation and reintroduction of individuals into species' historical ranges to restore extirpated populations, and the captive breeding or establishment of seed banks to restore or supplement wild populations (**Table 1**, **Supplementary Table 3**). For example, the substantial increase in the numbers of Aleutian Canada Geese (*Branta canadensis leucopareia*) that lead to their recovery was dependent on reestablishing this species to their former nesting islands. This was initially done through release of captive-bred birds on predator free islands with very little success. Greater success occurred from translocation of wild birds to these same islands, which resulted in reestablishment of multiple breeding colonies.

Incentive programs provided by the ESA (e.g., in section 10) and its implementing regulations, such as safe harbor agreements, habitat conservation plans, and conservation banks, have helped advance the recovery of several species (**Table 1**, **Supplementary Table 3**). This result is important because more than two-thirds of all listed species occur in part on private lands, and a third only on private lands (Evans et al., 2016). At the same time, much of current property rights regimes support private landowners to develop and access lands for commercial and private interests as opposed to maintaining or improving ecological processes, including habitat for imperiled species (Rissman and Sayre, 2012; Henson et al., 2018; Moon et al., 2020). The ESA extends habitat protections to private lands in limited circumstances: when federal actions are involved (in section 7 prohibiting agencies from carrying out, funding, or permitting activities that destroy or adversely modify designated critical habitat) or if habitat destruction were to demonstrably result in take (i.e., harm, harass, kill, etc.) of individuals of a listed species (section 9). The section 7 consultation process and the section 10 agreements noted above offer landowners permits to minimize the effects of these regulations, but additional recovery-focused incentives are likely needed. For

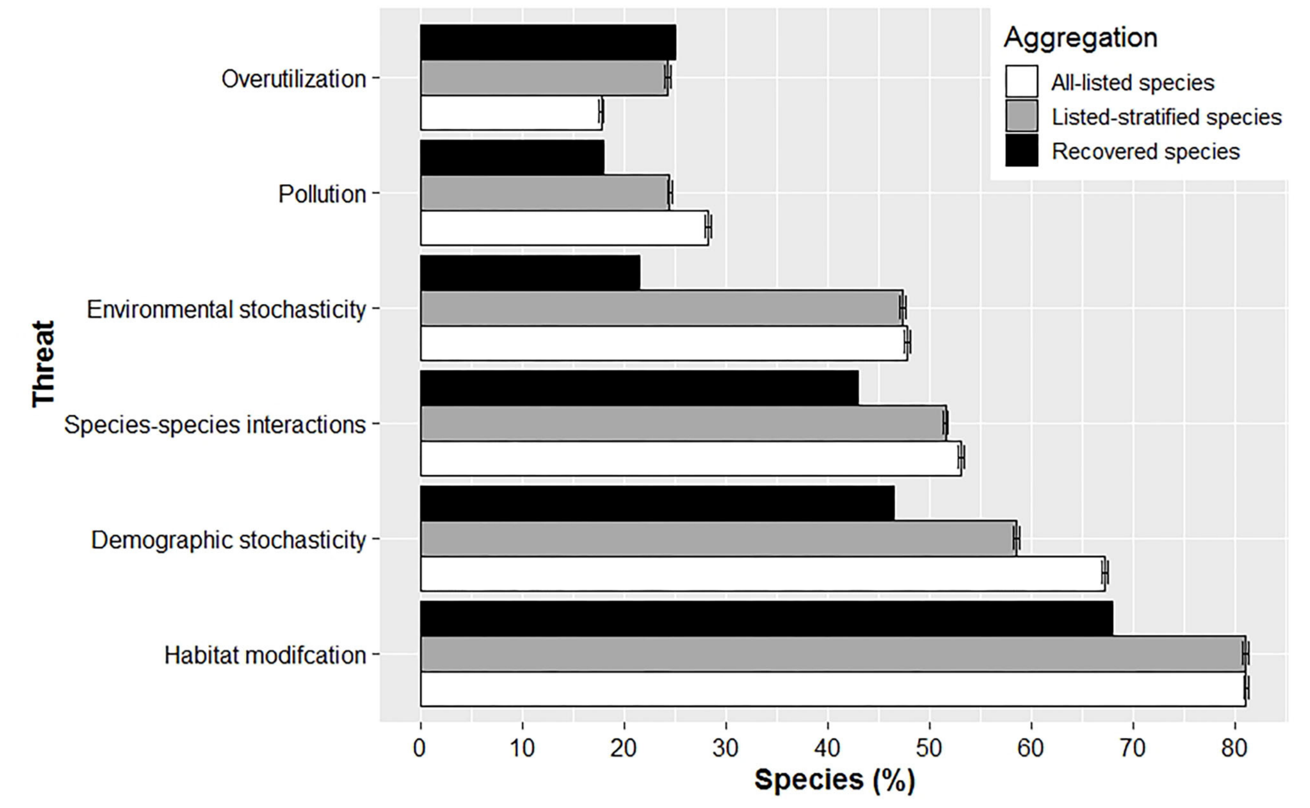

FIGURE 3 | Mean (± SE) percent of species listed with a given threat at time of listing for recovered, all-listed and stratified-listed species. Overutilization was the only threat that affected proportionally more recovered species compared to listed species at time of listing.

example, the overall effectiveness of current incentive programs remains uncertain, with many considered time-consuming and too complex for private landowners (Evans et al., 2016). Other landowner agreements such as Memoranda of Understanding and voluntary Recovery Management Agreements (Scott et al., 2005) have been successful in species recovery, especially for species that require active management to maintain their population numbers (i.e., conservation reliant, Scott et al., 2010). For example, the rebound and recovery of the Kirtland's Warbler (*Setophaga kirtlandii*, [[USFWS] US Fish Wildlife Service, 2020a) was made possible through development of a Memoranda of Understanding with governmental and private partners that put this species on the path to recovery (Frey, 2018). Expanding incentive programs such as Memoranda of Understanding and Recovery Management Agreements for private landowners to help advance the recovery of ESA-listed species will require programs that are innovative, integrate social sciences, tailored to the needs and values of the participating landowner, and increase the return-on-investment for the participant (Sorice and Donlan, 2015; Epanchin-Niell and Boyd, 2020).

With difficulties in working with private landowners and the ESA, it is no surprise that nearly two-thirds of recovered species (30 of 46) occurred predominately on protected areas (e.g., state parks, federal property, non-governmental organization property). Research suggests that protected areas benefit biodiversity by having reduced habitat loss that maintains species populations and providing more opportunities for implementation of recovery actions (Bruner et al., 2001; Hatch et al., 2002; Gray et al., 2016; Eichenwald et al., 2020). Several studies have found that listed species suffer less habitat loss and are more likely to be improving on public lands (Abbitt and Scott, 2001; Hatch et al., 2002; Evans et al., 2016; Eichenwald et al., 2020). Based on our review of delisting documents for recovered species, protected areas provide more opportunities for focused recovery efforts and implementation of recovery actions as outlined in **Table 1** (Hatch et al., 2002). For example, the biological control of invasive species on public lands has been important in the recovery of the Black-capped Vireo [*Vireo atricapilla*], Aleutian Canada Goose [*Branta hutchinsii leucopareia*], Tinian Monarch [*Monarcha takatsukasae*], Eggert's sunflower [*Helianthus eggertii*], Island night lizard [*Xantusia riversiana*] and others ([USFWS] US Fish Wildlife Service, 2018).

CONCLUSION

When reviewing the pattern of species recovery under the ESA, recovered species were more likely to be vertebrates, protected under the ESA for a longer period of time, affected by a lower number and diversity of threats, received protections from other policies outside the ESA, occurred more on protected lands, and received a higher proportion of recovery funding. Based on these observed patterns, recovery for species still listed, especially plants and invertebrates, could improve if they receive more

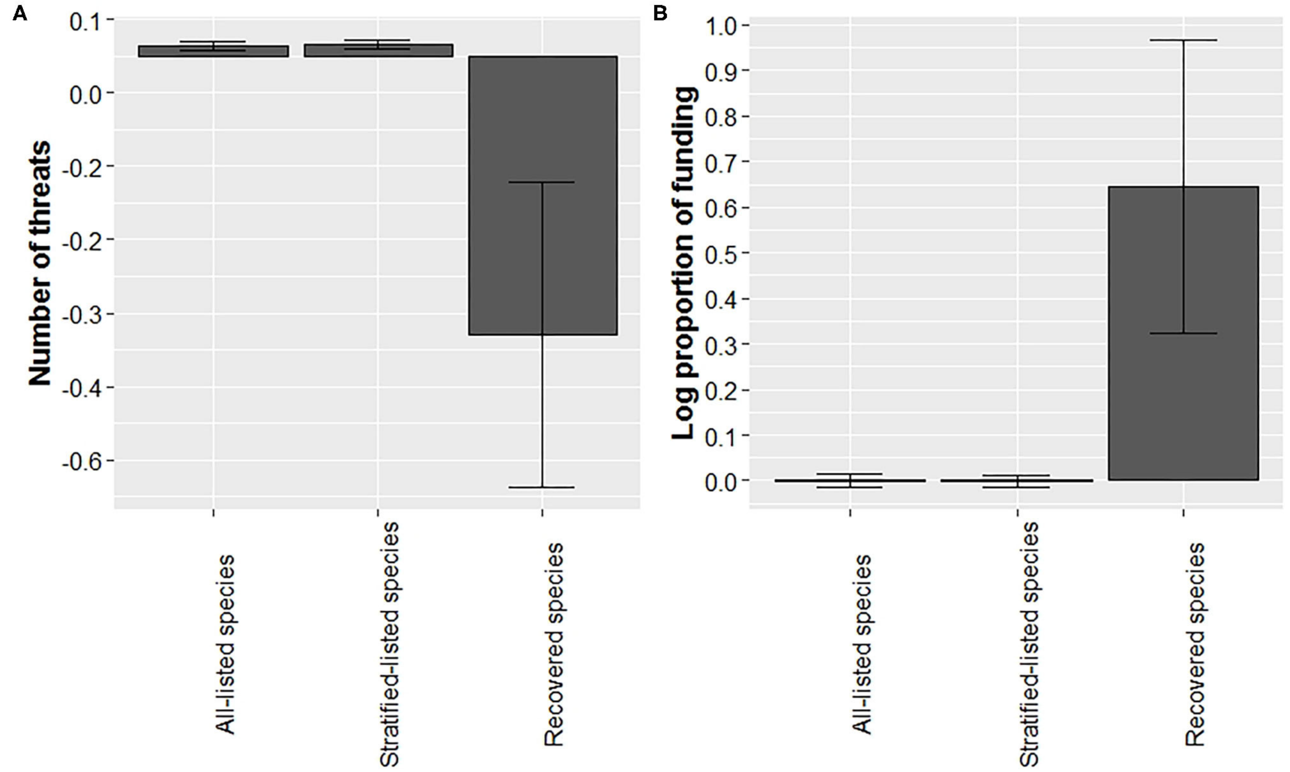

FIGURE 4 | Recovered species experienced fewer threats at time of listing and a higher proportion of funding (adjusted by year) than listed species. Bars represented mean (with ± SE error bars) residuals for number of threats at listing **(A)** and average log proportion funding allocated **(B)** for all-listed, listed-stratified, and recovered species.

recovery funding and are protected sooner under the ESA before suffering from a greater number and diversity of threats.

One purpose in developing an IUCN "green list" is to develop an optimistic vision of species conservation and provide learned lessons from species conservation success stories to provide a road map on how to achieve species recovery. Based on our observed patterns of species recovery under the ESA, we suggest five strategies to improve species recovery:

(1) Time: Allow species ample time to recover and list them sooner, recognizing that biological and ecological processes are time-limited, and acknowledge that it is incorrect to conclude the ESA is a failure based on duration of listings without accounting for the time requirements.
(2) Funding: Increase federal, state, and private sector financial support for effective recovery actions (e.g., direct population management, control of problem species and habitat restoration; Malcom et al., 2019) and prioritize funding within a resource allocation framework as part of a decision support tool (Gerber et al., 2018).
(3) Regulations: Reestablish, maintain and develop environmental governmental policies that support species recovery efforts (e.g., regulations on take, pollution, energy development and off-road vehicle activity) and provide assurances that recovered species maintain their recovered status post-recovery (e.g., Clean Water Act, Migratory Bird Treaty Act).
(4) Agreements: Increase federal and state governmental support to establish innovative and tailored private landowner incentive programs, including agency agreements such as Memoranda of Understanding and Recovery Management Agreements to protect habitat and implement recovery actions.
(5) Land protection: In collaboration with local communities, enhance the amount of protected space for listed species that provide habitat space and the flexibility to implement effective recovery actions.

The implementation of these recommendations in an adaptive management approach would help identify which strategies work best in specific situations (Canessa et al., 2016; Evans et al., 2016; Gosnell et al., 2017; Evansen et al., 2020). By monitoring these implemented recommendations over time, we expect to identify which actions are improving our ability to recover species and restore their ecosystem function and which are not. We note that the data are not available to determine which actions are not effective at recovery at this time, but that such information is needed for effective adaptive management and efficient resource allocation (Evansen et al., 2020). We also recommend future benchmarks of recovery be conducted to determine conservation strategies and policies that continue to work, or what new approaches to recovery are having success.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in https://osf.io/cxehu/.

AUTHOR CONTRIBUTIONS

AH contributed writing, data analysis, and overall construction of this manuscript. ML contributed writing, data analysis, and figure development. DC contributed writing and data collection. TT and CP contributed data collection. JMi and JMa contributed writing and policy review. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.630490/full#supplementary-material

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Wildlife-Friendly Livestock Management Promotes Mammalian Biodiversity Recovery on a Semi-Arid Karoo Farm in South Africa

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Agriculture is an essential production system used to feed the growing human population, but at the same time has become a major driver of biodiversity loss and environmental degradation. Employing production methods that restore degraded landscapes can have a positive impact on biodiversity, whilst improving food production. We assessed how mammalian biodiversity, specifically richness and their relative abundances varied on five Karoo farms in South Africa that had been amalgamated and subjected to a transition from traditional livestock grazing techniques (sporadic rotational grazing and lethal predator control) to wildlife-friendly non-lethal predator management, using human shepherding of livestock under a high-density short-duration grazing regime. We used camera trap data collected over a 4-year period, to measure mammalian species richness, distribution and relative abundance on the wildlife-friendly farm to investigate temporal changes throughout the conversion from traditional farming practices. In the last year of the study (2019) additional cameras were used to provide a spatial comparison of mammalian species on the wildlife-friendly farm to two neighboring farms, a traditional livestock farm using lethal predator controls, and a game farm. We found that mammalian species richness increased year on year resulting in a significant increase of 24% over the duration of the study. Herbivores showed an increase of 33% in the number of species detected over the years, while predator species increased by 8%. The relative abundance and distribution of most species also showed increases as the conversion process took place. For example, 73% of the herbivore species detected throughout the study increased in their relative abundance. Similarly, 67% of all species showed an increase in the number of sites occupied over the years. In the final year of the study the wildlife-friendly farm had more mammalian species compared to the game farm and traditional livestock farm, with the latter two sites having a similar number of species when compared to the commencement of the conversion of the wildlife-friendly site. These broad improvements in mammalian biodiversity demonstrate that livestock production can benefit local mammalian biodiversity through a combination of herder grazing management and wildlife-friendly farming.

Keywords: farming, predator, shepherding, abundance, herbivore, rangelands, fences, richness

INTRODUCTION

Conserving and restoring biodiversity has become a rising priority globally. Over the last two decades, ambitious targets set by the United Nations Convention on Biological Diversity (CBD) to curb the rate of biodiversity loss have failed (Butchart et al., 2010; Kok et al., 2018). While society increasingly realizes the value of biodiversity to human well-being (Hill et al., 2015), responses have been insufficient in achieving short-term goals and cast doubt on the ability of society to achieve the long-term goals of the CBD. These ongoing losses of biodiversity are predicted to result in ecosystem collapse by the turn of the century (Díaz et al., 2019; IPBES, 2019). Natural ecosystems around the world are shrinking, and with approximately a third of the world's land surface used for agriculture; either livestock or crop production (UN Food Agriculture Organization, 2017), these production lands and their impact on biodiversity is becoming increasingly important to conservation efforts (Kok et al., 2018). In South Africa, 69% of the land surface is reported to be suitable for livestock farming (Goldblatt, 2010), making this sector an important component of efforts to promote biodiversity conservation regionally.

However, agricultural landscapes are notorious for negative impacts on wildlife and ecosystems, and are attributed to causing the largest impact on terrestrial biodiversity loss (Kok et al., 2018). Livestock farming has been shown to negatively affect animal diversity (Filazzola et al., 2020), plant biodiversity (Nenzhelele et al., 2018), primary productivity, carbon sequestration, soil erosion, and water retention (du Toit et al., 2009, Stavi et al., 2016). In South Africa, livestock production practices have degraded landscapes through poor grazing practices (Milton et al., 1994; Hoffman, 2014), hunting and trapping to control predators and competing wildlife (Nattrass and Conradie, 2015) and erecting fences to control livestock movements (Roche, 2004; Dean et al., 2018). Apex predators that once roamed vast areas, including lions (*Panthera leo*), cheetah (*Acinonyx jubatus*), and spotted hyena (*Crocuta crocuta*), have long been extirpated from the landscape, leaving only the leopard (*Panthera pardus*), and meso-predators such as black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) as the last major free-roaming mammalian predators in South Africa. Furthermore, the historical herds of ungulates that occasionally migrated across the Karoo in their millions have also been removed through hunting and fencing (Roche, 2004; Harris et al., 2009). The long-term implications of extensive networks of fences are far reaching (Dean et al., 2018); they cut off vital migratory routes of animals, restricting dispersal patterns and genetic exchange (Hayward and Kerley, 2009) and continue to cause mortalities of faunal species, through entanglement or electrocution (Boone and Hobbs, 2004). These migrations would have played a vital role in nutrient cycles and healthy soils which ensured landscapes remained resilient during harsh climatic conditions. These compounding factors, together with hunting and lethal predator controls and associated by-catch, have resulted in brittle ecosystems in semi-arid regions which are more vulnerable to prolonged droughts and changing climate conditions.

Changing how we manage livestock rangelands to increase biodiversity and ecological function could have a profound impact on global ecological health. Alternative rangeland management strategies, such as using traditional grazing regimes, have been shown to increase biodiversity and ecosystem functioning (Mu et al., 2016) as opposed to commercial livestock farming. Using livestock to mimic the effect of historical mass migrations of ungulates can aid in restoring degraded landscapes (Savory and Parsons, 1980, Esler et al., 2010; McManus et al., 2018). These techniques have shown some positive effects on veld (uncultivated open scrub or grassland) production, particularly in degraded semi-arid landscapes, as they allow for longer resting and veld recovery periods and more nutritious grazing (McManus et al., 2018). Furthermore, the constant attendance of human shepherds who oversee livestock, manage herd health concerns, and direct their grazing routes, reduces predation threats and the need for fencing on rangelands. These impacts should reduce human-wildlife conflict as livestock are protected and rangelands are allowed time to recover in semi-arid landscapes and thus offer improved forage for both livestock and wildlife (McManus et al., 2018). The removal of fences facilitates the reconnection of previously isolated animal populations as species can disperse further, which will aid genetic resilience to disease and effects related to climate change (Woodroffe et al., 2014). Crucial to these efforts is the shift from indiscriminate lethal control methods aimed at eradicating predators to mitigation via non-lethal methods, focusing instead on livestock management such as human shepherding, kraaling (enclosing at night in pens) or using guardian animals (Hazzah et al., 2014, McManus et al., 2014; Van Eeden et al., 2017).

The semi-arid Karoo in South Africa is an ecologically sensitive region notorious for slow vegetation recovery rates of degraded landscapes (Seymour et al., 2010), and a key region for livestock production in the country. We use the conversion of the five amalgamated farms as a case study to determine if human shepherding of livestock under a high-density, short duration grazing regime, combined with wildlife coexistence and fence removal, and a cessation of hunting wildlife could play a positive role in ecosystem restoration, i.e., reversing land degradation, improving the quantity and quality of palatable grasses (Savory and Parsons, 1980) and improving biodiversity on livestock production landscapes (Landmark Foundation, 2017). Human shepherding also provides additional benefits for local economic development and employment, whilst improving herd health and productivity. These latter effects were not however evaluated in this study but were concurrent benefits.

We expected that changes at all levels of biodiversity, would occur as a result of the conversion to wildlife-friendly management practices. Although data was collected on the biodiversity of birds, insects and plants we elected initially to focus on the changes observed in mammalian species since a number of the new management practices (stopping all hunting and trapping, and fence removals) would directly impact these species. Mammals would additionally be less impacted by severe short term climatic conditions, such as droughts compared to birds and insects. Results of the changes of biodiversity of birds, and plants are being prepared for separate publication.

Three complementary metrics were chosen to document changes in mammalian biodiversity: (1) species richness was chosen as the most basic indicator of mammalian biodiversity of the local environment (Duelli and Obrist, 2003) and was predicted to increase during conversion, (2) species distribution was chosen to get a measure of whether changes in species richness were also reflected in the distribution of species in response to removal of fencing constraints and the concentration of livestock and associated human activity to only a small proportion of the farm at any on time as a result of moving to shepherding, (3) relative abundance index (RAI) of a species was chosen to provide an indication of the size of the population of each mammalian species.

In this study, we evaluated the mammalian biodiversity changes (mammalian species richness, distribution, and abundance) that took place over a 4-year period on a Karoo farm that was undergoing a transition from a traditional farming practice to wildlife-friendly farming. This Karoo farm was an amalgamation of five individual farms into a single management unit. The extensive size of this farm was an attempt to mimic the effect of the adoption of non-lethal shepherding at a landscape level and to limit edge-effects on the management treatment introduced, since it was embedded in a landscape dominated by lethal control. Mammalian species richness was also used to evaluate the biodiversity associated with three different land uses; (1) the wildlife-friendly system, (2) a traditional commercial livestock production strategy, and (3) a fenced game farm. The comparison across land uses was evaluated at a single point in time, when the conversion to wildlife friendly farming was completed on the experimental site. We predicted that after 4 years of wildlife-friendly conversion and management, the wildlife-friendly farm would have a higher mammalian species richness (number of species), higher mammalian species distribution (spatial extent), and would have seen an increase in abundance within mammalian species (frequency of occurrence). We predicted that this would hold true when compared to either the traditional livestock farm or the game farm.

MATERIALS AND METHODS

Study Area

The study was conducted on the Nuweveld Mountain range, ∼45 km north east of Beaufort West in South Africa, between 2015 and 2019 (**Figure 1**). Three sites were compared; the first site is a wildlife-friendly livestock farm (22,111 ha). The second site lies on the northern boundary and is a game farm that excludes domestic livestock (5,435 ha), and the third site is a traditional livestock farm (11,244 ha) ∼20 km to the north of the wildlife-friendly farm (**Figure 1**).

The study region falls within the semi-arid Nama Karoo biome and includes two dominant vegetation types: the Upper Karoo Hardeveld and the Eastern Upper Karoo (Mucina et al., 2006). The Upper Karoo Hardeveld is typically present on steep, hilly topography covered with large boulders, and comprises sparse dwarf Karoo scrub with drought-tolerant grasses. The Eastern Upper Karoo is present on flat or gently-sloping landscapes and characterized by a higher proportion of grasses among the low shrubs (Mucina et al., 2006).

The region is in the summer rainfall zone classification (Roffe et al., 2019) and receives an average annual rainfall of 270 mm, with peak rainfall occurring from October to April. During the 4-year study period a drought resulted in stochastic rainfall events, with lower-than-average rainfall measured on the wildlife-friendly farm of 186 mm per year (2016: 235.5 mm, 2017: 303 mm, 2018: 66 mm, 2019: 138 mm). Topographically the region varies from flat open plains to steep riverine gullies (**Figure 1**). The altitude above sea-level varies across the three sites from ∼1,100 m in the lower lying ravines to 1,700 m at the highest peaks.

Wildlife-Friendly Farm

Prior to mid-2015 the individual farms (that later became the wildlife-friendly farm) were managed in a traditional rotational grazing system and employed lethal control methods such as leg-hold traps (gin-traps), jackal-proof fencing and hunting (inclusive of night-time call and shoot hunting, and helicopter hunting), to limit the numbers of predators and damage causing animals, mainly black-backed jackal, caracal and chacma baboon (*Papio ursinus*), as well as other non-target species. Since July 2015 livestock (sheep and cattle) farming, as well as the ecological restoration of the consolidated properties, were considered as complimentary management goals. This conversion has entailed using (1) high-density, short duration grazing with a single herd of sheep and cattle and night-time kraaling of sheep and cattle using human shepherds, (2) non-lethal predator management, and (3) no hunting of wildlife, and (4) a cumulative removal of internal farm fencing allowing wildlife migrations.

The first phase of the management conversion started in July 2015 when all lethal predator control ceased, and the farm continued to operate under conventional rotational paddocking. The livestock were monitored sporadically by direct observation from a suitable distance that would not influence the livestock or wild animal behavior. All deaths and their associated cause were recorded. Since January 2017 the livestock where herded throughout the day by human shepherds employing a

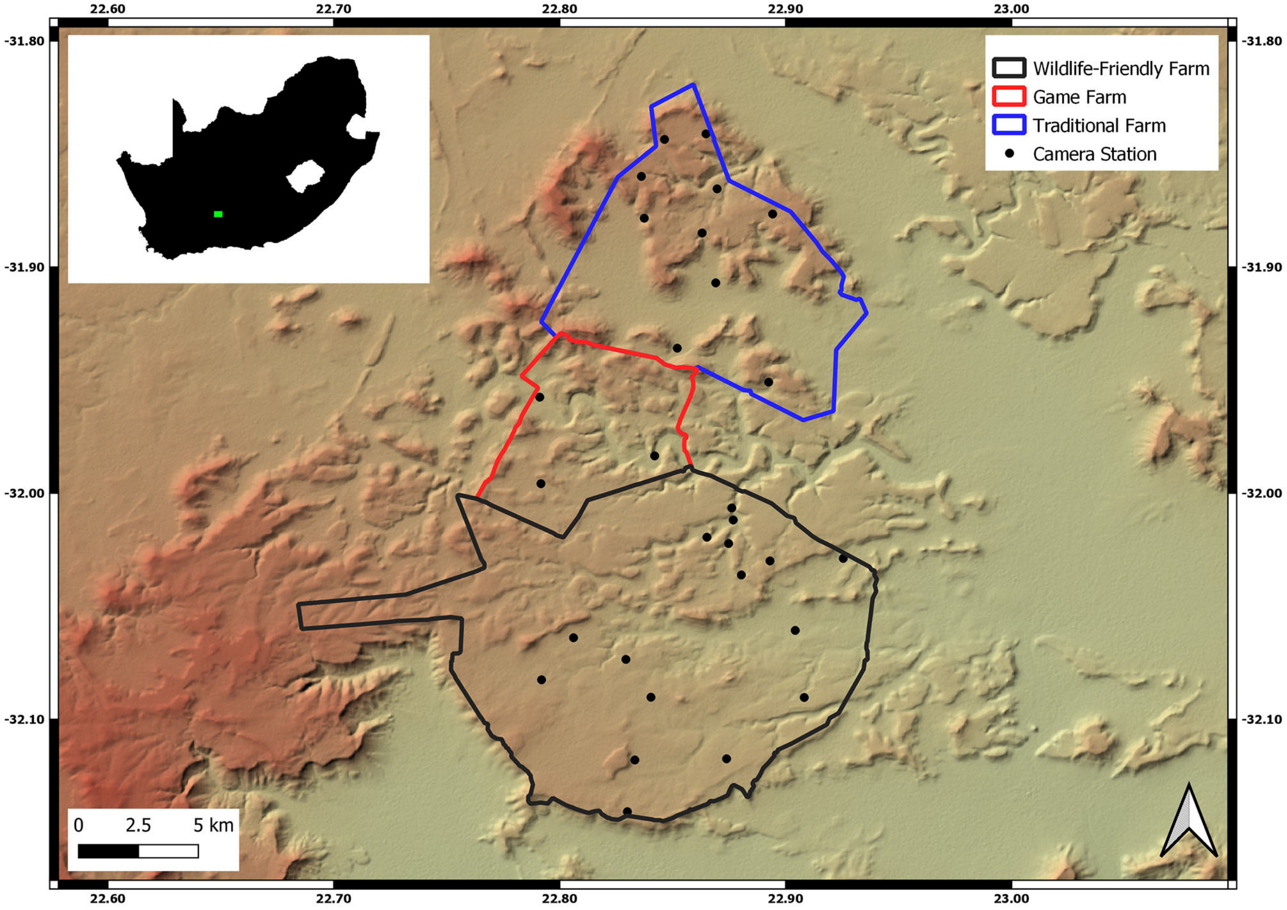

FIGURE 1 | Location of the three study sites, which included the wildlife-friendly farm (black), a game farm (red), and a traditional livestock farm (blue), on a hillshade projection of the Nuweveld Mountain range (Van Niekerk, 2015). Camera stations retained in the analysis are indicated by black dots. The inset shows the location of the study region (green) within South Africa.

high-density, short duration grazing technique. Additionally, the shepherds protect the livestock at night by using mobile kraal sites (as part of non-lethal livestock protection from carnivores). These kraal sites are relocated every 7 days. Kraal sites were placed on severely degraded locations and the dung, urine and hoof actions were rehabilitative on these sites. Shepherds maintain 24-h contact with the livestock 365 days per year which allows for herd-health interventions as well as preventing livestock depredation (McManus et al., 2018). In the 4 years of this management practice the number of adult sheep fluctuated between 1,500 and 1,650, while cattle varied between 200 and 350 (they were incorporated into the herd in May 2017). The livestock are checked and counted daily as they are released from the kraals, allowing heath issues to be attended to as well as deaths to be identified. Since January 2017 (the start of shepherding) only one lamb has been lost to predation, compared with 116 (12.3% of the herd) predation losses during 2016. Lamb survival at weaning also improved from 70 to 100%. These production and financial effects are part of other research projects.

Beginning in 2017 internal fences were sporadically and ongoingly removed from the wildlife-friendly farm. Due to labor constraints, key fence lines were targeted for initial removal, followed by short sections in strategic locations. This allowed the landscape to be efficiently opened up. Gates were also opened between paddocks and along roads (except a few that were still used to contain bulls and rams in non-breeding seasons). By the completion of the study a total of 28 km, out of a total 230 km, had been removed, allowing free migration of wildlife throughout the farm.

Traditional Livestock Farm

The traditional livestock farm was stocked with 1,800 sheep resulting in a carrying capacity of 0.16 livestock units per hectare. The rainfall was 127 mm in 2019, and historically has experienced the same rainfall regime as the wildlife-friendly farm as it is only 10 km away and is at the same altitude. It utilizes rotational paddocking, where the livestock are moved from one camp to another at one−3 months intervals, depending on veld conditions. Livestock roamed freely in paddocks ranging between 200 and 600 hectares in size, and lethal methods are used to reduce predator numbers. Predator controls include hunting via night-time call and shoot culling, helicopter predator culls, as well as trapping with cages, leg-hold traps and neck-snapping traps. The use of poison and hunting dogs on the property is denied. The total annual lamb losses for 2019 (due to predation, health issues, still birth etc.) amounted to 276 lambs. Both the outer boundary and internal fences are strictly maintained, and most are jackal proof (wire mesh up to 1.2 m high). Gates are typically kept closed to ensure livestock are kept in specific paddocks. This farming enterprise was located in a region of extensive livestock farming utilizing similar paddock rotations, lethal controls, and jackal proof fencing.

Game Farm

The game farm was converted from a traditional livestock farm in 1997. It is fully enclosed by a 2.2 m high non-electrified game fence which is jackal proof, as regulated by the provincial conservation authorities to contain all herbivores on the farm, allowing game ownership in South African laws. No lethal predator control reportedly takes place, but the farm is subject to very occasional game hunting. The game farm is well-established and is situated adjacent to a similarly managed game farm of twice its spatial extent.

Since its inception, Cape mountain zebra (*Equus zebra zebra*), eland (*Taurotragus oryx*), gray rhebok (*Pelea capreolus*), red hartebeest (*Alcelaphus buselaphus caama*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), mountain reedbuck (*Redunca fulvorufula*), and giraffe (*Giraffa camelopardalis giraffa*) were all introduced by 2017, thus the site contains indigenous and extralimital species. There are approximately 800 total game animals, with their numbers managed through live sales (∼50 individuals per year are removed), and the occasional introduction of new individuals and species (S. Lovemore, personal communication, 25 November 2020). There has been no direct evidence of predation on any game species. However, the game species are only occasionally monitored so predation events may be missed. In 2019 they also received a lower than average rainfall for the region of 170 mm, and would have had historically experienced the same rainfall regime as the farm is immediately adjacent to the wildlife-friendly farm and at the same altitude.

Study Design

We deployed 48 camera stations across the three sites (**Supplementary Table 1**) to detect terrestrial mammals. We used three different camera types; Cuddeback™ AttackIR, Cuddeback™ E2 (Wisconsin, 115 USA; www.cuddeback.com), and Bushnell® 119436 Trophy Cameras (Overland Park, KS, USA; www.bushnell.com). Each camera is triggered by passive infrared sensors and were set to 3-min intervals between triggers. All night-time images were taken with an infrared flash. Twenty-nine camera stations (762 ha per camera) were active on the wildlife-friendly farm since late 2015. These cameras operated throughout the 4-year study period to enable temporal variations within the wildlife-friendly study site to be evaluated as the conversion to new management practices unfolded. Two cameras were removed from the study due to malfunctions. Access to the traditional livestock and game farms, and camera resources, dictated that camera stations could only be deployed on the comparison sites in 2019, which was to evaluate the comparison after the wildlife friendly conversion was completed on the experimental farm. We placed thirteen camera stations (865 ha per camera) on the traditional livestock farm, and six (906 ha per camera) on the game farm. Camera stations were placed with the aim to cover all areas and habitat types across the three farms in order to capture the full mammalian biodiversity of the farms. The straight-line distance between a camera station and its nearest neighbor averaged 1,834 m (range 591–3,834 m, **Figure 1**) on the wildlife-friendly farm, 2,333 m on the traditional livestock farm (1,754–3,134 m) and 1,321 m on the game farm (894–2,161 m). All camera stations consisted of a single camera fixed ∼40 cm from the ground at locations where evidence of diverse animal species had been found (e.g., spoor), or was expected to occur, such as along low usage gravel roads, game trails and ephemeral river courses.

Data Extraction and Analysis

We used four study periods running for 6 months each year (July–December) to assess the mammalian species richness, distribution, and RAI of species during the surveyed years (2016–2019). The same 6-month period was analyzed for all three study sites in 2019. These periods were chosen to allow the management changes (initiated prior to, or at the start of years) to have an impact on the wildlife-friendly farm, and to ensure independence between measures. Camera images were processed using digiKam, version 5.9.0 (www.digikam.org). Camera station performance (camera effort) was assessed using the camtrapR package (Niedballa et al., 2016) run in the R statistical software version 3.6.2 (R Core Team, 2017). Cameras stations with a camera effort of <90 days were removed from the analysis to ensure adequate sampling took place. The mean (±SE) camera effort was 170.8 ± 3.0 days for the wildlife friendly farm (over the 4 study periods), 153.9 ± 10.6 days for the traditional farm, and 99.0 ± 6.5 days for the game farm. To ensure independence of photographic events, additional photographs of the same species captured within a 60-min timeframe were excluded from the analyses (Tobler et al., 2008). All domestic species, human and vehicle records were excluded.

The three measures used to evaluate changes to the mammalian population within the wildlife-friendly site were (1) species richness, a measure of the number of species observed at a camera station, (2) the distribution of a species being the number of camera stations within a study site where it was detected, and (3) RAI which is a measure of a species' capture frequency (i.e., number of independent captures of a species divided by the camera station effort) at each camera station (Wearn and Glover-Kapfer, 2017). The RAIs were standardized to 183 active capture nights (the 6-month survey period) to allow for reliable comparisons. Whilst the RAI is susceptible to various biases (behavioral activity being the most prominent), and it does not include species detection probability in the formulation (e.g., Sollmann, 2018), it contributes to understanding the community assemblage in relation to commonness and rarity of different species. Furthermore, this index is the best alternative when it is not possible to identify individuals (e.g., Wearn and Glover-Kapfer, 2017; Pardo et al., 2018). RAI values derived from large scale camera trapping have been shown to correlate strongly with independent density estimates for a range of species (Palmer et al., 2018). Variations in species richness over time at the wildlife-friendly farm were evaluated by a repeated measures ANOVA and paired-T test analysis using the rstatix package (Kassambara, 2020). Species accumulation curves were calculated using the iNEXT package (Hsieh et al., 2016). Only species richness and composition were compared between the three study sites due to no repeat measures during different years on the two comparison sites.

The detected species were grouped according to their foraging guild, either herbivore or predator. Baboons were placed with the predators due to their predatory role on livestock farms (killing lambs; Muriuki et al., 2017). The detected species were additionally grouped into two weight categories calculated from Stuart and Stuart (2015); herbivores with an average mass below 18 kg were classed as small and above as large. Predators below 5 kg were classed as small and above as medium.

RESULTS

We retained data from 16 camera stations on the wildlife-friendly farm site ($n = 16$). These were active for a total of 10,932 camera trap nights, ranging from 2,619 to 2,806 nights per year (**Supplementary Table 1**) and captured a total 10,206 independent mammalian species events. Data from ten camera stations ($n = 10$) at the traditional farm was retained in 2019, for a total 1,539 camera trap nights, capturing 1,372 independent records. The game farm retained only three camera stations ($n = 3$) tallying 297 camera trap nights, and capturing 695 independent records. Each 6-month analysis period, at all three sites, reached an asymptote for total species richness detected indicating that the sampling effort was adequate. Rainfall was measured on the wildlife-friendly study site and totalled for the year. During the period from 2016 to 2019 the total yearly rainfall decreased by 42% indicating the presence of a worsening drought. Rainfall values at each camera location were not measured and so no direct analysis of the local effects of rainfall on species richness or distribution could be made.

Species Richness Between Years on the Wildlife-Friendly Farm

The species accumulation curves for the wildlife-friendly farm (**Figure 2**) indicate that species richness had reached an asymptote for each year, despite differing number of capture events, indicating that these are reliable measures of species richness and that they represent a steady improvement in species richness over the 4-year study at the wildlife-friendly farm.

The number of observed species at the wildlife-friendly farm increased year on year from 28 in 2016 to 30 in 2017, 32 in 2018 and 34 species in 2019 (**Figure 3**, **Table 1**). The total number of species detected over the entire study period, increased by nine species (24%) to a total of 37 species, of which 24 were consistently detected in all four study periods (**Table 1**). Only two species which were present in the 2016 survey, meerkat (*Suricata suricatta*) and Cape clawless otter (*Aonyx capensis*), were not detected in 2019. The pattern of year on year increasing species richness held for herbivores and for predators (**Figure 3**), although the slope was steeper for herbivores (1.6, $R^2 = 0.98$, $p < 0.01$) than predators (0.4, $R^2 = 0.80$, $p = 0.1$), and it held for all size classes except medium predators which remained the same.

Over the 4 years of the study the species richness on the wildlife-friendly site was found to vary significantly [ANOVA, $F_{(3/45)} = 12.52$, $p < 0.0001$]. There is a clear indication of an increased species richness each year between 2016 and 2019 (**Figure 4**), with 2019 having significantly more species than 2016 ($p < 0.001$), 2017 ($p < 0.01$) and 2018 ($p < 0.05$). However, there was no significant difference detected between the years 2016 and 2017 or 2017 and 2018.

Species Distribution and Relative Abundance on the Wildlife-Friendly Farm

There was a general increase in the number of camera stations where a given species were detected. In total, 68% of species (25 of 37) were detected at more camera stations in 2019 than in 2016 (**Table 2**). Six species were detected at the same number of camera stations and six were present on fewer camera stations. The largest increases were seen with blue wildebeest and gemsbok (*Oryx gazella*), which were both captured at seven new camera stations. Other large increases were seen with ungulate species, namely, red hartebeest, waterbuck, common duiker (*Sylvicapra grimmia*), eland and plains zebra (*Equus quagga*). However, kudu (*Tragelaphus strepsiceros*) presented a slight decrease and was seen on one fewer camera station in 2019 compared to 2016. African wildcat (*Felis lybica*) exhibited the largest increase in distribution (three additional camera stations) in the predator guild. The larger of the predators detected on the farm, black-backed jackal and caracal, had smaller increases (two and one additional camera station, respectively) in their detections. Herbivores show the most notable improvements, with 16 out of 21 (76%) species appearing at more stations, compared to 9 out of 16 (56%) predator species showing increased distribution.

The RAI values for the common species detected in every year (**Table 3**) indicates that 67% (16 of 24) increased their relative abundance. Ten species more than doubled their RAI (blue wildebeest, eland, water mongoose (*Atilax paludinosus*), blesbok (*Damaliscus pygargus phillipsi*), red hartebeest, baboon, common duiker, gemsbok, vervet monkey (*Chlorocebus pygerythrus*), and porcupine), while only six [gray rhebok, steenbok (*Raphicerus campestris*), small-spotted genet (*Genetta genetta*), aardwolf, klipspringer (*Oreotragus oreotragus*), and dassie] decreased. Both the caracal and small-gray mongoose maintained an approximately constant relative abundance (<5% variation).

Comparison of Wildlife-Friendly Farm to Traditional Livestock and Game Farms

Species accumulation curves for the three different study sites from 2019 (**Figure 5**) show that at asymptote the game farm and traditional livestock farm presented a similar species richness (23 and 24, respectively). They were both significantly lower (outside of the 95% confidence interval) than that detected on the wildlife-friendly farm which recorded 34 species during the

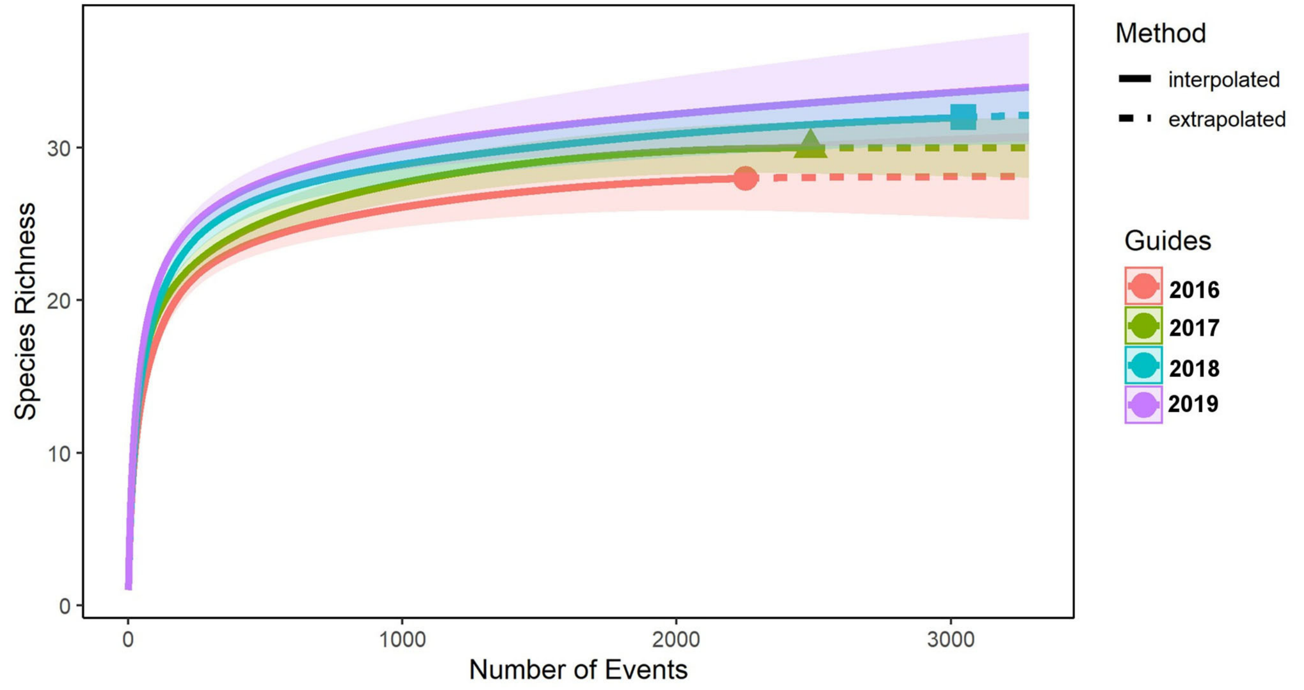

FIGURE 2 | Species accumulation curves for all camera sites on the wildlife-friendly farm.

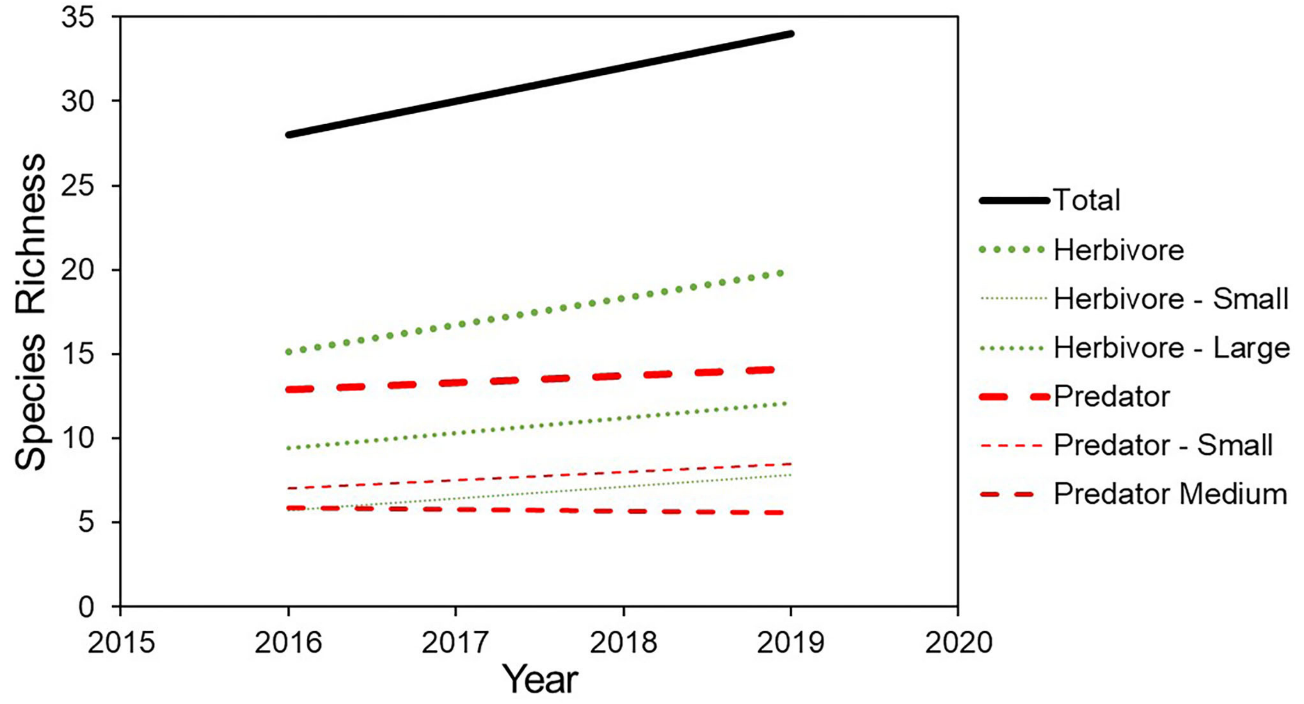

FIGURE 3 | Species richness detected on the wildlife-friendly farm per sample period and broken down by guild and body size.

same 6-month period in 2019. Only 14 species were detected on all three study sites (**Supplementary Table 2**). Three species (giraffe, Cape clawless otter, and Cape mountain zebra) were not detected on the wildlife-friendly farm but were present on the game farm. The traditional farm detected a single species (leopard) that was not present on the wildlife-friendly farm. All

TABLE 1 | Species detected per sample period (July to December of each year) on the wildlife-friendly farm.

Species number	2016	2017	2018	2019
1	Aardvark	Aardvark	Aardvark	Aardvark
2	Aardwolf	Aardwolf	Aardwolf	Aardwolf
3	Baboon	Baboon	Baboon	Baboon
4	Bat-eared Fox	–	Bat-eared Fox	Bat-eared Fox
5	Black-backed Jackal	Black-backed Jackal	Black-backed Jackal	Black-backed Jackal
6	Blesbok	Blesbok	Blesbok	Blesbok
7	Caracal	Caracal	Caracal	Caracal
8	Dassie	Dassie	Dassie	Dassie
9	Duiker – Common	Duiker - Common	Duiker - Common	Duiker - Common
10	Eland	Eland	Eland	Eland
11	Gemsbok	Gemsbok	Gemsbok	Gemsbok
12	Genet - Small Spotted	Genet - Small Spotted	Genet - Small Spotted	Genet - Small Spotted
13	Gray Rhebok	Gray Rhebok	Gray Rhebok	Gray Rhebok
14	Klipspringer	Klipspringer	Klipspringer	Klipspringer
15	Kudu	Kudu	Kudu	Kudu
16	Meerkat	Meerkat	Meerkat	–
17	Mongoose - Small gray	Mongoose - Small gray	Mongoose - Small gray	Mongoose - Small gray
18	Mongoose - Water	Mongoose - Water	Mongoose - Water	Mongoose - Water
19	Mongoose - Yellow	–	Mongoose - Yellow	Mongoose - Yellow
20	Otter	Otter	–	–
21	Porcupine	Porcupine	Porcupine	Porcupine
22	Red Hartebeest	Red Hartebeest	Red Hartebeest	Red Hartebeest
23	Scrub Hare	Scrub Hare	Scrub Hare	Scrub Hare
24	Springbok	Springbok	Springbok	Springbok
25	Steenbok	Steenbok	Steenbok	Steenbok
26	Striped Polecat	Striped Polecat	Striped Polecat	Striped Polecat
27	Vervet Monkey	Vervet Monkey	Vervet Monkey	Vervet Monkey
28	Wildebeest - Blue	Wildebeest - Blue	Wildebeest - Blue	Wildebeest - Blue
29	–	African Wild Cat	African Wild Cat	African Wild Cat
30	–	Cape Fox	Cape Fox	Cape Fox
31	–	Waterbuck	Waterbuck	Waterbuck
32	–	Zebra - Plains	Zebra - Plains	Zebra - Plains
33	–	–	Red Rock Rabbit	–
34	–	–	–	Ground Squirrel
35	–	–	–	Honey Badger
36	–	–	–	Mountain Reedbuck
37	–	–	–	Gerbil - Highveld

three sites were experiencing the same drought conditions and received approximately the same rainfall.

DISCUSSION

Despite the importance of livestock rangeland management to global biodiversity conservation few studies have evaluated the effect of different management practices at a farm scale. This study of a working Karoo farm is the only farm scale test we know of that investigates the effect of a change in management from traditional farming to wildlife-friendly farming. Our main findings suggest that the combination of stopping hunting and lethal predator control, the removal of internal fences, and replacing a camp grazing system with focused herding and night-time kraaling to produce a high intensity, short-duration, long rest grazing regime can increase mammalian biodiversity, distribution and relative abundance, even during an extreme and worsening drought period.

We found that species richness increased year-on-year on the wildlife-friendly farm since 2016, with a significant increase occurring in 2019 compared to previous years (**Figure 4**). We found that in comparison to the traditional livestock and game farm species richness was significantly higher on the wildlife-friendly farm (**Figure 5**). Species appeared to become increasingly distributed among camera stations between 2016 and 2019 (**Table 2**), whilst the majority (67%) of species that were detected in all 4 years showed increases in their relative

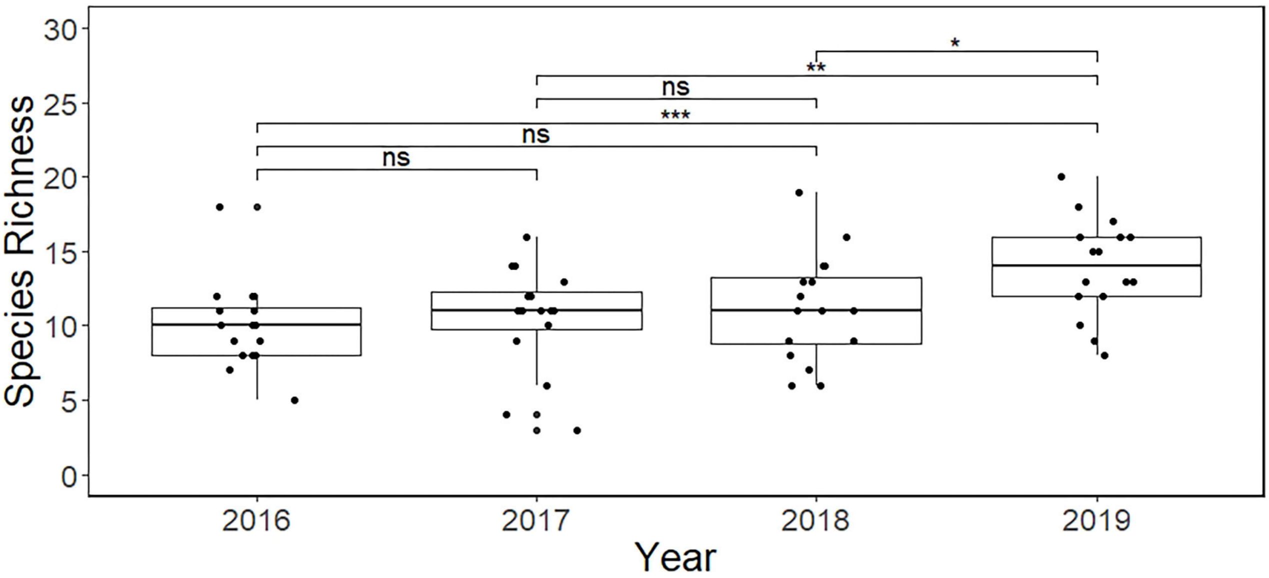

FIGURE 4 | Species richness (SR) detected over four consecutive years from the 16 camera sites retained on the wildlife-friendly farm. The median value, interquartile range and range are shown for each year. The letters above each plot indicate significant differences (ns-not significant, *'s indicate the degree of significance).

abundance (**Table 3**). These positive outcomes were evident despite a prolonged period of drought.

Why Did Medium Size Predator Diversity Remain the Same?

The lack of increase in medium size predator species numbers is at odds with the general pattern of increase in mammalian biodiversity. This can partly be explained by the fact that 85% of the medium sized predators that could be detected in this area were already present throughout the wildlife-friendly farm in the 2016 survey. This leaves only a small margin for potential recruitment into the guild, unlike the herbivore guild where many species were undetected in 2016. Additionally, non-lethal predator management commenced 1 year prior to the initial survey period which may have allowed early species recovery and population shifts to occur by the time of the first sampling. The social structures and territorial behavior of these species may also have resulted in early territorial establishment. In the final survey year, the Cape clawless otter disappeared, likely due to the intensified drought in the region at this time, causing a reduction in both the length of streams and quantity of water bodies such as dams and natural pools. At the same time, the honey badger (*Mellivora capensis*) was first detected on the wildlife-friendly site, possibly due to more favorable conditions in this arid environment. The swapping of these species explains the lack of change in the number species.

Only one large predator species, the leopard, was detected across all three study sites. It was identified from a single capture event on the traditional livestock farm during the 2019 survey. However, two independent captures of leopard were made on the wildlife-friendly farm by camera traps not used in this study. It is suspected that all these captures are of the same individual leopard that was moving through the area. Wildlife-friendly farming has the potential to enable the coexistence of resident large predators, like the leopard, on rangelands where there is an abundant natural prey base without the danger of livestock losses.

Comparison to Traditional and Game Farms

The comparison of a wildlife-friendly farm to both a traditional livestock farm and game farm in 2019 yielded a notable difference in species richness and composition. Both the game farm and lethal control livestock farm presented a similar species richness, which was lower than that detected on the wildlife-friendly farm (**Supplementary Table 2**, **Figure 5**). It should be noted that the species richness for the wildlife-friendly farm in 2016 (∼12 months after lethal control was stopped) was similar to the 2019 value for both the comparison properties. This suggests a common baseline in species richness across the region in the absence of shepherding. However, this should be interpreted cautiously due to the worsening drought and the comparison of different years. Follow up studies are needed to conclusively confirm the stability of the regional baseline. The direct comparison of the wildlife-friendly farm to the traditional farm reveals two groups of species absent from the latter: large game (blesbok, eland, red hartebeest, waterbuck, and blue wildebeest), and small predators [yellow mongoose (*Cynictis penicillate*), water mongoose, striped polecat (*Ictonyx striatus*), and small-spotted genet]. The large game species are easily controlled by fences and so their presence on any farm is generally due to reintroductions or retaining existing populations when fencing, conversely, their absence is largely due to human management. A traditional livestock production farm gains no

TABLE 2 | Number of cameras at which each species was detected, ordered by absolute (Δ) increase and then percentage increase.

Species	Guild	Size	Average mass (kg)	2016 stations	2017 stations	2018 stations	2019 stations	Δ(2019-2016)	% change (2016–2019)
Wildebeest – Blue	Herbivore	Large	215.0	1	2	8	8	7	+700
Gemsbok	Herbivore	Large	225.0	3	6	5	10	7	+233
Waterbuck	Herbivore	Large	260.0	0	1	1	5	5	+
Red Hartebeest	Herbivore	Large	135.0	3	1	4	8	5	+167
Vervet Monkey	Herbivore	Small	5.5	4	7	7	9	5	+125
Duiker – Common	Herbivore	Large	19.5	6	8	9	10	4	+67
Zebra - Plains	Herbivore	Large	315.0	0	1	1	3	3	+
African Wild Cat	Predator	Small	4.3	0	2	3	3	3	+
Eland	Herbivore	Large	575.0	1	4	4	4	3	+300
Bat-eared Fox	Predator	Small	4.0	3	0	2	6	3	+100
Baboon	Predator	Medium	32.0	11	12	14	14	3	+27
Porcupine	Herbivore	Small	17.0	12	12	11	15	3	+25
Mountain Reedbuck	Herbivore	Large	30.0	0	0	0	2	2	+
Cape Fox	Predator	Small	3.3	0	1	1	2	2	+
Blesbok	Herbivore	Large	70.0	2	4	3	4	2	+100
Springbok	Herbivore	Large	39.0	8	7	7	10	2	+25
Scrub Hare	Herbivore	Small	3.0	11	9	13	13	2	+18
Black-backed Jackal	Predator	Medium	8.0	12	11	12	14	2	+17
Gerbil – Highveld	Herbivore	Small	0.2	0	0	0	1	1	+
Ground Squirrel	Herbivore	Small	0.7	0	0	0	1	1	+
Honey Badger	Predator	Medium	11.0	0	0	0	1	1	+
Klipspringer	Herbivore	Small	11.5	2	3	2	3	1	+50
Mongoose - Small gray	Predator	Small	0.8	3	3	4	4	1	+33
Mongoose – Water	Predator	Small	4.0	3	4	1	4	1	+33
Caracal	Predator	Medium	13.0	9	10	8	10	1	+11
Red Rock Rabbit	Herbivore	Small	1.7	0	0	1	0	0	0
Dassie	Herbivore	Small	3.6	3	3	3	3	0	0
Mongoose - Yellow	Predator	Small	0.7	1	0	1	1	0	0
Striped Polecat	Predator	Small	1.0	4	4	5	4	0	0
Aardwolf	Predator	Medium	8.5	12	8	10	12	0	0
Aardvark	Predator	Medium	55.0	10	10	10	10	0	0
Kudu	Herbivore	Large	207.5	16	15	14	15	−1	−6
Steenbok	Herbivore	Small	11.0	11	12	9	10	−1	−9
Genet - Small Spotted	Predator	Small	2.0	4	3	3	3	−1	−25
Gray Rhebok	Herbivore	Large	20.0	2	3	2	1	−1	−50
Meerkat	Predator	Small	0.8	1	1	1	0	−1	−100
Otter	Predator	Medium	15.5	2	1	0	0	−2	−100

The percentage change of species detected in 2019 but not detected in 2016 are not calculated. Guild and size classifications for each species are also presented.

direct financial value from the presence of these species, they may even be perceived as a problem in the form of increased competition for grazing, and as a result these species may have been traded or hunted out entirely. The lack of small predators on rangelands has been linked to changes in vegetation structure (shrub encroachment) as a result of overgrazing (Blaum et al., 2007). The high-density, short duration grazing strategy implemented on the wildlife-friendly farm impacts the vegetation in a non-selective manner, reducing overall shrub cover and promoting grass re-growth (S. Goets, personal communication, 10 October 2020). This increase in grass cover may provide additional food resources for small carnivore prey species, which in turn provide an increase in resource availability for small predators. Conversely, the high general stocking density and selective grazing occurring on both the game and the traditional livestock farms, could result in an increase in shrub cover, causing a decline in small carnivore prey availability, and thus small predators. Additionally, some of these small predators may be removed as by-catch during periods of indiscriminate lethal predator control (gin traps, foot hold, and cage traps and poison usage), inclusive of neighboring properties that were not sampled.

TABLE 3 | Relative Abundance Index (RAI) of species that occurred in all 4 years on all 16 cameras retained on the wildlife-friendly farm.

Species	2016	2017	2018	2019	Δ (2019–2016)	% change (2016–2019)
Wildebeest – Blue	2	15.1	58.52	65.68	63.68	+3184.00
Eland	1	14.19	7.14	12.71	11.71	+1171.00
Mongoose – Water	5	10.34	1.08	44.14	39.14	+782.80
Blesbok	27	225	175.6	164.2	137.2	+508.15
Red Hartebeest	13	1.02	25	69	56	+430.77
Baboon	73.21	187.95	334.86	366.4	293.19	+400.48
Duiker – Common	18	24.69	37.22	80.79	62.79	+348.83
Gemsbok	25	55.3	40.65	88.2	63.2	+252.80
Vervet Monkey	37.39	68.63	56.39	124.96	87.57	+234.21
Porcupine	92.31	126.64	204.3	218	125.69	+136.16
Black-backed Jackal	107.39	128.36	123.23	192.78	85.39	+79.51
Aardvark	29.83	68.85	42.76	51.93	22.1	+74.09
Striped Polecat	17	7.51	17.52	23	6	+35.29
Springbok	168	103.43	164.27	226.12	58.12	+34.60
Kudu	370.96	399.76	573.25	476.77	105.81	+28.52
Scrub Hare	596.58	573.46	677.04	635.49	38.91	+6.52
Caracal	23.04	31.13	23.71	23.31	0.27	1.17
Mongoose – Small gray	31	43.18	40.13	31.23	0.23	0.74
Gray Rhebok	2	5.36	12	1	−1	−50.00
Steenbok	134.45	103.03	74.92	62.51	−71.94	−53.51
Genet – Small Spotted	24.63	70.21	9.31	10	−14.63	−59.40
Aardwolf	307.22	85.26	159.76	114.21	−193.01	−62.82
Klipspringer	17	14.02	18.15	5.46	−11.54	−67.88
Dassie	104	97.04	74.66	19.91	−84.09	−80.86

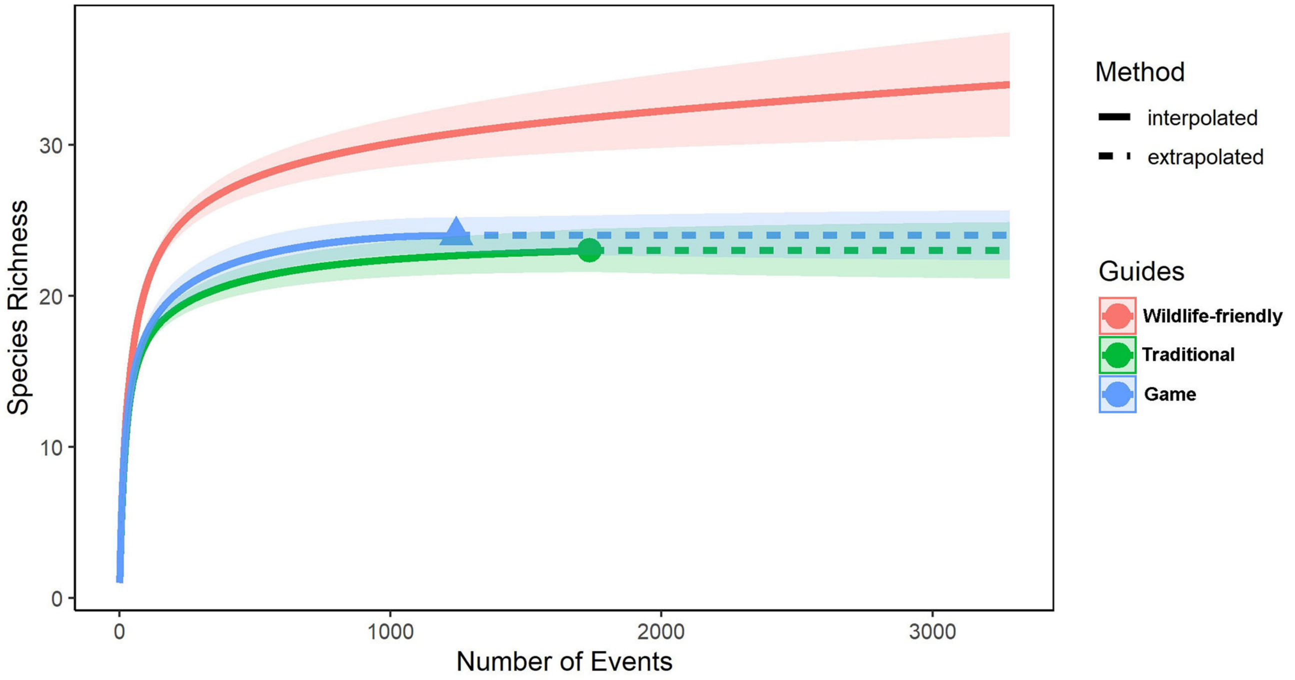

FIGURE 5 | Species accumulation curves for wildlife-friendly, traditional livestock and game farms for 2019, created using the individually corrected camera event histories (RAI values).

Mechanisms of Mammalian Species Recovery

Conversion of the farm from traditional management to wildlife-friendly management had a widespread positive effect on mammalian biodiversity. Identifying the particular mechanisms underpinning the recovery is however difficult, since many changes occurred simultaneously as part of the conversion of the farm: (1) all hunting was stopped; (2) all lethal control of damage causing animals (and by-catch) was stopped, including setting of indiscriminate gin-traps, as well as targeted shooting and trapping of black-backed jackals, caracals, porcupine, baboons, Cape foxes and otters; (3) fences were removed and gates left open allowing all species access to the entire farm; (4) human and livestock activity was concentrated in a single area at any one time leaving the rest of the farm undisturbed by production activities and rested; (5) high-density grazing was limited to small areas, increasing soil disturbance, and defecation with potentially higher water infiltration and concentrated nutrient enrichment; (6) animals were kraaled at high densities in small areas for consecutive nights resulting in even a higher magnitude of transformation of these kraaling sites through trampling, grazing and defecation with beneficial vegetation recovery on these sites (McManus et al., 2018).

Any of these changes or combinations of them might have contributed to the observed increase in biodiversity richness, distribution and abundance of mammal species, and most likely different factors affected different species.

1) Ceasing hunting would have the potential to increase the number of large ungulates who would have been the target of recreational hunting. We see evidence of this increase in that four of the five species that showed the greatest increase in abundance were popular hunting species (blue wildebeest - 31-fold increase, eland - 11-fold increase, blesbok - 5-fold increase, red hartebeest - 4-fold increase) (**Table 3**). All other traditionally hunted species, gemsbok, springbok and kudu also increased in abundance (**Table 3**). The increase of ungulates that were traditionally hunted would also be affected by the removal of fences (4) which would allow a larger area to sustain larger populations that were formally accidentally, or intentionally confined to certain camps.
2) Ceasing targeted lethal control of "problem animals" should have increased the distribution and occurrence of black-backed jackals, caracals, baboons, porcupines, aardvark, Cape Fox and honey badgers all of which have been recorded as problem animal targets either for "assumed" killing of livestock or causing damage to fencing and water infrastructure. We have evidence of increases in distribution and for all of these species (**Tables 2**, **3**, Cape fox and honey badger do not appear in **Table 3** as the former was only recorded from 2017 onward and the latter only in the final year of the study **Table 1**).
3) Stopping lethal control by trapping also has the potential to affect mammal species by-catch, potentially increasing the presence of aardvark, aardwolf, bat-eared fox, duiker, small-spotted genet, small gray mongoose, water mongoose, yellow mongoose, striped polecat, scrub hare, African wildcat, and ground squirrel all of which have been recorded as by catch of gin traps (Bothma, 2012). All of these species (duiker, small gray mongoose, water mongoose, scrub hare, African wildcat) that occurred in all years of the study and therefore qualified for analysis of distribution and abundance (RAI) increased in both distribution and relative abundance.
4) Opening of fences and gates would have potentially increased the presence of all large ungulates on camera stations which would have been previously confined by fences. By concentrating livestock and humans (shepherds and managers) in a single area where the single large mixed herd occurred essentially allowed that at any one time 95% of the farm to be totally natural and undisturbed by livestock farming operations (on any single week livestock were always confined to <1,000 ha of the 22,111 ha farm), this would have benefitted all wild species. There is strong evidence that this benefitted the species previously enclosed by these fences – blue wildebeest, gemsbok, red hartebeest, eland, mountain reedbuck, springbok all showing large increase in distribution and relative abundance, while kudu who are known to jump fences and the smaller antelope that go through the fence like steenbok (Lindsey et al., 2012) showed small or negative changes.

Changes to the vegetation structure in the arid Karoo due to grazing is known to take place over long timescales (Wiegand and Milton, 1996), thus the response of mammals to the changes brought about by kraaling and high-density grazing would only become evident over time scales longer than this study (a decade or more). The stopping of hunting, and lethal control with its direct effects on target species and by-catch, as well as opening the entire farm's resources to the large ungulates by removing fences and barriers to movement, while only operating on <5% of the farm at any one time while leaving the rest of the area undisturbed were immediate and had large implications for wildlife, yet it is impossible to separate the direct effects of each of these new management actions. In essence the combination of these practices turns a commercial livestock farm into a more natural landscape akin to a nature reserve or conservation area.

The results of this case study are important as this farm scale conversion illustrates the potential of changing a large part of the world's area (livestock rangelands) to a situation where wildlife coexists on productive rangelands providing the resources to feed a growing population while maintaining employment (the shepherds) and economic opportunities in rural areas. The key to this is conceiving rangelands as primarily conservation areas where the dividends of natural capital (palatable grazing and forage) produced in a biodiverse naturally functioning ecosystem is used to produce food and livelihoods. Whilst these findings are based on the conversion of a single Karoo farm, although itself being a combination of five farms, the range and size of the improvements observed in mammalian biodiversity should be seen as motivation to encourage further farms, both in the Karoo and in other regions, to adopt some or all of these farming methods.

Implications of Farming for Biodiversity

Globally, ecosystems are in decline and in order to reverse this trend, novel approaches to farming must be considered so that species diversity and ecosystem function can be restored. Samhouri et al. (2017) evaluated the implications of different approaches to facilitating wildlife recovery in a variety of scenarios. They identified that the fastest way to restore both predators and prey in an ecosystem was through a synchronized approach. Here, we have provided a case study demonstrating a significant and extensive improvement to mammalian biodiversity at a farm scale, achieved through a combination of wildlife-friendly management practices implemented on a commercial production farm, where both predator and prey species can recover simultaneously. Mammalian species have generally increased in variety, distribution, and density and the change was rapid occurring over a period of only 4 years. The recovery also demonstrated a resilience occurring as it did during a period of drought. Higher rainfall is known to increase species richness (Yarnell et al., 2007) while droughts result in reduced species diversity (Seabrook et al., 2011). However, we found that substantially lower rainfall occurred in 2018 and 2019 when the species richness was highest, demonstrating that even through the harshest conditions ecological recovery is possible. Whilst this study is limited by the constraints of not having replicate sites and the practicalities of sampling different sized farms, the trends observed are clear and informative. Going forward, we have implemented a modified monitoring protocol to ensure a more even sampling of the environments, and to allow an ongoing temporal analysis at all three study sites and we plan to expand farm scale studies to determine if these results are broadly applicable to similar conversions. This will provide for a future long-term evaluation of the implications of converting to wildlife-friendly farming.

This study has shed light onto the complex mammalian species responses to landscape modification and sustainable agriculture. We found that a continuing implementation of wildlife-friendly livestock practices has a positive effect on mammalian biodiversity by increasing species richness, as well as the number of sites occupied and the relative abundance of the majority of species. Although some changes where not evident on a yearly basis, the accumulated improvements suggest that a recovery time of at least 1 years is needed to start seeing the effect of restoration processes through better management practices. Should this restorative farming practice be applied to global rangelands, the implications for mammalian biodiversity recovery, and long-term security, are considerable.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

BS and JM conceptualized and designed the study. MS, SG, and JM carried out the field work. MS, LP, and JM performed the statistical analysis. MS and DG drafted the manuscript. IS, CC, and VC provided input into the data interpretation. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.652415/full#supplementary-material

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Conserving an Endangered Canid: Assessing Distribution, Habitat Protection, and Connectivity for the Dhole (Cuon alpinus) in Bhutan

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Most canids face population declines and range contractions worldwide. Although the dhole (*Cuon alpinus*) is widely distributed across 10 countries in South and Southeast Asia, limited studies exist on this species. Despite its globally "Endangered" status and ecological role as an apex predator, assessments on its distribution are limited to a few landscapes and countries. This explains the lack of a dhole-specific species conservation plan in most range countries, including Bhutan where no current population estimate exists. The species has also recovered from a country-wide poisoning campaign in the 1970s and 80s. In this study, we determine the dhole's distribution pattern and assess the protection and connectivity of dhole habitat in Bhutan. We anticipated dholes to be extant within their habitat well-represented in protected areas (PAs) and biological corridors (BCs). We used 721 georeferenced dhole occurrence records and eight environmental variables in MaxEnt software to model potential dhole distribution and habitat suitability. The model output was overlaid on the spatial layers of PAs and BCs to assess habitat protection and connectivity. As anticipated, we found the dhole widely distributed in all districts, PAs, and BCs in Bhutan. Dholes were recorded at the highest elevation range limit of 4,980 m above sea level, which overlapped with the "Vulnerable" snow leopard (*Panthera uncia*). Our model identified 72% (27,634 km^2) of the country as suitable areas for dholes, of which, 31% (11,899 km^2) was highly suitable and 41% (15,735 km^2) was moderately suitable. Contrary to our expectation, PAs and BCs encompassed only 29% (8,046 km^2) and 12% (3,185 km^2) of suitable areas for dholes, respectively. A vast majority of the areas we deemed suitable for dholes currently remain unprotected, thus making dholes more vulnerable to human persecution and local extermination. We recommend adjusting PA boundaries to fully encompass suitable dhole habitat, and also advocate improved livestock husbandry to reduce dhole related livestock predation and minimize conflict, thereby ensuring its long-term survival in Bhutan.

Keywords: Bhutan, biological corridors, dhole conservation, dhole distribution, endangered canid, protected areas

INTRODUCTION

With 13 genera encompassing 37 species in 81% of countries, canids are widespread across diverse habitats and environments in all continents except Antarctica (Fleming et al., 2017). As apex predators, large canids can influence prey populations and cause trophic cascades when their populations fluctuate (Newsome and Ripple, 2015; Fleming et al., 2017). Globally, canid distributions overlap with human-modified landscapes (Srivathsa et al., 2019b) to pose conservation challenges (Lamb et al., 2020), resulting in population declines caused by habitat loss, prey decrease, human persecution, disease, and overexploitation (Ripple et al., 2014). The most notable examples include the extermination of the Mexican wolf (*Canis lupus baileyi*) from its natural range (Brown, 1983), a 93% range contraction of the African wild dog (*Lycaon pictus*; Woodroffe and Sillero-Zubiri, 2020), eradication of gray wolves (*Canis lupus*) from most of the United States and Europe (Mech, 1995), and extinction of the Falkland Islands wolf *(Dusicyon australis*; Sillero-Zubiri, 2015).

The dhole (*Cuon alpinus*, Pallas 1811), or Asiatic wild dog, is one of the most widely distributed members of the 10 canid species described from Asia (Din et al., 2013). It is an apex social carnivore that preys mostly on ungulates (Kamler et al., 2012, 2020) in forested areas across most of South and Southeast Asia and parts of China (Srivathsa et al., 2014; Kamler et al., 2015). Although largely restricted to protected areas (Kamler et al., 2015), dholes have also been recorded in unprotected secondary forests, multi-use forest fragments, and agro-forest plantations adjacent to protected areas (Srivathsa et al., 2014). Despite being shy and elusive with infrequent contacts with humans (Srivathsa et al., 2020), this canid has been extirpated from ∼82% of its original range through human persecution and habitat loss (Wolf and Ripple, 2017). It is currently listed as globally "Endangered" by the IUCN based on an estimated population of 4,500–10,500 individuals comprising <2,500 adults, with India housing substantial populations concentrated to the south of the Ganges River in the Western Ghats and central forested regions (Kamler et al., 2015).

Although endangered, the dhole has received less conservation attention than other charismatic carnivores (Widodo et al., 2020). Much of the focus on dholes is related to their depredation on livestock (e.g., Katel et al., 2015; Srivathsa et al., 2020). While basic information from camera-trapping (presence and relative abundance) has been reported for site-specific dhole populations in India (Datta et al., 2008; Bashir et al., 2014), Myanmar (Rao et al., 2005), Peninsular Malaysia (Kawanishi and Sunquist, 2008), and Laos (Johnson et al., 2006), there remains a lack of country-specific consolidated distribution data and range maps for dholes. This hinders the assessment of their population status (Karanth et al., 2009) for both in-country and regional conservation planning (Srivathsa et al., 2014; Punjabi et al., 2017), because knowledge of suitable sites where species occur and survive can aid in conservation planning (Papeş and Gaubert, 2007).

Several modeling studies on dhole distribution and occupancy have been carried out at varying scales. At local scales, park-wide potential dhole distribution modeling was carried out by Namgyal and Thinley (2017) in Bhutan's Jigme Dorji National Park and by Rahman et al. (2018) in Indonesia's Ujung Kulon National Park, whereas Singh et al. (2020) recently reported on dhole occupancy in India's Dampa Tiger Reserve. At the broader landscape scale, Srivathsa et al. (2014), Punjabi et al. (2017), and Srivathsa et al. (2019a) modeled dhole occupancy across the Western Ghats of Karnataka, India. Similarly, Srivathsa et al. (2019b) also assessed occupancy by dholes across the Pench-Kanha Landscape in Madya Pradesh, India. Recently, Widodo et al. (2020) modeled potential dhole distribution across the Rimbang Baling and Tesso Nilo landscapes in Sumatra. At the country level, Jenks et al. (2012) used maximum entropy modeling to predict potential dhole distribution in Thailand based on dhole occurrence data from 15 protected areas while Karanth et al. (2009) used occupancy modeling to predict areas of dhole occurrence in India.

In Bhutan, dholes are apex predators similar to tigers (*Panthera tigris*; Thinley et al., 2018) and snow leopards (*Panthera uncia*; (Leki and Shrestha, 2018). There is no current population estimate for dholes in Bhutan. They were, however, almost extirpated from the country in the 1970s and 80s by mass poisoning campaigns due to blames over persistent livestock depredation (Wang and Macdonald, 2006; Thinley et al., 2011; Namgyal and Thinley, 2017). Because dholes are known to control populations of wild pig (*Sus scrofa*), the principal crop-raiding species in Bhutan (Wangchuk, 2004; Thinley et al., 2018), it is believed that wild pig populations in Bhutan substantially increased and intensified crop damage after the mass extermination of dholes (Wangchuk, 2004). Despite the dhole population recovering and re-establishing itself in Bhutan from the late 1990s with some probable recolonization from the neighboring Indian states of Assam and West Bengal (Wangchuk, 2004), little is known on its current distribution in Bhutan (Namgyal and Thinley, 2017). The dhole is still not listed as a protected species in Schedule I of Bhutan's Forests and Nature Conservation Act despite being globally endangered (Namgyal and Thinley, 2017). Therefore, it is important to ascertain dhole distribution in Bhutan at the landscape level to promote efficient research and planning decisions (Guisan et al., 2013). The only previous attempt to discern dhole distribution in Bhutan was by Wangchuk (2004) who interviewed 67 field forestry staff members and surveyed residents in 18 villages across seven *dzongkhags* (districts) of Gasa, Paro, Punakha, Thimphu, Trongsa, Wangduephodrang, and Zhemgang (**Figure 1**). However, no distribution map was produced in addition to the anecdotes of localities where dholes were present or absent. As such, there is no information on how well dhole habitats are protected within Bhutan's protected area network.

An adequate knowledge of distribution, including associated environmental and anthropogenic variables, further enables appropriate modeling to predict additional areas where dholes are likely to occur, both within and outside protected areas, as recently demonstrated by Thinley et al. (2021) for the tiger in Bhutan. Because dholes are prominently linked to livestock predation in Bhutan (Thinley et al., 2011; Katel et al., 2015; Rajaratnam et al., 2016), determining and modeling

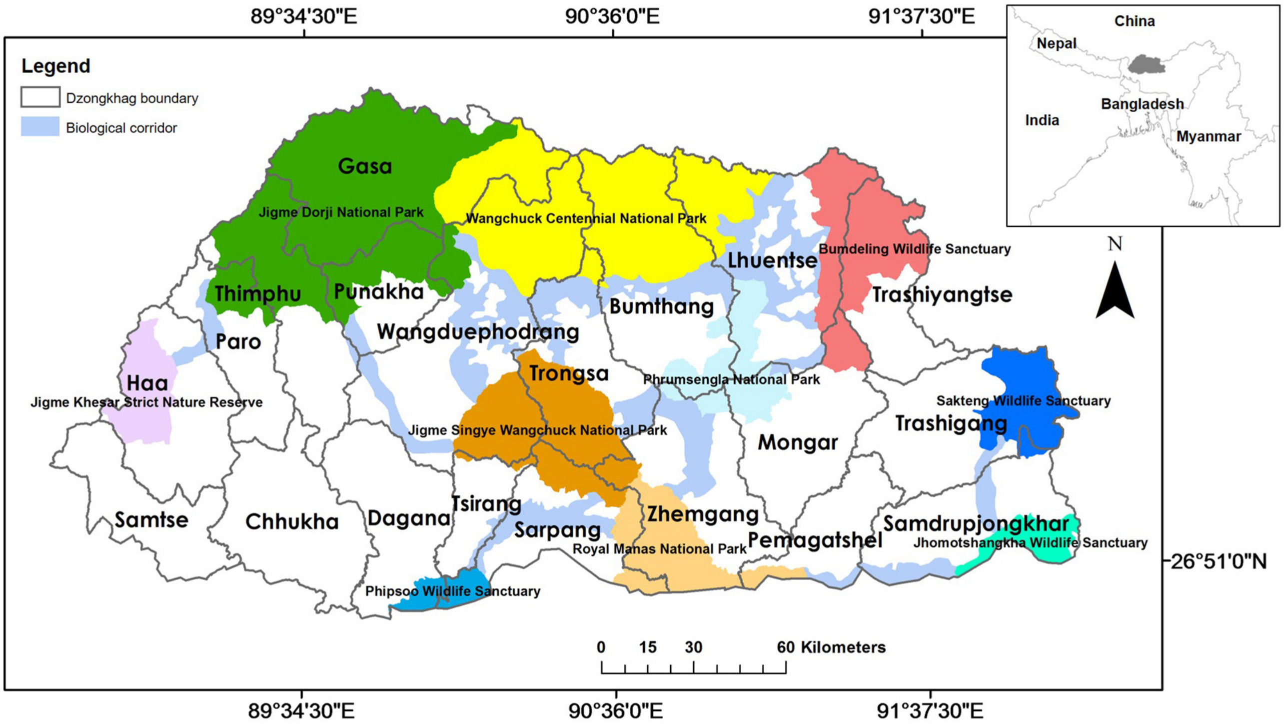

FIGURE 1 | Protected areas, biological corridors, and dzongkhags (districts) of Bhutan. The inset depicts Bhutan's location relative to its neighboring countries in South Asia. Source: Environmental Systems Research, Inc.

their distribution further enables an identification of potential human-wildlife conflict hotspots to prioritize mitigation efforts (Sharma et al., 2020). Juxtaposing conflict hotspots and habitat protection against the current and predicted dhole distribution can provide the spatial framework to develop an appropriate dhole conservation plan for Bhutan.

In this study, we investigated dhole distribution based on current presence records across Bhutan and assessed the protection and connectivity of its habitat. Specifically, we modeled potential dhole distribution and suitable habitat coverage in Bhutan's protected areas (PAs) and interconnecting biological corridors (BCs). Based on Bhutan's strong conservation policy and high proportion of land dedicated to nature conservation, we anticipated dholes to be extant in their habitats well-represented in PAs and BCs.

MATERIALS AND METHODS

Study Area

Bhutan (**Figure 1**) is one of the least-populated countries of Asia with only 735,553 people (NSB, 2017). Situated in the eastern Himalayas (**Figure 1** inset) and administratively divided into 20 *dzongkhags* (district), Bhutan encompasses an area of 38,394 km^2 (NSB, 2018) and is well-known for its rich biodiversity. Approximately 71% of the country is forested (FRMD, 2016) and encompasses 11,248 species of plants and animals, including 129 mammal species (NBC, 2017). This mammalian community includes four wild canid species, namely dhole, Tibetan wolf (*Canis lupus chanco*), golden jackal (*Canis aureus*), and red fox (*Vulpes vulpes*) (Wangchuk et al., 2004). The country's Constitution mandates the government to maintain a minimum of 60% forest cover for eternity. As such, more than half of the country (51%) is designated as a protected area network (**Figure 1**) comprising protected areas and interconnecting biological corridors (Dorji et al., 2019). The country's topography is mountainous and highly rugged with a pronounced elevation range from 97 m above sea level (a.s.l.) in the southern foothills to 7,750 m a.s.l. in the greater Himalayas near the Chinese border (Tshering et al., 2020).

Modeling Potential Dhole Distribution or Habitat

We modeled potential dhole distribution and habitat suitability in Bhutan using MaxEnt program *version 3.4.3* (Phillips et al., 2020) which uses a widely employed maximum entropy method of modeling species distribution based on presence-only data (Phillips et al., 2006). In MaxEnt, georeferenced occurrence points of a target species are associated with environmental variables to yield a spatial layer representing the most widespread probability of its presence, given constraints imposed by these environmental layers (Elith et al., 2011). The resulting layer also constitutes a habitat suitability layer of a species and depicts its realized niche, which is a subset of its fundamental niche (Phillips et al., 2006). MaxEnt modeling was chosen because our dataset solely comprised dhole presence points, thereby, precluding the use of a boosted regression tree based on additional absence data (Yu et al., 2020) and species occupancy modeling based on repeated surveys (MacKenzie et al., 2006).

We utilized a database of 721 georeferenced dhole occurrence points in Bhutan from 2014 to 2019 based on cumulative pooling of dhole records from: (a) a 2014–2015 nationwide camera trapping survey on tigers (Thinley et al., 2015) up to 4,500 m a.s.l.; (b) a 2015–2016 nationwide camera trapping survey on snow leopards (Lham et al., 2016) between 3,500 and 5,500 m a.s.l.; (c) camera trap and sign surveys across protected areas between 2014 and 2019; (d) SMART (Spatial Monitoring and Reporting Tool) patrolling reports submitted by wildlife personnel between 2015 and 2019; and (e) camera trapping of wildlife in catchment studies (Thinley et al., 2020) in Wangchu and Kholongchhu sub-basins between 2018 and 2019.

Following Thinley et al. (2021), we selected eight environmental (geophysical and anthropogenic) variables deemed to influence dhole occurrence based on its ecology (Johnsingh and Acharya, 2013), particularly prey selectivity (Wangchuk, 2004; Wang and Macdonald, 2009; Thinley et al., 2011) and habitat use (Aryal et al., 2015; Namgyal and Thinley, 2017). All environmental variables were processed in ArcMap *version 10.7.1* where spatial layers were classified into 10 categories based on suitability to dholes and standardized with a spatial resolution of 30×30 m cell corresponding to the spatial resolution of the Digital Elevation Model (DEM), Transverse Mercator projection, DRUKREF 03 coordinate system, and geographic extent of Bhutan. Dhole points co-occurring within the same 30×30 m cell were omitted to minimize errors from spatial autocorrelation (Kanagaraj et al., 2011).

Categorization of spatial layers for environmental variables was based on Thinley et al. (2021) as follows:

1) Elevation: reclassified from Bhutan's Digitial Elevation Model (Jarvis et al., 2006) into 10 classes such that lower elevations were ranked more suitable than higher elevations (**Table 1**);
2) Slope: extracted from the DEM such that lower slope classes were ranked more suitable than higher classes (**Table 1**);
3) Prey richness: prey densities are ecological determinants of carnivore densities (Karanth et al., 2004) and dholes generally prey on medium to large ungulates (Wang and Macdonald, 2009; Kamler et al., 2020; Srivathsa et al., 2020). We, therefore, merged the distribution of nine potential wild prey species (Wangchuk, 2004; Wang and Macdonald, 2009; Thinley et al., 2011)—wild pig, sambar (*Rusa unicolor*), muntjac (*Muntiacus muntjac*), Himalayan goral (*Naemorhedus goral*), serow (*Capricornis sumatraensis*), hog deer (*Axis porcinus*), alpine musk deer (*Moschus chrysogaster*), gaur (*Bos gaurus*), and Bhutan takin (*Budorcas taxicolor whitei*). Spatial layers were obtained from the Field Guide to Mammals of Bhutan (Wangchuk et al., 2004), rasterized, and reclassified with higher suitability values assigned to areas with higher prey richness (**Table 1**);
4) Distance from rivers and streams: rasterized from the Drainage Map of Bhutan based on Euclidean distance; areas closer to rivers and streams were assigned higher suitability values than those farther away (**Table 1**);
5) Distance from human settlements: rasterized from the Settlement Map of Bhutan 2006 (OCC, 2005) based on Euclidean distance; assigned suitability scores increasing with distance away from the settlements (**Table 2**), because dholes avoid human settlements and presence (Srivathsa et al., 2014);
6) Land cover: reclassified from the Land-use Map of Bhutan 2011 (NSSC and NSSC, 2011) with higher suitability values assigned to forested areas compared to open areas (**Table 2**), because the dhole primarily inhabits forested areas (Srivathsa et al., 2014);
7) Distance from roads: rasterized from the latest Road Map of Bhutan obtained from the Department of Roads based on Euclidean distance; assigned suitability scores increasing with the distance away from roads (**Table 2**);
8) Distance from religious sites: digitized areas occupied by Buddhist temples, monasteries, meditation centers, and other religiously significant areas from Google Earth^{TM}; areas were rasterized with an inverse relationship between suitability values and Euclidean distance (**Table 2**), as demonstrated by snow leopards finding safe sanctuaries near Buddhist monasteries in Tibet (Li et al., 2013).

Following Jenks et al. (2012), Namgyal and Thinley (2017), and Thinley et al. (2021), in our generated MaxEnt model we used the default setting of 500 iterations with a convergence threshold of 0.00001, a regularization multiplier of 1, and a maximum background of 10,000 background pseudo-absence points with 50% random tests and 10 replicates. We assessed model performance using AUC (Area under the Receiver Operating Curve) whereby values $\leq$0.5 indicate very poor fit, >0.5 indicate good fit, and equal to 1 indicate perfect fit (Fielding and Bell, 1997). The resulting MaxEnt probability surface was exported to ArcMap and reclassified into the probabilities of dhole occurrence ("highly probable," "moderately probable," and "not probable"). These probabilities correspond to the suitability surfaces ("highly suitable," "moderately suitable," and "unsuitable") because a relatively high number of dhole occurrence points collected across a wide range of environmental conditions optimally reflects the dhole's fundamental niche. Following Thinley et al. (2021), we used the Jenks (natural breaks) classification in ArcMap to classify model surface values from 0 to 0.254 as not probable/unsuitable; 0.255 to 0.461 as moderately suitable/probable; and >0.461 as highly suitable/probable.

Assessing Dhole Protection and Habitat Connectivity

We overlaid protected area (PA) and biological corridor (BC) layers on the dhole suitability layer to assess how much of the habitat that we deemed suitable for dholes is encompassed within PAs (assessing dhole protection) and corridors (assessing dhole habitat connectivity between protected areas). Using the Field Calculator tool in ArcMap, we computed areas (km^2) for each of the dhole suitability classes falling within and outside PAs and BCs.

TABLE 1 | Geophysical and biological variables with suitability values for dholes (*Cuon alpinus*) in Bhutan.

Spatial layers	Classes	Suitability
Elevation (meters above sea level)	28–500	9
	501–1,000	8
	1,001–1,500	7
	1,501–2,000	6
	2,001–2,500	5
	2,501–3,000	4
	3,001–3,500	3
	3,501–4,000	2
	4,001–5,000	1
	>5,000	0
Slope (degrees)	0–5.5	9
	5.6–10.5	8
	10.6–15.5	7
	15.6–25.5	6
	25.6–35.5	5
	35.6–45.5	4
	45.6–55.5	3
	55.6–65.5	2
	65.6–75.5	1
	>75.5	0
Prey richness	9	9
	8	8
	7	7
	6	6
	5	5
	4	4
	3	3
	2	2
	1	1
	0	0
Distance from rivers and streams (meters)	0–300	9
	301–1,000	8
	1,001–2,000	7
	2,001–3,000	6
	3,001–4,000	5
	4,001–5,000	4
	5,001–6,000	3
	6,001–7,500	2
	7,500–10,000	1
	>10,000	0

Higher values reflect higher suitability based on dhole ecology and habitat utilization.

TABLE 2 | Land-use and anthropogenic variables with suitability values for dholes (*Cuon alpinus*).

Spatial layers	Classes	Suitability
Distance from human settlements (meters)	0–30	0
	31–100	1
	101–500	2
	501–3,000	3
	3,001–8,000	4
	8,001–11,000	5
	11,001–14,000	6
	14,001–18,000	7
	18,001–25,000	8
	>25,000	9
Land cover	Broadleaf forest	9
	Broadleaf with conifer forest	8
	Mixed conifer forest	7
	Fir forest	6
	Scrub forest/Meadows	5
	Bluepine forest	4
	Chirpine forest	3
	Improved pasture/Plantations	2
	Agriculture/Horticulture	1
	Glaciers/Rocky outcrops/Settlements/Mining	0
Distance from roads (meters)	0–5	0
	6–100	1
	101–500	2
	501–1,000	3
	1,001–2,000	4
	2,001–3,000	5
	3,001–4,000	6
	4,001–5,000	7
	5,001–6,000	8
	>6,000	9
Distance from religious sites (meters)	0–300	9
	301–1,000	8
	1,001–2,000	7
	2,001–3,000	6
	3,001–4,000	5
	4,001–5,000	4
	5,001–6,000	3
	6,001–7,000	2
	>7,000	1

Higher values reflect higher suitability based on dhole ecology and habitat utilization.

RESULTS

Dhole Distribution

Dholes were distributed throughout Bhutan across all 20 districts and in all PAs and BCs (**Figure 2**), and occurred within a broad elevation range from 110 m a.s.l. in Royal Manas National Park (RMNP) in the southern foothills to 4,980 m a.s.l. in Jigme Dorji National Park (JDNP) in the upper Himalayas (**Figure 1**). They were also present in almost all habitat types ranging from sub-tropical forests in the lowlands to alpine meadows in the uplands. The highest concentration of dhole occurrence records was observed in JDNP whereas the least was recorded in Wangchuck Centennial National Park (WCNP) (**Figure 2**).

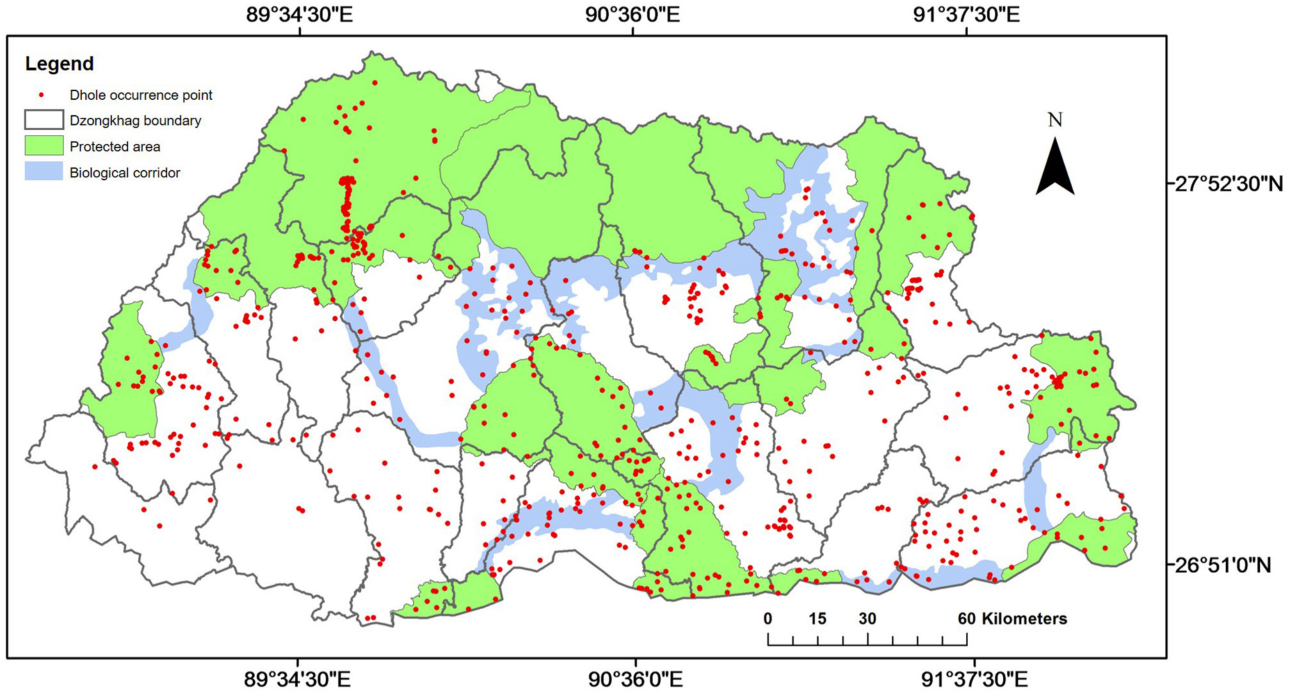

FIGURE 2 | Dhole (*Cuon alpinus*) presence records overlaid on protected areas, biological corridors, and dzongkhags (districts) of Bhutan.

Suitable Areas for Dholes

The MaxEnt model (AUC = 0.73 for training data; 0.72 for test data) predicted that suitable area for dholes covered 72% (27,634 km^2) of Bhutan (**Figure 3**; **Table 3**). This comprised 31% (11,899 km^2) of highly suitable area and 41% (15,735 km^2) of moderately suitable area (**Figure 3**; **Table 3**). Among the eight environmental variables, model prediction (or gain) was maximally influenced by slope (26.4%), followed by distance from human settlement (24.3%), elevation (16.5%), and land cover (13.1%; **Table 4**). Distance from water bodies (**Table 4**) contributed least (1%) to model prediction. Overall, suitable area for dholes coincided with flat and moderately flat area situated further away from human settlements in forested areas below 5,000 m a.s.l. The remaining 28% (10,760 km^2) of modeled area was unsuitable for dholes (**Figure 3**; **Table 3**) and overlapped with steep areas closer to human settlements and roads, and with areas above 5,000 m a.s.l. which were either too cold or permanently covered with snow and glaciers.

Dhole Protection and Habitat Connectivity

When PA and BC layers were overlaid on the suitability layer for the dhole, PAs encompassed only 29% (8,046 km^2) of suitable area for dholes in Bhutan (**Figure 3**; **Table 3**), of which, 39% (3,151 km^2) was highly suitable and 61% (4,895 km^2) was moderately suitable. Similarly, BCs encompassed merely 12% (3,185 km^2) of suitable area for dholes (**Figure 3**; **Table 3**), which comprised 51% (1,631 km^2) of highly suitable and 49% (1,554 km^2) of moderately suitable area. In contrast, a substantial proportion of suitable area for dholes (59%; 16,403 km^2) occurred outside the protected area network (**Figure 3**; **Table 3**), of which, 43% (7,117 km^2) and 57% (9,286 km^2) were highly and moderately suitable for dholes, respectively.

DISCUSSION

Dhole Distribution

We mapped the first-ever nation-wide distribution of dholes in Bhutan (**Figure 2**), which also constituted the first study of its kind amongst dhole range countries in the Himalayan Mountains. Dholes were present in high elevation alpine meadows and screes, and their distribution overlapped with "Vulnerable" snow leopards which are known to range between 3,400 and 5,186 m a.s.l. (Thinley et al., 2016). Dholes are reported to be sympatric with snow leopards in the arid region of the Altun Mountains in western China (Xue et al., 2015). We documented the highest elevation occurrence (4,980 m a.s.l.) for dholes in Bhutan, which also constitutes the highest across its entire distribution range, thus representing an uppermost range limit for dholes. Whether this range extreme is attributed to climate change or prey availability, including livestock such as yak (*Bos grunniens*), needs further investigation. To date, high altitude livestock predation in Bhutan has been mainly attributed to snow leopards (Rajaratnam et al., 2016). Further investigation is required on a potential dietary overlap with the snow leopard (Namgyal and Thinley, 2017) to ascertain the competitive impact of dholes on this iconic flagship carnivore species for the montane Himalayas.

As anticipated, we also discovered that the dhole has the widest distribution amongst large carnivores in Bhutan. It was previously not reported in the three eastern districts of Trashigang, Samdrupjongkhar and Pemagatashel (Wangchuk, 2004), but is now confirmed to be present in all 20 districts of Bhutan. Its wide distribution also indicates the possibility of frequent conflicts with humans due to livestock depredation (Namgyal and Thinley, 2017) given that dholes are principal livestock predators in western Bhutan (Katel et al., 2015; Tshering and Thinley, 2017) and neighboring Arunachal Pradesh in India (Lyngdoh et al., 2014). Increased prevalence of livestock predation by dholes is a distinct possibility in Jigme Dorji National Park (Thinley et al., 2011) which harbored the highest concentrations of dhole occurrence records. Livestock loss presents a significant socioeconomic setback for rural farmers in Bhutan's predominantly agrarian society because the loss of yak results in sizable income loss to upland pastoralists, while the loss of cattle compromises agricultural production and nutrition for lowland agro-pastoralists (Sangay and Vernes, 2008; Rajaratnam et al., 2016).

In relation to agricultural crop loss, wild pigs are responsible for more crop damage compared to any other species in Bhutan. Such losses have major negative impacts on subsistence farmers throughout Bhutan. In fact, the crop damage caused by wild pigs is so severe that wild pigs are considered a national pest with significant funding allocated by the government to control this species. Consequently, the controlling effect by dhole on wild pig populations (Wangchuk, 2004) suggests that increasing the number and expanding the distribution of dholes in Bhutan may lead to lowered numbers of wild pig, which ultimately, would benefit local farmers.

Slope was the top contributor to dhole distribution and habitat suitability (**Table 4**), indicating the influence of Himalayan rugged topography on dhole distribution in Bhutan. Aryal

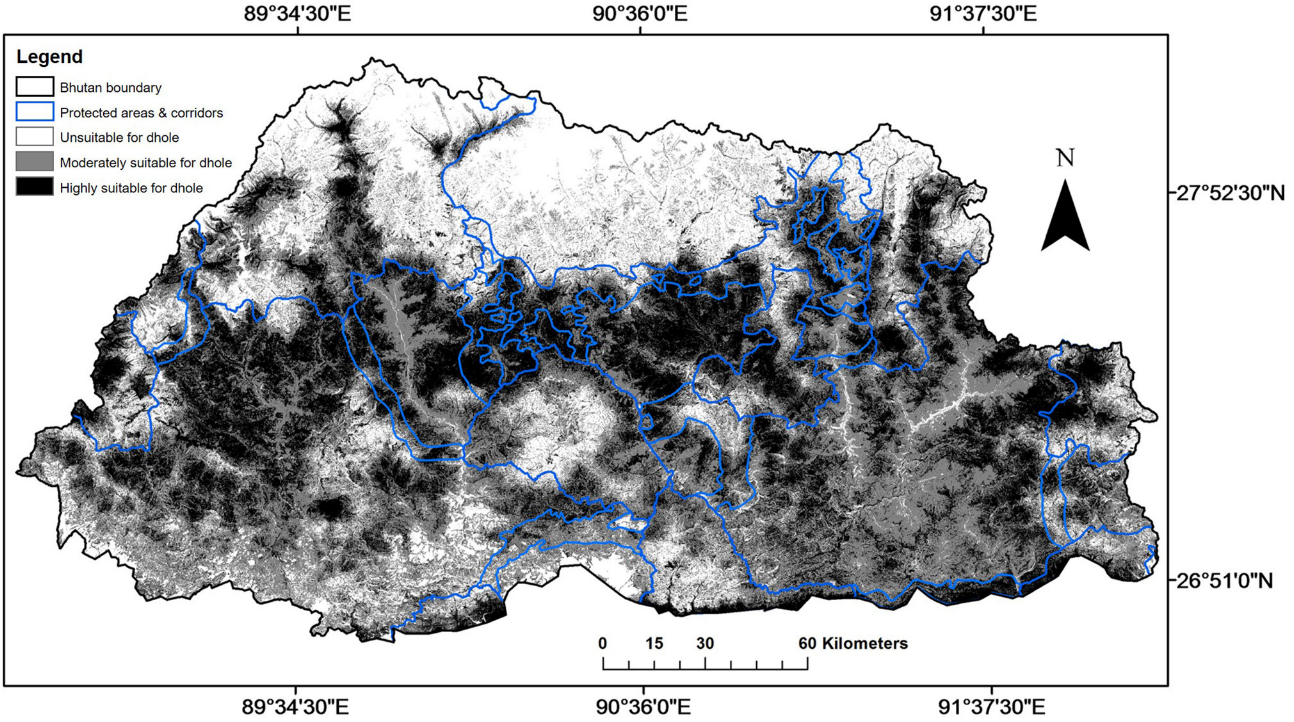

FIGURE 3 | The extent of highly suitable, moderately suitable, and unsuitable areas for dholes (*Cuon alpinus*) in Bhutan as generated by the MaxEnt model.

TABLE 3 | Suitable and unsuitable areas for dholes (*Cuon alpinus*) in Bhutan distributed inside and outside the protected area network (PAN) comprising protected areas (PA) and biological corridors (BC).

Suitability for dholes	Area (km^2)	% of Bhutan	Inside PA	%	Inside BC	%	Outside PAN	%
Highly Suitable (HS)	11,899	31	3,151	26	1,631	14	7,117	60
Moderately Suitable (MS)	15,735	41	4,895	31	1,554	10	9,286	59
Suitable Area (HS + MS)	27,634	72	8,046	29	3,185	12	16,403	59
Unsuitable	10,760	28	7,808	73	648	6	2,304	21

TABLE 4 | Relative contributions of the input variables to the MaxEnt model of dhole (*Cuon alpinus*) distribution/habitat suitability in Bhutan.

Variable	Percent contribution
Slope	26.4
Distance from human settlements	24.3
Elevation	16.5
Land cover	13.1
Distance from religious sites	7.9
Distance from roads	7.4
Prey richness	3.4
Distance from rivers and streams	1.0

et al. (2015) also determined slope to be the most significant factor influencing dhole presence and occupancy in Nepal's Dhorpatan Hunting Reserve, whereby dholes used gently sloped land more than steep areas. This is likely related to the cursorial hunting strategy of dholes which is more effective on flatter terrain and gentle slopes compared to more rugged terrain or areas with steeper slopes (Kamler et al., 2012). In contrast to Jenks et al. (2012), contribution of prey richness to modeled potential dhole distribution in our study was minimal and much lower than that of land cover. This is possibly because forested habitats throughout Bhutan naturally harbor a high richness of potential prey species (Wangchuk et al., 2004). We do, however, acknowledge the greater role of prey density in influencing dhole distribution. This variable was excluded due to the lack of its spatial layer, which constitutes a limitation to our study.

Dhole Conservation Mismatch

We assessed whether protected areas and biological corridors are adequate for conserving dhole habitats. Although protected areas in Bhutan were designated for multiple species, we found them inadequate for protecting and connecting wide-ranging species like the dhole, similar to that observed for the tiger (Thinley et al., 2021). Contrary to expectations, only 29% of total suitable habitat for dholes was available in protected areas, reflecting an increased vulnerability of the species to further human persecution and habitat loss through livestock depredation and land-use changes outside protected areas. Similarly, only 30% of potential habitat for dholes in Thailand was encompassed within protected areas (Jenks et al., 2012) while 41% of areas occupied by dhole were inside protected wildlife reserves in the Western Ghats landscape within Karnataka, India (Srivathsa et al., 2014). As such, the current level of landscape protection may be insufficient to support functional dhole meta-populations (Bargelt et al., 2020) across Bhutan as equally demonstrated by the meager 33–35% of suitable areas captured by Bhutan's protected areas for the wide ranging tiger (Thinley et al., 2021).

Dhole as a Potential Umbrella Species

Dholes are also estimated to require five times more land area than large-bodied carnivores such as tigers (Kamler et al., 2012), mainly because of the social structure of populations living in exclusive territories (Johnsingh, 1982), unlike solitary tigers with overlapping territories (Carter et al., 2015). Large space requirements in conjunction with a hypercarnivorous diet (Van Valkenburgh, 1991) make dholes more vulnerable to extirpation, as evidenced by their disappearance from more reserves than tigers (Woodroffe and Ginsberg, 1998). Most reserves in Asia are typically focused on conserving umbrella species such as tigers (e.g., Wikramanayake et al., 2011) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal (e.g., Aryal et al., 2017) to highlight conservation efforts. As exemplified above, umbrella species are typically large-bodied animals which require large areas to ensure species persistence. They are good surrogates for overall biodiversity but are more sensitive than other species to human activities, ecosystem changes, and habitat destruction whilst having the largest land requirements and most stringent ecological needs (Woodroffe and Ginsberg, 2005). Recently, Kaszta et al. (2020) advocated habitat prioritization for the medium-sized clouded leopard (*Neofelis nebulosa*) as a good indicator and focal species to address limited resources for immediate biodiversity conservation actions to conserve forest ecosystems and forest-dependent biodiversity in Southeast Asia. Based on this premise and the results of our study, we suggest that the dhole, given its unusually high requirements for space and prey, could constitute a more effective umbrella species in Asia and a driver for future designation of protected areas and/or expansion of current reserves with dhole metapopulations.

Dhole as a Keystone Species

In most terrestrial ecosystems, large carnivores have been identified as "keystone species" (Terborgh et al., 1999; Ripple et al., 2014) based on the premise that keystone species exert disproportionately larger influence on an ecosystem relative to their abundance (Power et al., 1996). Although the top-down effects of dholes are loosely described (see Thinley et al., 2018), previous research showed that dholes killed more ungulates than sympatric leopards (*Panthera pardus*) and tigers (Venkataraman, 1999), indicating that dholes have a greater impact on ungulate numbers relative to other large Asian carnivore species. As such, there may be a parallel to pack-living wolves in North America which cause trophic cascades primarily via predation on large ungulates which, in turn, affects vegetation growth patterns across the landscape (Ripple et al., 2001; Beschta and Ripple, 2009). Further repercussions from the decline of dholes are exemplified in Bhutan, whereby wild pig populations thrived and increased crop depredation after dholes were exterminated from many areas (Wangchuk, 2004). The dhole may, therefore, be a top keystone carnivore in Bhutan, and probably across its range. Consequently, their presence may have a greater impact on biodiversity in Asia, compared to other large carnivores. Thus, if protected areas in Asia are to preserve entire ecosystem functions, adequate protection and conservation of dholes should be equally considered.

Conservation Implications

Based on our study, Bhutan is a stronghold for dholes in the eastern Himalayas due to their widespread distribution and availability of large tracts of suitable habitat. In order to ensure long-term survival of the dhole in Bhutan, we recommend replicating the recommendations of Thinley et al. (2021) for tigers in terms of readjusting PA boundaries to encompass prime dhole habitats and extending dhole conservation efforts outside the PAs. However, local people exhibit resentment to dholes and their conservation due to persistent dhole-related livestock predation (Katel et al., 2015). This is principally driven by socio-economic losses because pastoral communities experiencing human-carnivore conflict tend to have low income with low tolerance to carnivores and their conservation (Ahmad et al., 2016). As such, there is likelihood for retaliation against dholes reminiscent of historic poisoning efforts against the species in the 1970–80s (Wangchuk, 2004). Therefore, dhole conservation efforts both within and outside the PAs need to incorporate efforts to improve livestock husbandry like grazing livestock in and around villages, including stall-feeding and cooperative herding of livestock in forests during the day (Katel et al., 2015). Tshering and Thinley (2017) further recommended stock improvement, fodder development, pasture development, and livestock insurance schemes to reduce livestock predation by dholes, while Sangay and Vernes (2008) advocated non-grazing of livestock in depredation hotspots. Dhole-specific livestock insurance schemes are also feasible to alleviate socio-economic loss from livestock predation by dholes. Local people should also be educated about the positive impacts that dholes have on ecosystems, including suppression of major crop-destroying species such as wild pigs. Based on this control of crop depredators, rural farmers might be inclined to adopt livestock protection measures against dholes as well. This will alleviate livestock losses in addition to a reduction in crop damage. We further advocate the listing of the dhole in Schedule I of Bhutan's Forests and Nature Conservation Act, urging for increased legal protection of this globally endangered canid. Lastly, we recommend other dhole range countries to conduct a similar study on the role of protected areas in conserving dhole populations to ensure species viability across its distribution area.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The study was reviewed and approved by Department of Forests and Park Services, Bhutan.

AUTHOR CONTRIBUTIONS

PT: conceptualization, data collection, data curation, formal analysis, and writing—original draft. RR: conceptualization, validation, writing—review, and editing. JK: validation, writing—review, and editing. CW: data collection, data curation, formal analysis, and writing—review. All authors contributed to the article and approved the submitted version.

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Stable Isotope Analysis of Specimens of Opportunity Reveals Ocean-Scale Site Fidelity in an Elusive Whale Species

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Elusive wildlife are challenging to study, manage, or conserve, as the difficulty of obtaining specimens or conducting direct observations leads to major data deficiencies. Specimens of opportunity, such as salvaged carcasses or museum specimens, are a valuable source of fundamental biological and ecological information on data-deficient, elusive species, increasing knowledge of biodiversity, habitat and range, and population structure. Stable isotope analysis is a powerful indirect tool that can be used to infer foraging behavior and habitat use retrospectively from archived specimens. Beaked whales are a speciose group of cetaceans that are challenging to study *in situ*, and although Sowerby's beaked whale (*Mesoplodon bidens*) was discovered >200 years ago, little is known about its biology. We measured $\delta^{13}C$ and $\delta^{15}N$ stable isotope composition in bone, muscle, and skin tissue from 102 Sowerby's beaked whale specimens of opportunity collected throughout the North Atlantic Ocean to infer movement ecology and spatial population structure. Median $\delta^{13}C$ and $\delta^{15}N$ values in Sowerby's beaked whale bone, muscle, and skin tissues significantly differed between whales sampled from the east and west North Atlantic Ocean. Quadratic discriminant analysis that simultaneously considered $\delta^{13}C$ and $\delta^{15}N$ values correctly assigned $>85\%$ of the specimens to their collection region for all tissue types. These findings demonstrate Sowerby's beaked whale exhibits both short- and long-term site fidelity to the region from which the specimens were collected, suggest that this species is composed of two or more populations or exhibits a metapopulation structure, and have implications for conservation and management policy. Stable isotope analysis of specimens of opportunity proved a highly successful means of generating new spatial ecology data for this elusive species and is a method that can be effectively applied to other elusive species.

Keywords: bone, muscle, skin, Sowerby's beaked whale, *Mesoplodon bidens*, δ^{13} C and δ^{15} N, museum collections

INTRODUCTION

Knowledge of a species' population structure and spatial ecology is essential for effective wildlife conservation, particularly in potentially highly migratory marine species. Species of concern are often by definition rare or elusive, resulting in large gaps in knowledge regarding their biology and ecology (Cunningham and Lindenmayer, 2005). As a result, the conservation needs of these species are often unknown, presenting challenges to those tasked with developing conservation and management plans. Traditional field research techniques may be ineffective when species are rarely encountered, live in remote or inaccessible habitats, or actively avoid human researchers and equipment (Green and Young, 1993; Breck, 2006; Meek et al., 2014). In such cases, alternative, often indirect, approaches to the generation of basic ecological and biological knowledge may be needed to fill essential knowledge gaps (Piggott and Taylor, 2003; Joseph et al., 2006).

Specimens of opportunity provide sources of ecological and biological information that may be particularly valuable for rare and elusive species (Roberts et al., 2016). These sources include museum specimens, salvaged carcasses, or specimens collected in the wildlife trade or for human consumption and sold in the marketplace. Museums are critically important repositories of biological data, and museum specimens have been used in comparative studies, to identify new species and to understand historical biodiversity (Newbold, 2010; Holmes et al., 2016; MacLean et al., 2019). Salvaged carcasses, such as roadkill or stranded marine mammals, have provided new information on range and population structure (Coombs et al., 2019; Schwartz et al., 2020). Similarly, animals collected for the pet trade or human consumption have yielded new species and information on hybridization events (Erdmann, 1999; Baker et al., 2007; Ebert et al., 2019). As research tools develop, the quantity and quality of information that can be gained from these specimens of opportunity grow, providing an invaluable resource to investigate the biology and ecology of elusive species.

Stable isotope analysis is a powerful and efficient tool that can be used on specimens of opportunity for addressing biological and ecological questions that may otherwise be challenging or impossible to answer (McKechnie, 2004; West et al., 2006; MacKenzie et al., 2011). Using a combination of tissues synthesized at different times or at different rates, researchers can infer spatial origin and diet across time (Phillips and Eldridge, 2006; Vander Zanden et al., 2015). The rate that stable isotopes are incorporated into a specific tissue is determined by that tissue's growth and replacement rates. Some tissues grow rapidly and are replaced within months, while others are incrementally grown and replaced depending on environmental and physiological pressures (Fry and Arnold, 1982). Stable isotope analysis conducted on specimens of opportunity has been used to infer animal migrations, the spatial origin of wildlife products, and even historical trophic structures (Hobson, 1999; Chasar et al., 2005; Hopkins and Ferguson, 2012). Two of the most commonly used isotopes for wildlife studies are carbon (expressed as δ^{13}C values), used to evaluate habitat range and latitudinal shifts, and nitrogen (expressed as δ^{15}N values), used for obtaining foraging and trophic information (Ben-David and Flaherty, 2012). As the body of literature on the application of stable isotope analysis to wildlife studies grows, in conjunction with more high-resolution maps documenting the spatial relationship of stable isotope abundance (i.e., isoscapes), this analytical approach creates more opportunities to utilize specimens of opportunity to increase knowledge regarding elusive species (Vander Zanden et al., 2018; Trueman et al., 2019).

Although beaked whales comprise more than 25% of extant whale and dolphin species, they are poorly understood and elusive, with most questions regarding their basic biology unanswered (Dalebout et al., 2004; Mead, 2009). This paucity of data is largely attributable to the challenge of locating beaked whales and distinguishing among species due to their elusive behavior and similar appearance (MacLeod et al., 2005). Beaked whales generally inhabit deep ocean, off-shelf habitats, and their relatively small size, limited time spent at the surface, and deep-diving behavior protected most species from being targeted by commercial whaling operations and contribute to a lack of observational data. Consequently, visually identifying and studying beaked whales *in situ* is challenging, and many field sightings of beaked whales can only be reliably identified to genus, with possibly a suggestion of species. Specimens of opportunity already have proven critical to increasing our understanding of beaked whale diversity and ecology (Feyrer et al., 2020; Landrau-Giovannetti et al., 2020). For example, three species (*Mesoplodon bowdoini*, *M. traversii*, and *M. hotaula*) have never been observed alive and are known only from stranded carcasses, and several other species are known from stranded carcasses and a few unconfirmed sightings (van Helden et al., 2002; Dalebout et al., 2014). Similarly, during the last 20 years, four new species were discovered by re-examining museum specimens (Dalebout et al., 2002, 2014; Yamada et al., 2019).

Sowerby's beaked whale (*Mesoplodon bidens*) was first described in 1804, yet in more than 200 years, little has been learned about its life history (Sowerby, 1804; MacLeod et al., 2005; Ellis et al., 2017). Most information on the species' basic biology, such as its spatial and foraging ecology, is still largely unknown, explaining why it is considered "data deficient" by the IUCN and a species of special concern by the Committee on the Status of Endangered Wildlife in Canada (Taylor et al., 2008; COSEWIC, 2019). The species' range encompasses much of the North Atlantic Ocean, and although individuals of this species have been observed and collected from both North American and European waters, it is unknown if this is one continuous and highly mobile population, or if the species is structured into spatially distinct subpopulations.

Based on the lack of data on the population structure and spatial ecology of Sowerby's beaked whales, management needs of this species are unclear and effective conservation plans cannot be developed across this species' range. Site fidelity has been recorded in other beaked whales, such as Cuvier's (*Ziphius cavirostris*) and Blainville's (*M. densirostris*), but this has not been investigated or documented in Sowerby's beaked whale (McSweeney et al., 2007). Analysis of seven cranial elements from 112 Sowerby's beaked whale museum specimens identified significant morphological differences between specimens collected in the east and west Atlantic Ocean, suggesting there may be distinct populations of Sowerby's beaked whale (Smith et al., 2021). However, mitochondrial DNA analysis of 14 individuals identified both regionally distinct and shared haplotypes between animals collected from both sides of the Atlantic Ocean (COSEWIC, 2006). Thus, the spatial ecology and population connectivity of this species are largely unknown. Additional data regarding the spatial ecology of Sowerby's beaked whale are needed to identify conservation threats and aid in the development of management plans.

In this study, we measured $\delta^{13}C$ and $\delta^{15}N$ compositions of three tissues with distinct growth and isotopic turnover rates from Sowerby's beaked whale specimens of opportunity from the east and west Atlantic. Our research brings together tissues from museum specimens, stranded carcasses, and bycaught animals to create a robust and diverse collection of specimens of opportunity. Our objectives were to (i) evaluate the general efficacy of specimens of opportunity in spatial ecology studies, (ii) identify and characterize regional patterns in isotopic values among Sowerby's beaked whale individuals, and (iii) determine if isotope values from specimens of opportunity can be used to illuminate the spatial ecology of Sowerby's beaked whales across months and years.

METHODS

Sampling

We sampled 102 opportunistically collected Sowerby's beaked whale specimens from museums, stranding programs, and research centers for bone ($n = 71$), muscle ($n = 40$), and skin ($n = 50$) tissue samples (**Supplementary Table 1**). For 46 specimens, we acquired more than one tissue type: bone, muscle, and skin from 13; bone and muscle from 4; bone and skin from 12; and muscle and skin from 17. Original specimen collection locations were from the east and west North Atlantic Ocean, here defined as being on either side of the 35th meridian west (**Figure 1**). East Atlantic specimens ($n = 64$) were stranded or recovered in dredging operations, whereas west Atlantic specimens ($n = 38$) were stranded or bycaught in the former swordfish (*Xiphias gladius*) pelagic drift gillnet fishery of the western North Atlantic (Wenzel et al., 2013). Original specimen collection dates ranged across all months and seasons from 1980 to 2019; included male, female, and unknown sex individuals; and spanned age classes (**Supplementary Table 1**).

We used a handheld drill to remove 1 g of bone tissue from the occipital bone, when available. In 17 specimens, this bone was not available, and we sampled an alternate location. We sampled 0.5 g from soft tissues and stored them in 95% ethanol for transportation. Soft tissues are commonly preserved in ethanol, which can contribute to lipid removal but has insignificant effects on $\delta^{13}C$ and $\delta^{15}N$ values (Sarakinos et al., 2002; Javornik et al., 2019).

Stable Isotope Analysis

We subsampled ∼200 mg of bone tissue for collagen extraction and followed the protocol outlined by Smith et al. (2020), including lipid extraction and HCl and NaOH baths to remove the mineral component. Analysis was completed at the Cornell Isotope Laboratory at Cornell University using a Thermo Delta V isotope mass spectrometer interfaced with a NC2500 elemental analyzer (Thermo Fisher Scientific, 168 Third Avenue Waltham, MA, USA 02451). We calibrated our sample values using two in-house protein standards with known $\delta^{13}C$ and $\delta^{15}N$ values relative to Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}C$ and Atmospheric Air for $\delta^{15}N$. An in-house animal tissue standard was included between every 10 samples, with an analytical precision of ±0.1‰ (1σ) for $\delta^{13}C$ and $\delta^{15}N$.

Soft tissue samples were freeze-dried, finely ground, and lipid extracted with 2:1 chloroform:methanol for 30 min, manually agitating every 5 min; additional lipid extractions were performed as necessary if the supernatant was not clear. We dried samples at 60°C after extraction. Analysis was completed at the Smithsonian Museum Conservation Institute Stable Isotope Mass Spectrometry Laboratory using a Thermo Delta V Advantage mass spectrometer coupled to an Elementar vario ISOTOPE Cube Elemental Analyzer *via* a Thermo Conflo IV (Thermo Fisher Scientific, 168 Third Avenue Waltham, MA, USA 02451). We calibrated our sample values to V-PDB and Air *via* two standards, an in-house Costech Acetanilide (Costech Analytical, 26074 Avenue Hall, Suite 14 Valencia, CA, USA 91355) and Urea-UIN3, calibrated to USGS40 and USGS41 L-glutamic acid (Schimmelmann et al., 2009). Standards were included between every 10 samples, with an analytical precision of ±0.2‰ (1σ) for $\delta^{13}C$ and $\delta^{15}N$.

We use delta notation (δ) to express our stable isotope results. This is the parts per thousand difference between the sample and international standards, expressed as $\delta^{y}X = [(R_{\text{sample}} - R_{\text{standard}}) / (R_{\text{standard}})]$, where X is the element, y is the atomic mass of the stable isotope, and R is the ratio of heavy to light isotopes. In order to account for the Suess effect (i.e., changing atmospheric carbon isotope ratios due to fossil fuel input) (Keeling, 1979), we Suess-corrected the data by adding 0.015‰

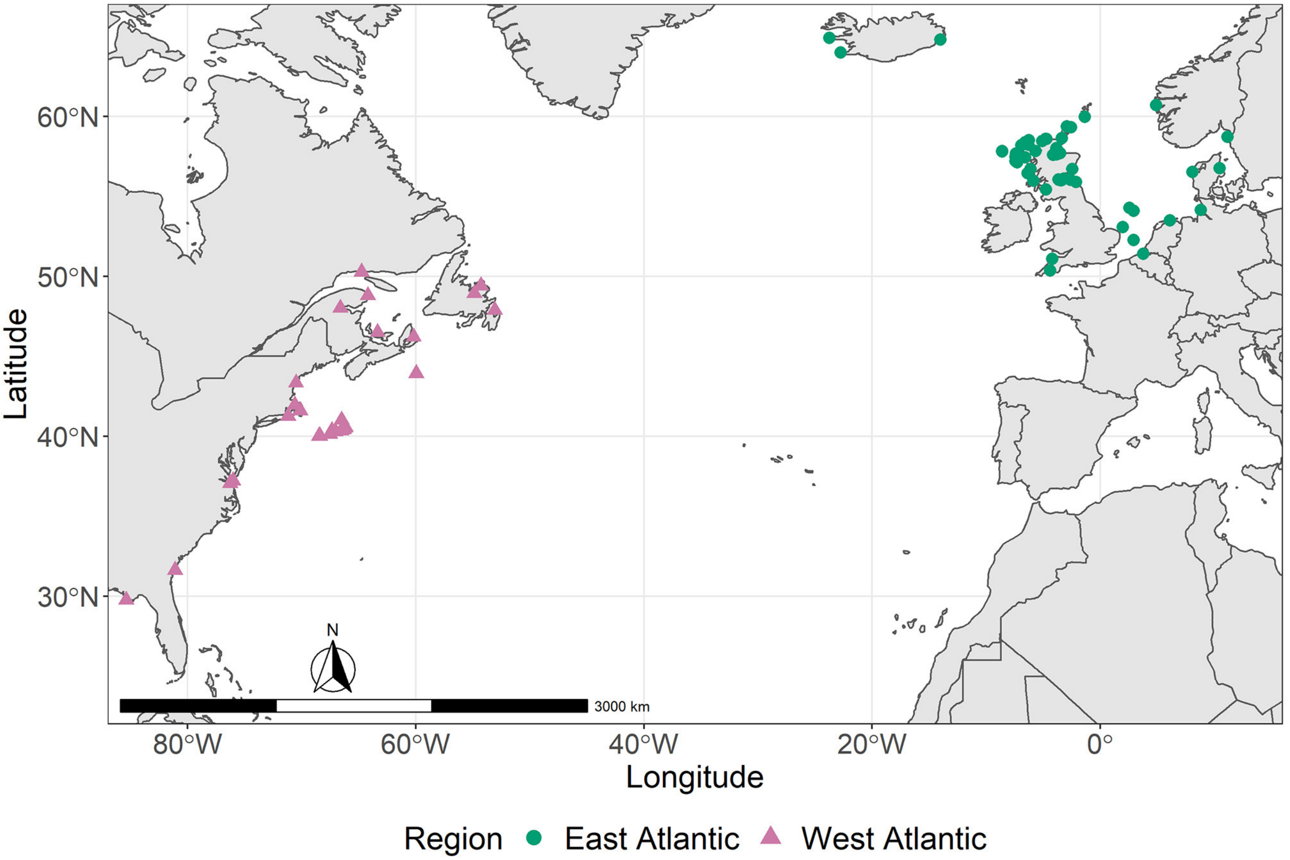

FIGURE 1 | Collection locations for 102 opportunistically collected Sowerby's beaked whale specimens housed in museums, stranding programs, and research centers collected in the east ($n = 64$) and west ($n = 38$) Atlantic Ocean basin, defined here as being on either side of the 35th meridian west.

to the δ13C value for each year since 1980 to the date the sample was collected (Sonnerup et al., 1999; Young et al., 2013). Because the cumulative change in δ^{13}C values caused by the Suess effect across the time the samples in this study were collected exceeded the analytical precision of our standards, failure to account for this variation could result in the mischaracterization of δ^{13}C values for this species.

Data Analysis

We first explored differences in isotopic values between samples collected from the east and west Atlantic graphically and using descriptive statistics. We performed Mann–Whitney *U*-tests to explore differences in median tissue isotope values between regions and considered $p \leq 0.05$ significant. This test was selected because some data categories were non-normally distributed. We then assessed the ability to assign samples to their collection location in the east or west Atlantic based on stable isotope values using jackknife quadratic discriminant analysis of δ^{13}C values alone, δ^{15}N values alone, or δ^{13}C and δ^{15}N values simultaneously. Quadratic discriminant analysis was used because it is appropriate for analyzing data which are unequally sampled across regions and have unequal variance. We performed all analyses using R (R Core Team, 2018) with RStudio (RStudio Team, 2016) and JMP (SAS, 2019).

RESULTS

δ^{13}C and δ^{15}N biplots demonstrated that stable isotope values differed between tissues from Sowerby's beaked whales collected from the east and west Atlantic (**Figure 2**). Of the three tissues sampled, bone had the most overlap in isotope values between regions, whereas the regional groups for both skin and muscle samples were more distinct. Box and whisker plots demonstrated differences in median isotope values in all three tissues between collection regions, and that specimens collected in the west Atlantic consistently displayed higher median δ^{13}C and δ^{15}N values (**Figure 3**). East Atlantic specimens exhibited a larger range in δ^{13}C and δ^{15}N values than west Atlantic specimens except for muscle δ^{15}N, which was the same between regions (**Table 1**). In both regions and for both isotopes, bone was more enriched than muscle and skin. Median δ^{13}C values in muscle were higher than those in skin in both regions. Median δ^{15}N values were higher in skin compared with muscle in specimens from the east Atlantic but lower than muscle in specimens from the west Atlantic. Mann–Whitney *U*-tests

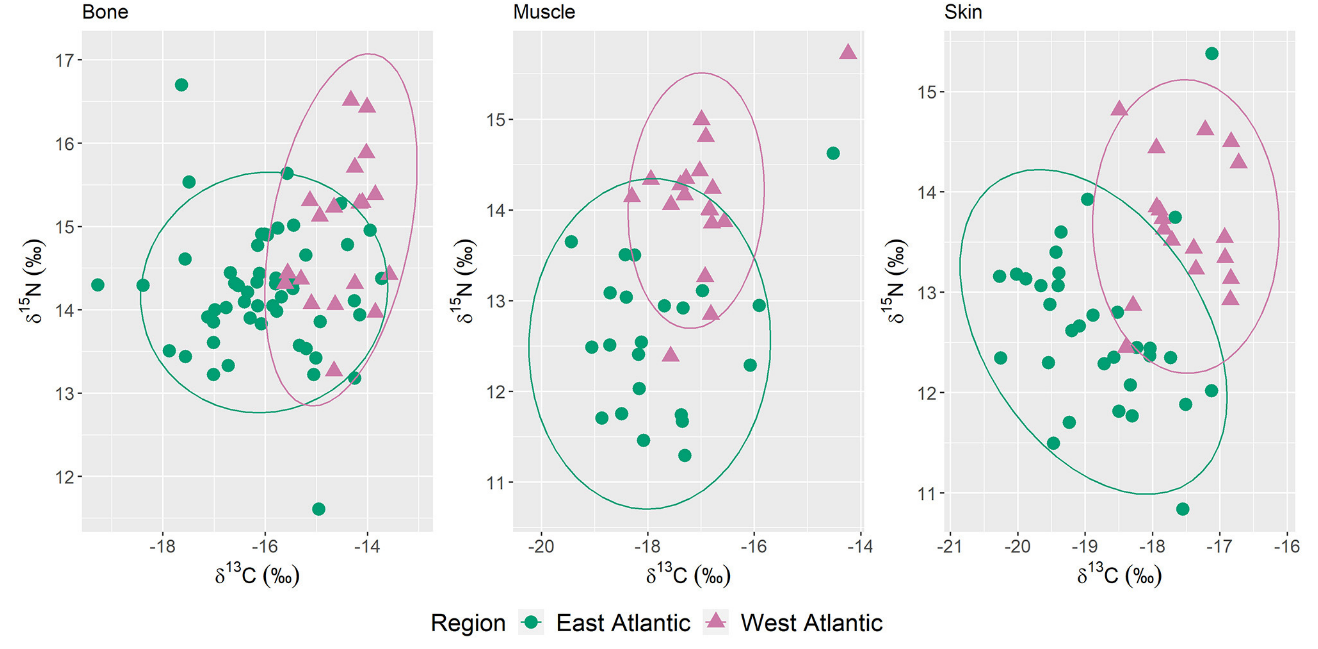

FIGURE 2 | $\delta^{13}C$ and $\delta^{15}N$ of bone ($n = 71$), muscle ($n = 40$), and skin ($n = 50$) samples from Sowerby's beaked whale specimens of opportunity collected 1980–2019. Ellipses are 95% normal confidence ellipses.

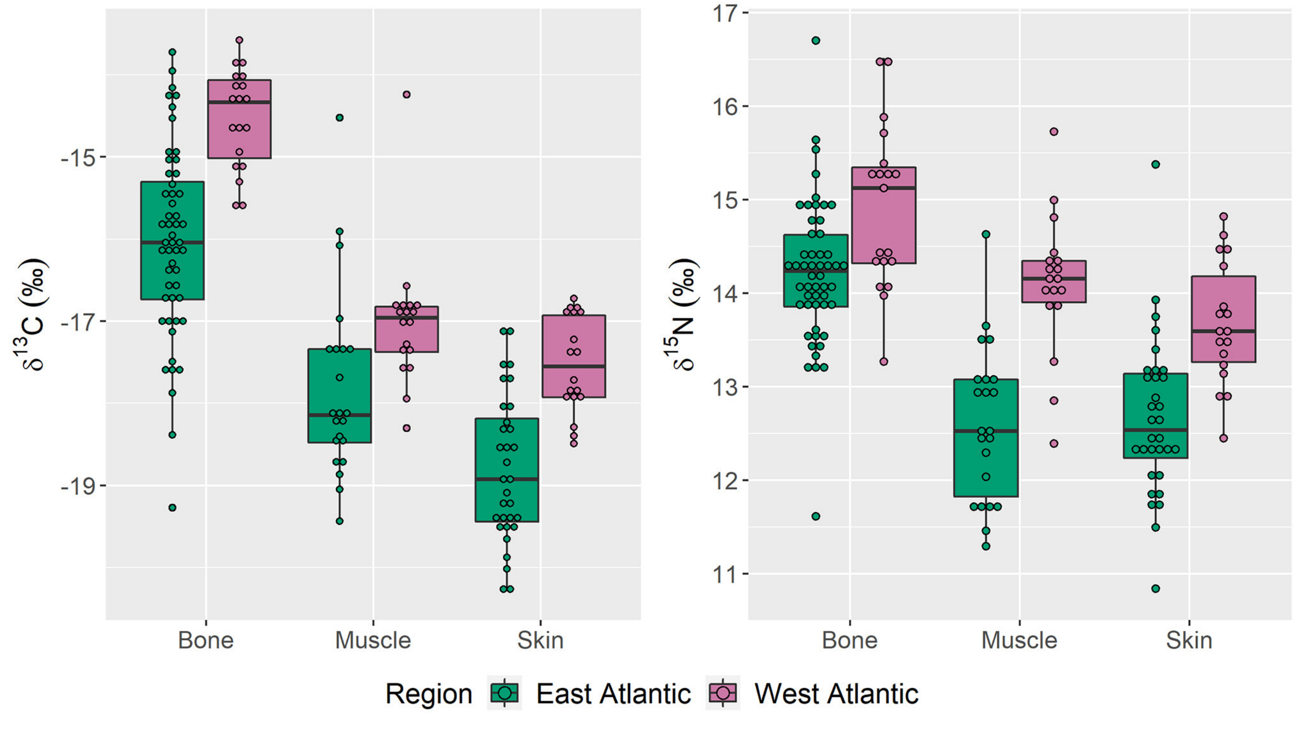

FIGURE 3 | $\delta^{13}C$ and $\delta^{15}N$ values from Sowerby's beaked whale specimens of opportunity collected in the east ($n = 64$) and west ($n = 38$) Atlantic Ocean basin, 1980–2019. Boxes present median and interquartile range and whiskers represent 95% confidence intervals.

demonstrated significant differences in median $\delta^{13}C$ and $\delta^{15}N$ values between east and west Atlantic samples in all three tissue types (**Table 1**).

Quadratic discriminant analysis assigned specimens to their collection location with a high degree of success (**Table 2A**). Analysis that simultaneously considered both $\delta^{13}C$ and $\delta^{15}N$

TABLE 1 | δ^{13}C and δ^{15}N values of Sowerby's beaked whale specimens of opportunity collected in the east and west Atlantic Ocean basin, 1980–2019.

Isotope	Tissue	East Atlantic				West Atlantic				*P*
		n	Median ‰	SD	Range ‰	*n*	Median ‰	SD	Range ‰	
δ^{13}C	Bone	52	−16.0	1.16	5.5	19	−14.5	0.60	2.0	<0.001
	Muscle	22	−18.1	1.15	4.9	18	−17.0	0.83	4.1	0.003
	Skin	32	−18.8	0.89	3.2	18	−17.5	0.59	1.8	<0.001
δ^{15}N	Bone	52	14.2	0.77	5.1	19	14.9	0.87	3.2	0.002
	Muscle	22	12.5	0.83	3.3	18	14.2	0.75	3.3	<0.001
	Skin	32	12.7	0.85	4.5	18	13.7	0.66	2.4	<0.001

P values pertain to Mann-Whitney U tests to evaluate differences in median tissue isotope values by region; P values <0.05 are significant.

TABLE 2 | Quadratic discriminant analysis assignment percent probabilities for δ^{13}C and δ^{15}N values of Sowerby's beaked whale specimens of opportunity collected in the east and west Atlantic Ocean basin, 1980–2019.

A. Quadratic discriminant analysis by tissue type

Tissue	*n*	Correct percent assignment			Simultaneous δ^{13}C and δ^{15}N misclassifications					
		δ^{13}C	δ^{15}N	δ^{13}C and δ^{15}N	*n*	East	West	Male	Female	Unknown sex
Bone	71	80.0	70.4	84.5	10	7	3	4	5	2
Muscle	40	75.07	82.5	90.0	4	2	2	1	3	0
Skin	50	78.0	77.8	92.0	4	2	2	1	1	1

B. Specimens correctly assigned across tissue combinations

Tissues sampled	*n*	Correctly assigned	Tissues misassigned across specimens
Bone, muscle, and skin	13	9	2 bone only, 1 muscle only, 1 muscle and skin
Bone and muscle	4	3	1 muscle only
Bone and skin	12	10	2 bone only
Muscle and skin	17	15	1 muscle only, 1 skin only

(A) *is individual and simultaneous δ^{13}C and δ^{15}N assignments per tissue type.* ***(B)*** *presents the results for tissue assignments in 46 specimens where more than* ***one*** *tissue type was available. This allowed us to explore intraspecimen variation in isotope assignments by evaluating combinations of tissues synthesized at different rates from the same specimen; 80.4% percent of specimens sampled for more than* ***one*** *tissue type were correctly assigned across tissue types.*

values was more successful at correctly assigning specimens than analysis of either isotope separately. Skin, muscle, and bone samples analyzed simultaneously for δ^{13}C and δ^{15}N were correctly assigned for 92.0, 90.0, and 84.5% of the samples, respectively. Single isotope assignment percent probabilities for all tissue types were >70.0% (70.4–82.5%; **Table 2A**). We found no consistent trends in sex, age, or collection location among misassigned samples. Of the 46 specimens sampled for more than one tissue type, simultaneous δ^{13}C and δ^{15}N quadratic discriminant analysis correctly assigned 80.4% ($n = 37$) to their collection location across all tissues (**Table 2B**).

DISCUSSION

Our results suggest that Sowerby's beaked whales exhibit short- and long-term regional site fidelity. The regional differences in δ^{13}C and δ^{15}N values across three tissue types with different growth and turnover rates imply these Sowerby's beaked whales were not only present in the region from which they were collected during the final months of their lives, but over a long-term, possibly decadal, scale. Exact tissue growth and turnover times are species-dependent and influenced by animal health and body condition, where the sample was taken from the carcass, and environmental factors such as temperature. These values are not known for Sowerby's beaked whales, or indeed for most cetaceans; however, we can make broad approximations based on other marine mammals, which experience similar ecophysiological pressures, and large terrestrial mammals (Newsome et al., 2010; Vander Zanden et al., 2015).

Stable Isotope Values by Tissue Type

Skin is the fastest growing tissue we evaluated, and the isotopic composition of skin proteins represent short-term movement and foraging behavior. Skin can be relatively easily sampled in wild cetacean populations using biopsy darts, its growth rate has been studied in bottlenose dolphins (*Tursiops truncatus*) and beluga whales (*Delphinapterus leucas*), and skin isotope incorporation rate has been studied in captive bottlenose dolphins and killer whales (*Orcinus orca*). Hicks et al. (1985)

estimated complete skin turnover in bottlenose dolphins at 73 days, while Aubin et al. (1990) found similar results (70–75 days) in beluga whales. Williams et al. (2008) found that captive bottlenose dolphins and killer whales fed controlled diets for 5–7 months had reached isotopic equilibrium in their skin and had isotope values that reflected their diets. Thus, we estimate the skin isotope signatures in the Sowerby's beaked whales in our study reflect habitat and foraging behavior ~3–7 months prior to sampling.

Skin samples from the east Atlantic had lower mean $\delta^{13}C$ values than those from the west Atlantic, a pattern which parallels the distribution of $\delta^{13}C$ values in Atlantic Ocean isoscape models (Magozzi et al., 2017). Nitrogen isotope values followed the same pattern, with east Atlantic samples showing lower $\delta^{15}N$ values than west Atlantic samples. The clear distinction in median $\delta^{13}C$ and $\delta^{15}N$ isotope values between east and west Atlantic specimens and the high assignment percent probabilities for simultaneous $\delta^{13}C$ and $\delta^{15}N$ values suggest that the animals in our study were living and foraging in the region from which they were collected several months prior to their deaths (**Tables 1**, **2**, **Figure 3**). This indicates these animals were not moving between the east and west Atlantic during the months prior to their collection, suggesting regional site fidelity on the order of months at a time.

Muscle is a more challenging tissue to study than skin due to the invasive nature required to collect samples, which is often limited to animals that have died and been opportunistically sampled, or to non-cetacean animals that have been sacrificed in feeding studies. As a result, there is a lack of information on cetacean muscle growth and isotope turnover time. Vander Zanden et al. (2015) found a positive correlation between body mass and isotope half-life in mammal muscle tissue, and muscle isotope turnover rate has been studied in cattle, which provide the best current approximation to Sowerby's beaked whale due to similar body mass (i.e., ~700 kg). Bahar et al. (2009) switched diets of beef cattle 5 months before slaughter and found that carbon and nitrogen isotopic equilibrium was not reached in that time, implying that muscle turnover time and isotopic integration in mammals of this size likely takes more than 5 months. They suggested it may take a year or more for sampled muscle tissue to reflect diet. For these reasons, we estimate that muscle isotope signatures in Sowerby's beaked whales reflect foraging and habitat use from about 1 year prior to sampling.

Muscle samples followed the same isotopic patterns as skin, with lower $\delta^{13}C$ and $\delta^{15}N$ values in whales from the east Atlantic compared with those from the west Atlantic (**Table 1**, **Figure 3**). These results suggest that animals were in the region of collection about 1 year prior to sampling. Combined with the shorter temporal snapshot of skin, muscle values strongly suggest that Sowerby's beaked whales are not frequently moving between regions, instead demonstrating regional site fidelity for 1 year or more.

No data are available on cetacean bone growth and turnover rates. However, in other large mammals, bone can represent a decade or more of growth and has a turnover rate of 3–10% per year in adults (Clarke, 2008; Charapata et al., 2018). Thus, bone tissue presents a consolidated isotopic signature from several years, making this the most complex tissue to analyze in our study. Despite this complexity, bone tissue followed the same patterns as skin and muscle, with lower $\delta^{13}C$ and $\delta^{15}N$ values in east Atlantic specimens and with distinct isotopic median values between regions (**Table 1**, **Figure 3**). Bone had the lowest simultaneous assignment percent probability; however, with an assignment percent probability of 84.5%, isotopic variation among specimens from the same region may reflect changing ecosystem isotope values rather than trans-Atlantic movement patterns (**Table 2A**). Ecosystem variables, such as the Atlantic meridional mode, which contributes to interannual and decadal variation in Atlantic Ocean sea surface temperature, the confluence of shallow and deep-water currents particularly in the western Atlantic, and globally changing $\delta^{13}C$ values due to the Suess effect, may drive within-region bone isotope variation (Reverdin et al., 2003; Hakkinen and Rhines, 2009; Doi et al., 2010; Lorrain et al., 2020). Additionally, Smith et al. (2020) found that Sowerby's beaked whale skeletons exhibit median intraskeletal $\delta^{13}C$ variation of ~4‰, which may explain some of the isotope variation and misassigned specimens in our study because we could not sample the occipital bone in 17 specimens. Thus, the bone isotopic values in our study demonstrate that bone tissue is largely being grown in a single geographic region, and even in this complex and slow-growing tissue, we see long-term east and west Atlantic site fidelity, with the possibility of infrequent broader movements.

Spatial Population Structuring

Distinct median $\delta^{15}N$ values were observed between east and west Atlantic specimens across tissue types, suggesting long-term differences in foraging locations between these groups (**Table 1**, **Figure 3**). Few data are available regarding Sowerby's beaked whale foraging, as most specimens strand without stomach contents. In the east Atlantic, stomach contents have been analyzed from specimens that were stranded in the Azores and the Bay of Biscay, where both studies found that small- to medium-sized mid-water fish species, such as hake and cod (e.g., *Micromesistius poutassou*, *Trisopterus* spp., and *Merluccius merluccius*), comprised the majority of stomach contents (Pereira et al., 2011; Spitz et al., 2011). In the west Atlantic, stomach contents from healthy Sowerby's beaked whales bycaught in the former pelagic driftnet fishery revealed similarities in prey items: fish comprised the majority of stomach contents, with short beard codling (*Laemonema barbatulum*), Cocco's lanternfish (*Lobianchia gemellarii*), marlin-spike grenadier (*Nezumia bairdii*), lanternfishes (*Lampanyctus* spp.), and longfin hake (*Phycis chesteri*) being the most abundant (Wenzel et al., 2013). Despite the similarities in types of prey items between east and west Atlantic specimens, the differences we observed in $\delta^{15}N$ values indicate that east and west Atlantic Sowerby's beaked whales demonstrate spatial variation in their foraging behavior and long-term fidelity in their foraging locations.

Distinct median $\delta^{13}C$ values in our specimens indicate long-term regional fidelity rather than continuous or seasonal movement throughout the Atlantic Ocean basin (**Table 1**, **Figure 3**). We observed a pattern of lower $\delta^{13}C$ values in whales sampled from the east Atlantic compared with the west Atlantic across tissue types; this trend is consistent with δ^{13}C isoscape models of the Atlantic Ocean basin (Magozzi et al., 2017; Trueman and St John Glew, 2019). Although we Suess-corrected our samples to account for the long-term increase in isotopically light carbon being incorporated into marine ecosystems due to fossil fuel use (Keeling, 1979; Sonnerup et al., 1999), recent studies have shown more extreme declines in some marine ecosystem δ^{13}C values than previously recorded (Lorrain et al., 2020). These changing regional δ^{13}C values could account for some of the δ^{13}C variation we observed among specimens collected from the same region; however, δ^{13}C values alone still successfully assigned >70% of the specimens across all tissue types to their collection region (**Table 2A**). The trends in δ^{13}C values in our samples aligned with trends in regional δ^{13}C isoscape values, suggesting that if it we had sufficient ecosystem data to account for environmental fluctuations in δ^{13}C values for these samples, assignment percent probability would increase.

Among the specimens sampled for more than one tissue type, simultaneous δ^{13}C and δ^{15}N discriminant analysis correctly assigned a high degree (80.4%, **Table 2B**) of specimens to their collection location across tissues. Analysis of combinations of tissues synthesized at different times from the same specimens provided an opportunity to explore intraspecimen variation in isotope assignments. Of the 46 specimens sampled for a combination of tissues, 37 were correctly assigned to their collection region across all tissue types. This indicates that these specimens were continuously living in the region of their collection prior to their deaths and that trans-Atlantic movements may be rare in this species, providing further insight into the long-term site fidelity patterns of these specimens. The results of this study provide the first stable isotope evidence for spatial structuring in Sowerby's beaked whale. Coupled with previously identified morphological differences in skull measurements (Smith et al., 2021), our results suggest that Sowerby's beaked whale exhibits a metapopulation structure of two or more populations with limited movement of individuals between regions. However, genetic analysis is also needed to further explore whether these are distinct population segments or if this is a panmictic species with habitat preference among individuals and regional mixing for mating.

The Atlantic Ocean basin is a complex ecosystem, and environmental factors such as seasonal productivity, temperature, and ocean currents likely influence Sowerby's beaked whale spatial distribution. Future studies focused on exploring the nuances of these factors, and on evaluating how Sowerby's beaked whale isotope values align with seasonally changing Atlantic isoscapes, are needed. East Atlantic specimens are better represented than west Atlantic specimens in our dataset; this may be due to multiple oceanic currents in the west Atlantic acting to carry distressed animals and carcasses away from shore. For example, the Gulf Stream may be carrying specimens east and out to sea, resulting in less stranded carcasses in the west Atlantic. We do not think that west Atlantic carcasses are being carried to strand in the east Atlantic, as the level of decomposition in many strandings had not progressed sufficiently to suggest long-term drift and the isotopic data suggest that it is unlikely. Similarly, in the east Atlantic, the North Atlantic Drift Current may explain why Sowerby's beaked whales strand in the British Isles, particularly in Scotland, with such a high frequency as compared with other locations.

CONCLUSIONS

Our results provide critical data regarding spatial structuring in Sowerby's beaked whale populations, demonstrate the value of specimens of opportunity for conservation science, and illustrate the usefulness of stable isotope analysis for elusive species research. The methods we used can be applied to other beaked whales, providing much needed information about this enigmatic group of animals. Due to the paucity of data on beaked whales in general, analysis of specimens of opportunity for some species may be the only way to garner sufficient baseline data to reliably inform future research and conservation plans for beaked whales. For beaked whales assumed to have large distributions, stable isotope analysis of specimens of opportunity can provide an efficient and inexpensive means to test this assumption and thus provide insight into population units or regional fidelity among groups or individuals.

Specimens of opportunity are vital sources of biological information regarding elusive species, and stable isotope analysis is an efficacious means of quickly generating data to address ecological questions. The methods used in this study can be applied to an array of other marine or terrestrial animals, narrowing the knowledge gap for elusive species and aiding in the development of conservation plans. Museum and research institutions often store multiple tissues from specimens of opportunity, and with the increase in frozen tissue repositories, researchers have access to multiple temporal snapshots and can reconstruct short- and long-term foraging and movement behavior. Our results demonstrate the usefulness of these samples to elusive species research and provide a framework to apply these methods to other species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

KS, CT, and MP conceived the study. CF and JS advised on the study design. AB, MD, ND, GG, KK, AK, BL, VL, HM, JO, RS, ZT, GV, and FW contributed the samples. KS, CF, and JS processed the samples for analysis. KS and MP analyzed the data. KS led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

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Emotions and Cultural Importance Predict the Acceptance of Large Carnivore Management Strategies by Maasai Pastoralists

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Management strategies to reduce human-carnivore conflict are most effective when accepted by local communities. Previous studies have suggested that the acceptance depends on emotions toward carnivores, the cultural importance of carnivores, and livestock depredation, and that it may vary depending on the types of strategies and carnivores involved. However, no study so far considered these factors simultaneously to compare their influence on the acceptance of management strategies. We quantified the predictive potential of these factors on the acceptance of three management strategies frequently applied to mitigate human-carnivore conflict: no action, relocation, and lethal control. We interviewed 100 members of the Maasai community in Ngorongoro Conservation Area in Tanzania. We used structured, closed questionnaires and focused on the three large carnivores involved in the most depredation regionally: spotted hyenas (*Crocuta crocuta*), lions (*Panthera leo*), and leopards (*Panthera pardus*). We found that the majority of respondents accepted no action and rejected relocation and lethal control for all three carnivores. The acceptance of the management strategies was strongly influenced by the emotion joy and by the cultural importance of carnivores, and the effects of joy and cultural importance were stronger than the effect of livestock depredation. We conclude that authorities should evaluate the emotions and cultural importance that local communities associate with carnivores when seeking to gain acceptance of management strategies and account for differences between species. Finally, we recommend that future human-carnivore coexistence studies should consider the socio-psychology of local communities and be done longitudinally to detect shifts in cultural, emotional, and ecological factors over time.

Keywords: large carnivores, emotions, human dimensions, livestock depredation, human-wildlife conflict, non-weird people, culture, pastoralism

INTRODUCTION

Local communities play a crucial role in conservation and determine whether wildlife can persist in shared landscapes (Kiss, 1990) and in protected areas adjacent to human settlements (Emerton and Mfunda, 1999; Mwakatobe et al., 2014). Fortress conservation, whereby local communities are expelled and excluded from a protected area's resources, has been suggested to be ineffective at reducing human-carnivore conflict (see glossary in **Table 1**) due to its adversarial nature and displacement of stakeholders (Hulme and Murphree, 1999; Galvin and Haller, 2008). In multi-use landscapes, where human communities reside alongside wildlife, neglecting the need for community support can exacerbate conflict, whereas implementing management strategies that communities accept can ameliorate conflict, enhance tolerance, and benefit wildlife (Catalano et al., 2019). Accordingly, it is important for authorities to seek community acceptance to ensure the sustainability and effectiveness of management strategies (**Table 1**).

Areas with large carnivores and pastoralists are of particular interest in human-wildlife conflict studies due to the potential for livestock depredation (Bagchi and Mishra, 2006) and attacks on humans (Shepherd et al., 2014). Despite these challenges, large carnivores are among the most culturally important and emotionally evocative animals to people who live alongside them (Bruskotter et al., 2017; Albert et al., 2018). Previous studies separately examined the effect of the emotions a species elicits, its importance to the local community's culture (hereafter "cultural importance") (**Table 1**), and the amount of livestock depredation it causes on the acceptance of management strategies to reduce conflict between humans and large carnivores. Negative emotions toward wildlife have been suggested to predict acceptance of management strategies that can kill or hurt them, whereas positive emotions have been suggested to predict acceptance of protective management strategies (Jacobs et al., 2014; Sponarski et al., 2015). In addition, the cultural importance placed on wildlife has been suggested to have a positive relationship with conservation-oriented management strategies (Frank, 2016). Other studies found that livestock depredation by large carnivores can predict whether people accept relocation and lethal control (Kaczensky, 1999; Gusset et al., 2009; **Table 1**). Many studies focused on one of the three factors and may have linked them to the acceptance of different management strategies, but did not compare them directly. It therefore remains unclear whether one factor is more influential than the other and should be prioritized for conflict mitigation.

We simultaneously assessed emotions, cultural importance, and livestock depredation to determine which has the greater predictive potential among the Maasai community in the Ngorongoro Conservation Area (NCA), Tanzania. We assessed whether the predictors differ for three large carnivore species—spotted hyenas (hereafter "hyenas"), lions, and leopards—to find the mechanism underlying the acceptance of three management strategies. These species were chosen because they are the primary livestock predators in Tanzania (Kissui, 2008; Mkonyi et al., 2017) and can pose a direct threat to human lives (Peterhans

TABLE 1 | Glossary of main concepts as applied in this study.

Concept	Definition	References
Acceptance	The degree to which someone agrees with, supports, or tolerates a situation or concept on a discrete scale or continuum. When applied to our seven-point scale, it describes cases where a respondent gave a score of > 4.	Treves and Naughton-Treves, 2005
Coexistence	A state in which humans and large carnivores occur in shared landscapes where human interactions with carnivores are governed by institutions that ensure long-term carnivore persistence, social legitimacy, and tolerable levels of risk.	Carter and Linnell, 2016
Cultural importance	The significance that a human community or ethnic group places on or associates with a wild animal; the degree to which the animal plays a role in the social practices, traditions, and/or rituals therein.	Schwartz, 2006
Disgust	An emotion in which a person feels intensely repulsed by the exposure to or the thoughts of a stimulus and wants it to be kept far away.	Rozin et al., 1999
Emotion	Transient, discrete neurological state in an individual brought on by external or internal stimuli. Associated with behavioral responses, physiological conditions, and indicative of a degree of pleasure or displeasure.	Ekman, 1999
Fear	An emotion in which a person feels threatened or intimidated by a stimulus out of a sense of danger.	Lang, 1985
Human-carnivore conflict	Interactions between humans and large carnivores that are deemed problematic, e.g., livestock depredation or man-eating.	Broekhuis et al., 2017
Joy	An emotion in which a person feels happy and positive due to a stimulus.	Watkins et al., 2018
Lethal control	The killing of a wild animal in an effort to reduce the number of wild animals and mitigate human-wildlife conflict, and/or protect domestic animals to improve human livelihoods.	Treves and Naughton-Treves, 2005
Management strategy	A policy implemented by a local governing body or authority to mitigate conflict between humans and carnivores.	Treves and Karanth, 2003
No action	Letting wild animals exist in their natural state without persecution, i.e., maintaining the conservation status quo.	Harcourt et al., 1986
Relocation	Moving a wild animal deemed as a nuisance to human livelihoods to another location in order to mitigate human-wildlife conflict.	McCoy and Berry, 2008
Tolerance	Human willingness to share landscapes with large carnivores.	Lischka et al., 2019

and Gnoske, 2001). Several studies have also suggested that, in other communities, there are differences in the emotions that people have toward the species (Sibanda et al., 2020), the cultural importance the species have (Gebresenbet et al., 2018), the extent of livestock depredation the species cause (Okello et al., 2014; Lichtenfeld et al., 2015), and how people want them managed (Mitchell et al., 2019). Each variable involves different psychological levels and pathways: emotions are linked to affective pathways (inferring feelings or emotions), cultural importance to cognitive pathways (inferring thoughts or beliefs; Healey and Grossman, 2018), and livestock depredation is largely external to individual control. By simultaneously investigating the predictive potential of these variables on the three carnivores, we can disentangle their respective effects, assess whether the differences hold true among the NCA Maasai, and understand the mechanisms that shape acceptance across the large carnivore guild. We studied the acceptance of no action, relocation, and lethal control, three management strategies commonly applied where large carnivores and humans co-occur (Linnell et al., 1997; Treves and Karanth, 2003; Karanth and Gopal, 2005; **Table 1**). All three management strategies have a precedent for being applied in the NCA and are within the mandate of the Ngorongoro Conservation Area Authority, the local governing body (Ikanda and Packer, 2008). Other management strategies for large carnivores (e.g., compensation, improved construction of livestock corrals, or accompanying livestock on foot) have also been applied in the NCA, but we opted to select these three as they are the most commonly used in our study area and are more widely applicable to other study areas, irrespective of their expected effectiveness (Van Eeden et al., 2018).

Previous studies have suggested that animals can trigger emotions in people that can predict the acceptance of management strategies (Gore et al., 2009; Jacobs, 2009). For example, the positive emotion joy (**Table 1**) predicted the acceptance of the protection of chipmunks in Italy (Cerri et al., 2020). Negative emotions can also predict management strategy acceptance. Disgust and fear (**Table 1**) toward carnivores have been suggested to undermine conservation efforts and be more significant drivers of human-carnivore conflict than livestock depredation (Dickman, 2010). In communities bordering Iguaçu National Park, Brazil, fear of pumas (*Puma concolor*) was found to be lower than fear of jaguars (*Panthera onca*); the presence of jaguars was rejected while the presence of pumas was accepted (Conforti and de Azevedo, 2003). Lions were found to bring negative emotions among farmers in Zimbabwe which in turn predicted how accepting they were of protective management strategies toward lions (Sibanda et al., 2020). Hyenas tend to bring about negative emotions across human communities, which in turn may drive a desire to see them killed (Glickman, 1995). We predicted that joy would be a negative predictor of relocation and lethal control, and a positive predictor of the acceptance of no action. In contrast, we predicted that disgust and fear would be positive predictors of relocation and lethal control and negative predictors of no action.

The cultural importance of a wildlife species can have ramifications on how likely people are to accept different management strategies (Dickman, 2010). The more culturally important or iconic a species is, the more likely a community is to accept protective management strategies for the species and the less likely they are to accept lethal control or other invasive management strategies. The high cultural importance of the lion has been suggested to have led to a general acceptance of lion conservation among the Maasai (Hazzah et al., 2019). High cultural importance placed on blackbuck antelope (*Antilope cervicapra*) among the Bishnoi in India was also found to predict their acceptance of conservation of that species (Hall and Chhangani, 2015). In Australia, cultural importance was found to be a negative predictor for the acceptance of lethal control of koalas (*Phascolarctos cinereus*) (Drijfhout et al., 2020). Communities also may place different cultural importance on different species of large carnivore. For example, a study in Kenya found that leopards were more culturally important to the Samburu community than African wild dogs, which in turn predicted the differing acceptance of the protection of the two species (Mitchell et al., 2019). Thus, to understand the relationship between cultural importance and the acceptance of different management strategies for wildlife, it is important to recognize inter-specific differences in perception. We predicted that cultural importance would be a positive predictor of acceptance of no action and a negative predictor of acceptance of relocation and lethal control.

The focus of human-carnivore conflict studies has traditionally been livestock depredation, which has also been suggested to predict the acceptance of management strategies. Depredation was found to have a positive correlation with lethal control of carnivores in South Africa (Daly et al., 2006). After disease, hyenas were found to be the second-most important source of livestock loss, and communities which suffered more livestock depredation by carnivores were more likely to accept lethal control in Tanzania (Nyahongo, 2007). Livestock depredation was also a positive predictor of acceptance of lethal control of Brazilian carnivores (Engel et al., 2016). We predicted that reported livestock depredation, i.e., perceived conflict, would be a significant negative predictor of the acceptance of no action and a significant positive predictor of the acceptance of relocation and lethal control.

MATERIALS AND METHODS

Study Area

This study took place in the NCA located in Tanzania (03°12′36″S 35°27′36″E; **Figure 1**). The NCA is a multi-use protected area and United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site noted for its high density of large mammals and popularity as a tourist destination (Charnley, 2005). It is inhabited by members of the Maasai tribe, a semi-nomadic pastoralist ethnic group that ranges from central Kenya to southern Tanzania (Fratkin, 2001). The NCA has a double mandate to conserve wildlife while protecting the interests of the Maasai (Charnley, 2005). Within the NCA is the Ngorongoro Crater, a 300 km^2 volcanic caldera with high densities of both hyenas and lions on the Crater floor and leopards along the rim forests (Packer et al., 1991;

Höner et al., 2012). The wider NCA also supports populations of hyenas, lions, and leopards. The Maasai and cattle populations in the NCA have grown from ∼8,000 and 162,000 upon the establishment of the NCA in 1959 to ∼93,000 and 243,000, respectively, as of 2017, putting them at increased risk of conflict with carnivores (National Bureau of Statistics Tanzania, 2017).

Survey

Our survey instrument included five sections with closed questions. Section 1 focused on livestock depredation. Respondents were asked to report the average number of cattle, sheep, goats, and donkeys that they lost annually over the past 3 years due to depredation by hyenas, lions, and leopards and to drought/disease. Section 2 focused on a set of Wildlife Value Orientations (Manfredo et al., 2009). Sections 3–5 were used to score the cultural importance of, emotions (joy, disgust, and fear) toward, and the acceptance of three management strategies (no action, relocation, and lethal control) for each carnivore. Sections 2–5 relied on the usage of a discrete, numeric scale, where respondents would respond to a prompt and give a score between 1 (strongly disagree/reject) and 7 (strongly agree/accept). Section 6 focused on socio-demographic factors. Due to the Cronbach's Alpha (internal consistency) scores for the domination ($\alpha = 0.15$) and mutualism ($\alpha = 0.67$) dimensions of Wildlife Value Orientations falling below the critical threshold of 0.70, they were not included in our study. Furthermore, other prompts in the questionnaire were not included in the analyses for this study; they were not the focus of this comparative study on the predictive potential of different and often separately tested variables.

We first tested the survey instrument and explored the suitability of using selected items with the Maasai in a pilot survey conducted in February 2018 with 20 participants in Ngorongoro ward (**Supplementary Material**, Appendix A). The main survey (**Supplementary Material**, Appendix B) was then undertaken in March 2019 with 100 respondents. Respondents who participated in the pilot survey were not interviewed again for the main survey. The beginning and end time, ward, and geographic coordinates were noted for each questionnaire while further information such as the respondents' names were not included to maintain anonymity.

To accurately represent the local community, the 100 questionnaires were split between 50 men and 50 women and categorized into the following age sets: *endasati* ($n = 25$) and *siangiki* (25) for elder and young women, respectively, and *ilmoruak* ($n = 17$), *korianga* ($n = 17$), and *morani* ($n = 16$) for elder, middle-aged, and young men, respectively (McCabe et al., 2014; National Bureau of Statistics Tanzania, 2017). On each survey day, we visited pre-selected wards (**Figure 1**) and walked through the villages until an individual suspected to be of a target demographic was randomly sighted and approached between 08:00 h and 18:00 h. The aim of the survey was introduced and respondents were asked if they consented to participation and to state their age class and gender. Each respondent represented a single household. Owing to low literacy amongst the Maasai in the NCA (Goldman and Milliary, 2014), questionnaire items were read aloud, translated into Maa—their native language—and responses again translated from Maa to English, then recorded on a printed questionnaire copy. Participation by respondents was voluntary and unpaid. Each respondent was then presented with photographs of the three carnivores in this study as well as the African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), and striped hyena (*Hyaena hyaena*), three carnivores that are transient in the parts of the NCA we covered (Kennedy and Kennedy, 2014). Respondents were asked to name the carnivores; all 100 respondents accurately identified the carnivores.

Quantification of Livestock Depredation

We quantified herd size and livestock loss based on the number of heads of each species of livestock owned by each respondent and on the number of heads that died. Total financial loss incurred by each respondent was calculated by multiplying the number of heads of the livestock species lost by their per capita financial value on the local market. At the time of the study, NCA market prices for cattle, sheep, goats, and donkeys were TSH 400 000 (USD 174), TSH 110 000 (USD 48), TSH 110 000 (USD 48), and TSH 200 000 (USD 87), respectively. Proportional financial loss was then calculated by dividing the total financial value lost to the particular carnivore divided by the financial value of the livestock owned by the respondent prior to the loss. We used proportional financial loss (hereafter "livestock depredation") instead of the raw number of livestock heads that died as a predictor because (i) the market value differs between livestock species and may impact the perception of livestock depredation by respondents, (ii) herd size varies greatly in the NCA (this study; National Bureau of Statistics Tanzania, 2017), and (iii) the relative cost of livestock depredation may matter more than the absolute cost in shaping the perception of an experience as negative (Mkonyi et al., 2017). For an overview of the number of heads of the different livestock species that were killed by the different carnivores and the ensuing financial costs, see **Supplementary Table 1**.

Data Analyses

Statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020). The threshold for statistical significance was set to $\alpha = 0.05$, and data are presented as mean ± S.E. unless stated otherwise.

We compared the scores for the emotions of joy, disgust, and fear each carnivore elicited and their cultural importance using Friedman rank sum tests and Dunn *post-hoc* pairwise multiple comparisons with Bonferroni corrected p-values (package "dunn.test"; Dinno, 2017). Responses to the prompts on emotions, cultural importance, and the acceptance of management strategies were plotted as diverging stacked bar plots (package "likert"; Bryer and Speerschneider, 2016).

The livestock depredation caused by each carnivore (independent variable with three levels: hyena, lion, and leopard) was compared using a generalized linear mixed effects model (GLMM), with a beta distribution and logit link (package "glmmTMB"; Brooks et al., 2017; Douma and Weedon, 2019). Proportions (for the response variable, livestock depredation)

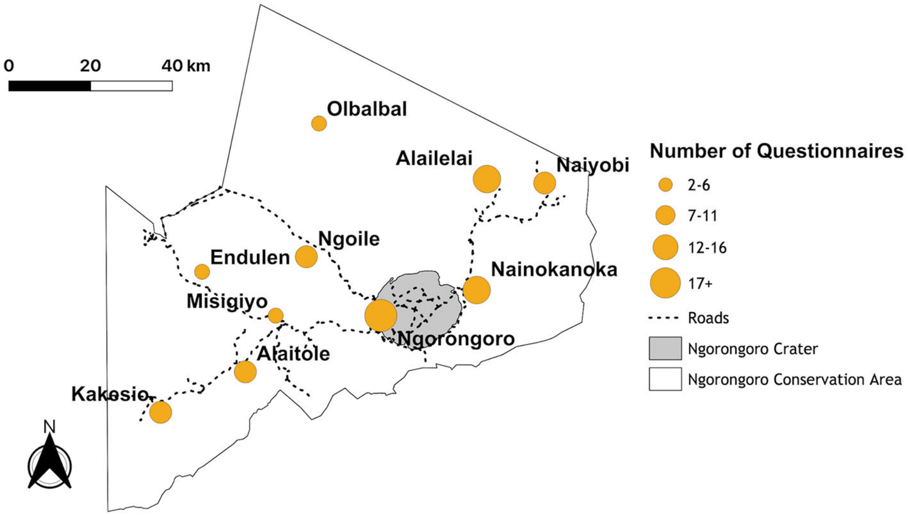

FIGURE 1 | Location and distribution of the 100 questionnaires conducted in the Maasai community living in Ngorongoro Conservation Area, Tanzania. The size of the orange circles indicates the number of questionnaires conducted within each of the ten labeled wards.

were transformed using the formula for beta distributions with values that include 0 and/or 1: $y^*(n - 1) + 0.5)/n$, where y is the original proportion and n is the sample size (100 respondents * 3 carnivores = 300) (Cribari-Neto and Zeileis, 2009). Because each respondent was assigned a value for livestock depredation pertaining to each carnivore, data included repeated measures. We therefore included the unique identifier for each respondent as a random factor.

The influence of the type of management strategy (no action, relocation, lethal control), the carnivore species (hyena, lion, leopard), emotions (joy, disgust, fear), cultural importance, and livestock depredation on the acceptance scores was tested using an ordinal logistic regression (OLR) model (function "clmm" in package "ordinal"; Christensen, 2019). We included an interaction term between management strategy and all other covariates to disentangle and quantify the effects of the predictors. The identity of the respondent (100 levels) was included as a random factor.

To avoid multicollinearity, numeric predictors were centered at their means using function "center.numeric" from the package "psycholing" (Fraundorf, 2020). All predictors fell below the critical variance inflation factor (VIF) threshold of 10 (package "HH"; James et al., 2013; Heiberger, 2020). Note that most studies involving a Likert-type dependent variable, i.e., a score on a discrete ordinal scale, traditionally conduct ordinary least-squares regressions (OLS) (Bishop and Herron, 2015; Bürkner and Vuorre, 2019). When applied to ordinal scores, metric models such as OLS assume that spacing between each score is the same, e.g., that a switch from 1 to 2 involves the same cognitive process as a switch from score 4–5 on a seven-point scale. This assumption is likely to be violated (Liddell and Kruschke, 2018). OLR, which allows for cognitive flexibility and account for the ordered nature of Likert-type data, are therefore more appropriate (Harrell, 2015).

The significance of the effects of each focal predictor and the interaction terms on acceptance was assessed using likelihood ratio tests (function "anova" in package "stats;" R Core Team, 2020). The likelihood ratio tests determined the marginal contribution of the focal predictor to the full model by comparing the fit of the full model with that of a reduced model with the focal predictor removed.

Both the GLMM and OLR models generated estimates as log(odds) which we converted to odds ratios and 95% confidence intervals using the function "exp(confint(model))" for ease of interpretation. Odds ratios > 1 and odds ratios < 1 indicate a relative increase and decrease, respectively, in the likelihood of the dependent variable to increase by one unit when the predictor variable increases by one unit. For example, if the odds ratio for a given predictor in the OLR is 1.50, then a one-unit increase in the predictor (e.g., from 4 to 5) leads to the probability of an increase (e.g., from score 4 to score 5) in acceptance being 50% higher when all other variables in the OLR are held constant. In the case of the livestock depredation GLMM, a one-unit "increase" in the predictor refers to a switching of the carnivore species—the reference species was set as the hyena, so a one-unit "increase" in this model refers to a shift in the predictor from hyena to lion or leopard. The OR expressed therefore refers to the odds of livestock depredation increasing when hyenas are replaced by lions or leopards. An OR > 1 would therefore mean that the focal species causes more livestock depredation than hyenas, and the opposite would be true for an OR < 1. Further information on how to construct and interpret OLR using the "clmm" function can be found in Lorenzo-Arribas (2019, p. 57–71). Cumulative predicted probabilities of acceptance (score > 4) of the management strategies as a function of the different predictors were calculated based on the OLR with the package "emmeans" (Lenth, 2021) and then plotted using the package "ggplot2" (Wickham, 2016).

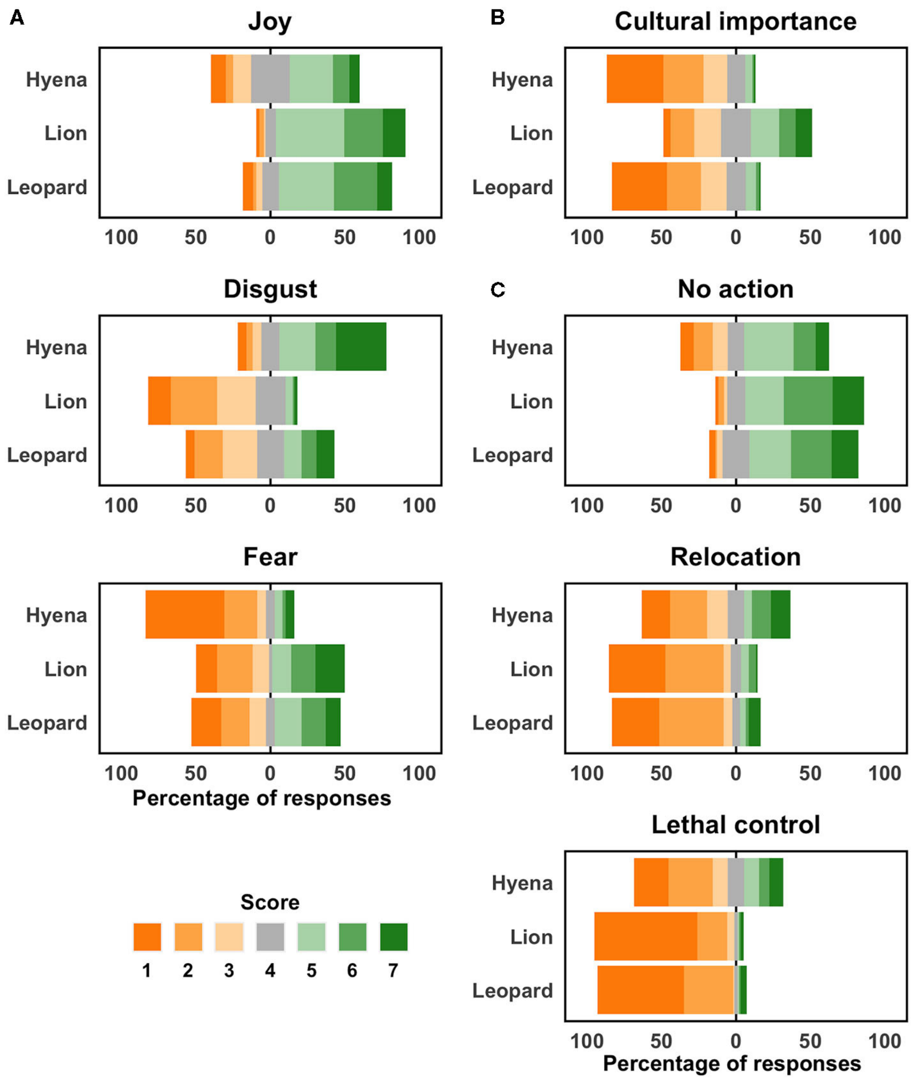

FIGURE 2 | Distribution of scores (percentage of responses) for the emotions joy, disgust, and fear **(A)**, cultural importance **(B)**, and the acceptance of the management strategies no action, relocation, and lethal control **(C)** toward hyenas, lions, and leopards by Maasai pastoralists in Ngorongoro Conservation Area, Tanzania. Data correspond to scores on a seven-point scale in questionnaires ($n = 100$). Diverging stacked bar plots display the distribution of scores ranging from 1 (strongly disagree/reject) to 7 (strongly agree/accept), with 4 representing a neutral score. The left side (orange range) of the figure shows the percentage in disagreement and the right side (green range) the percentage in agreement with the prompt.

RESULTS

Emotions

47% of respondents felt joy toward hyenas (score > 4), compared to 87% for lions and 76% for leopards (**Figure 2A**). 72% of respondents found hyenas disgusting (score > 4), compared to 8% for lions and 34% for leopards. 13% of respondents feared hyenas (score > 4), in contrast to 49% for lions and 44% for leopards. Scores for the emotions differed significantly between carnivores (Friedman test; joy: $\chi^2 = 41.58$, $df = 2$, $p < 0.001$; disgust: $\chi^2 = 88.10$, $df = 2$, $p < 0.001$; fear: $\chi^2 = 70.54$, $df = 2$, $p < 0.001$). Hyenas brought less joy ($\text{median}_{\text{hyena}} = 4.0$) than both lions ($\text{median}_{\text{lion}} = 5.0$, $p < 0.001$) and leopards ($\text{median}_{\text{leopard}} = 5.0$, $p < 0.001$). There was no difference in joy toward lions and leopards ($p = 0.26$). Respondents felt greater disgust toward hyenas ($\text{median}_{\text{hyena}} = 5.0$) than to both lions ($\text{median}_{\text{lion}} = 3.0$; $p < 0.001$) and leopards ($\text{median}_{\text{leopard}} = 4.0$; $p < 0.001$), and greater disgust toward leopards than lions ($p < 0.001$). Hyenas were feared less ($\text{median}_{\text{hyena}} = 1.0$) than both lions ($\text{median}_{\text{lion}} = 4.0$, $p < 0.001$) and leopards ($\text{median}_{\text{leopard}} = 3.5$, $p < 0.001$), whereas fear of lions and leopards did not significantly differ ($p = 0.39$).

Cultural Importance

7% of respondents found hyenas culturally important (score > 4), compared to 41% for lions and 10% for leopards (**Figure 2B**). Respondents attributed different cultural importance to the carnivores ($\chi^2 = 90.08$, $df = 2$, $p < 0.001$). Hyenas were seen as culturally unimportant overall ($\text{median}_{\text{hyena}} = 2.0$) and less culturally important than lions, which were seen as neither culturally important or unimportant ($\text{median}_{\text{lion}} = 4.0$; $p < 0.001$). There was no difference in cultural importance between hyenas and leopards ($\text{median}_{\text{leopard}} = 2.0$; $p = 0.85$). Leopards were seen as less culturally important than lions ($p < 0.001$).

Livestock Composition and Depredation

All respondents belonged to a household that owned livestock, with a mean of 137.4 ± 26.8 heads of livestock per household. Nearly all respondents (97%) owned herds that were composed of at least two species. Respondents owned a mean of 40.2 ± 5.4 cattle, 70.9 ± 20.4 sheep, 23.0 ± 3.6 goats, and 3.3 ± 0.5 donkeys. The carnivores differed in the livestock depredation they caused. Compared to hyenas (beta GLMM; OR = 0.14, $\text{CI}_{95\%} = 0.11$–0.16, $p < 0.001$), both lions (OR = 0.25, $\text{CI}_{95\%} = 0.19$–0.33, $p < 0.001$) and leopards (OR = 0.35, $\text{CI}_{95\%} = 0.27$–0.45, $p < 0.001$) caused less livestock depredation. Lions also caused less livestock depredation than leopards (OR = 0.72, $\text{CI}_{95\%} = 0.55$–0.94, $p = 0.016$). Hyenas accounted for a mean of 13.4 ± 1.3% of livestock depredation, lions 1.9 ± 0.3%, and leopards 4.1 ± 0.7% (**Supplementary Figure 1**).

Acceptance of Management Strategies

The majority of respondents accepted (score >4) no action for all three carnivores (hyenas: 57%, lions: 80%, leopards: 73%; **Figure 2C**). In contrast, both relocation and lethal control were mostly rejected (relocation: hyenas: 31%, lions: 11%, leopards: 14%; lethal control: 26%, 4%, and 6%).

Management strategy (OLR, likelihood ratio test; LR = 563.22, $p < 0.001$) and carnivore species (LR = 36.82, $p < 0.001$) had significant effects on acceptance scores (**Figure 3**; **Table 2**). Acceptance of no action was similar for all three carnivore species. In contrast, acceptance scores of relocation and lethal control were higher for hyenas than for lions and leopards (**Supplementary Tables 2**, **3**). There was no difference in acceptance scores of relocation and lethal control between lions and leopards (**Supplementary Table 4**).

Emotions had a significant effect on the acceptance score of management strategies (LR = 97.80, $p < 0.001$). Joy had a strong effect (LR = 68.31, $p < 0.001$), disgust a weak effect (LR = 7.20, $p = 0.066$) and fear no effect (LR = 3.94, $p = 0.27$) (**Table 2**; **Figure 4A**). The effect of joy differed between the management strategies (**Table 2**). It had a strong, positive effect on the acceptance of no action and a negative effect on the acceptance of relocation and lethal control. When the joy score changed from 1 to 7, predicted acceptance changed from 27% ($\text{CI}_{95\%}$: 14–40%) to 83% ($\text{CI}_{95\%}$: 77–89%) for no action, from 26% ($\text{CI}_{95\%}$: 14–39%) to 14% ($\text{CI}_{95\%}$: 8–19%) for relocation and 37% ($\text{CI}_{95\%}$: 21–53%) to 2% ($\text{CI}_{95\%}$: 1–4%) for lethal control (**Figure 4A**). The effect of disgust also differed between the management strategies (**Table 2**). It had no significant effect on the acceptance of no action and relocation but a weak, positive effect on the acceptance of lethal control. When the disgust score changed from 1 to 7, predicted acceptance changed from 71% ($\text{CI}_{95\%}$: 61–80%) to 60% ($\text{CI}_{95\%}$: 49–71%) for no action, from 15% ($\text{CI}_{95\%}$: 8–21%) to 21% ($\text{CI}_{95\%}$: 14–29%) for relocation and 5% ($\text{CI}_{95\%}$: 2–7%) to 12% ($\text{CI}_{95\%}$: 6–17%) for lethal control (**Figure 4A**).

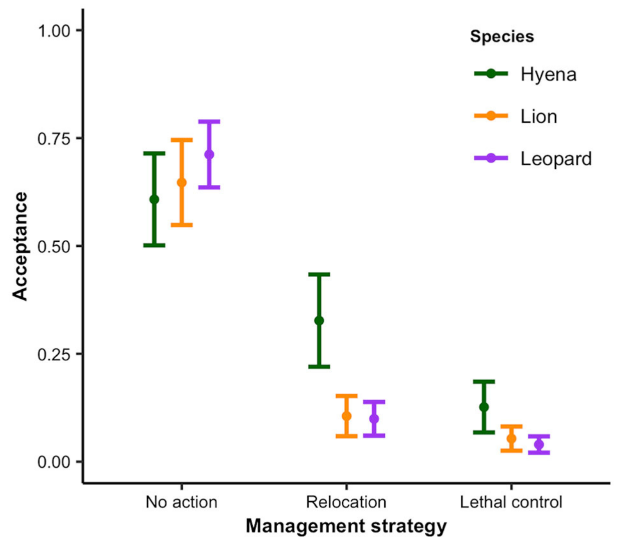

FIGURE 3 | Cumulative predicted probability of the acceptance (score > 4) of no action, relocation, and lethal control as management strategies toward hyenas, lions, and leopards by Maasai pastoralists in Ngorongoro Conservation Area, Tanzania. Points represent mean predicted probabilities from an ordinal logistic regression model and bars represent the 95% confidence intervals when continuous predictors are held at their population means.

Cultural importance had a significant effect on the acceptance of management strategies (LR = 20.39, $p < 0.001$; **Table 2**). It was positive for no action and weakly negative for relocation and lethal control. When the score for cultural importance changed from 1 to 7, predicted acceptance changed from 58% ($\text{CI}_{95\%}$: 50–66%) to 79% (69–89%) for no action, from 23% ($\text{CI}_{95\%}$: 17–29%) to 9% ($\text{CI}_{95\%}$: 4–15%) for relocation, and from 11% ($\text{CI}_{95\%}$: 7–15%) to 3% ($\text{CI}_{95\%}$: 1–5%) for lethal control (**Figure 4B**).

Livestock depredation had a significant effect on the acceptance of management strategies (LR = 14.17, $p = 0.003$; **Table 2**). It had no effect on no action and lethal control but a negative effect on relocation. When proportional financial loss (livestock depredation) changed from 0.0 to 0.8, predicted acceptance changed from 65% ($\text{CI}_{95\%}$: 59–71%) to 73% ($\text{CI}_{95\%}$: 40–100%) for no action, from 22% ($\text{CI}_{95\%}$: 17–27%) to 1% ($\text{CI}_{95\%}$: 0–2%) for relocation and 8% ($\text{CI}_{95\%}$: 5–11%) to 0% ($\text{CI}_{95\%}$: 0–1%) for lethal control (**Figure 4C**).

DISCUSSION

Our results suggest that the Maasai pastoralists living in the NCA are generally against the relocation and lethal control of large carnivores. Our results further suggest that the acceptance of management strategies is strongly influenced by emotions and cultural importance and that emotions and cultural importance are stronger predictors of the acceptance of management strategies than livestock depredation. These

TABLE 2 | Variation in acceptance scores by Maasai pastoralists as a function of management strategies, carnivore species, emotions, cultural importance, and livestock depredation.

Predictor	OR	CI$_{95\%}$	*p*
Threshold coefficients			
1|2	0.04	0.03–0.07	-
2|3	0.21	0.13–0.33	-
3|4	0.34	0.21–0.53	-
4|5	0.65	0.41–1.01	-
5|6	1.71	1.10–2.68	-
6|7	5.62	3.48–9.06	-
Management strategies			
Relocation	**0.31**	**0.17–0.59**	**<0.001**
Lethal control	**0.09**	**0.05–0.18**	**<0.001**
Species			
Lion	1.18	0.60–2.37	0.64
Leopard	1.59	0.89–2.85	0.12
Emotions			
Joy	**1.55**	**1.31–1.82**	**<0.001**
Disgust	0.92	0.81–1.06	0.24
Fear	1.03	0.93–1.14	0.59
Cultural importance	**1.19**	**1.04–1.36**	**0.013**
Livestock depredation	1.57	0.17–14.97	0.70
Interaction terms			
Relocation*Lion	**0.21**	**0.07–0.57**	**0.002**
Lethal control*Lion	**0.33**	**0.11–0.96**	**0.042**
Relocation*Leopard	**0.14**	**0.06–0.34**	**<0.001**
Lethal control*Leopard	**0.18**	**0.07–0.44**	**<0.001**
Relocation*Joy	**0.56**	**0.44–0.71**	**<0.001**
Lethal control*Joy	**0.37**	**0.29–0.48**	**<0.001**
Relocation*Disgust	1.18	0.97–1.44	0.10
Lethal control*Disgust	**1.28**	**1.05–1.57**	**0.017**
Relocation*Fear	1.05	0.91–1.21	0.53
Lethal control*Fear	0.90	0.76–1.05	0.17
Relocation*Cultural importance	**0.70**	**0.57–0.85**	**<0.001**
Lethal control*Cultural importance	**0.67**	**0.54–0.83**	**<0.001**
Relocation*Livestock depredation	**0.01**	**0.00–0.19**	**0.003**
Lethal control*Livestock depredation	0.22	0.01–6.59	0.39

Shown are the odds ratios (OR), their associated 95% confidence intervals (CI$_{95\%}$), and p-values for each predictor, as derived from an ordinal logistic regression model (individual-level random effect variance = 0.07). OR > 1 and OR < 1 indicate a relative increase and decrease, respectively, in the acceptance score associated with a 1-unit increase or shift in the focal predictor when all other covariates are held constant at their population mean or reference level. The reference carnivore species is the hyena and the reference management strategy is no action. Threshold coefficients refer to the cumulative probability that an acceptance score is at or below the threshold cut point, e.g., the OR for the threshold 2|3 compares the probability of the acceptance score falling within the range of 1–2 to the probability of the acceptance score falling within the range of 3–7. Data in bold were deemed significant ($p < 0.05$).

variables had the most significant results and had large effect sizes. The effect of emotions was mostly driven by joy: a positive effect on no action and a negative effect on relocation and lethal control, as predicted. The effects of the positive emotion joy are consistent with previous findings that suggested that joy is connected to a desire not to see animals killed or moved (Sponarski et al., 2015). Disgust had only a weak effect and fear had no significant effect on the acceptance of management strategies. The effect of cultural importance was positive for no action and negative for relocation and lethal control, as predicted. Despite controlling for several important predictors in our model, there was a significant difference in the acceptance of relocation and lethal control between the carnivores. These differences warrant further investigation to identify additional drivers of the inter-specific variation in acceptance of invasive management strategies within the large carnivore guild.

The key role of emotions and cultural importance as predictors of the acceptance of management strategies has potential conservation implications and applications. Being cognitive and affective variables, they are influenced by shifts in external factors. For emotions, our findings may facilitate

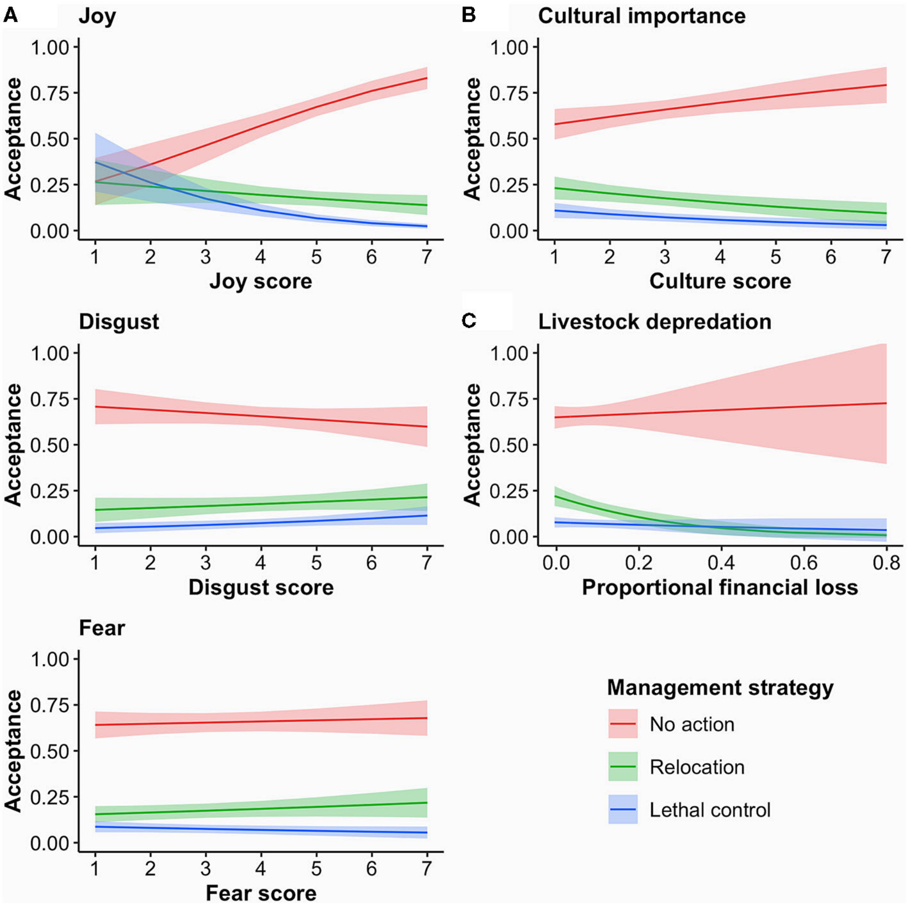

FIGURE 4 | Cumulative predicted probability of the acceptance (score > 4) of no action, relocation, and lethal control as management strategies toward hyenas, lions, and leopards by Maasai pastoralists in Ngorongoro Conservation Area, Tanzania. Plots show how emotions **(A)**, cultural importance **(B)**, and livestock depredation **(C)** influenced the acceptance of the management strategies. For emotions and cultural importance, scores range from 1 (strongly disagree/reject) to 7 (strongly agree/accept), with 4 representing a neutral score. For livestock depredation, the x-axis is limited to the range of observed values (0.0–0.8). Lines represent mean predicted probabilities from an ordinal logistic regression model and shading represents the 95% confidence intervals when continuous predictors are held at their population means and using the mean effect of the carnivore species.

local authorities' investment in outreach initiatives. We found that the positive emotion joy was a more important predictor of management strategy acceptance than the more negative emotions disgust and fear; we recommend an increased emphasis on positive emotions rather than the traditional focus on negative emotions toward wildlife (Espinosa and Jacobson, 2012). Education and awareness about predators can sometimes ameliorate negative emotions (Bruskotter and Wilson, 2014; Lyngdoh et al., 2017) and mitigate conflict due to improved knowledge of the risks and drivers of conflict (Treves and Karanth, 2003). As charismatic species such as lions continue to be represented positively, emotions toward these animals remain positive while negatively represented species continue to be subject to negative emotions (Albert et al., 2018). To incite change, it may be fruitful to depict hyenas positively in the NCA. For example, mentioning the value of social support in hyena society (Vullioud et al., 2019) may place them in a positive light due to the Maasai community's strong family focus (Kipuri, 2020) and further reduce the acceptance of relocation or lethal control of hyenas. Moreover, ecosystem services that hyenas provide as predators and scavengers may contribute to the control of diseases (O'Bryan et al., 2018) by reducing disease transmission within livestock herds and between wild herbivores and livestock (Stronen et al., 2007). This could also be highlighted as a benefit of having hyenas around. Such efforts can be put into place at workshops and outreach efforts for schoolchildren in order to instill positive emotions toward carnivores in Maasai community members from a young age (Mkonyi et al., 2017). There is a precedent for the efficacy of such efforts elsewhere, with children (Johansson et al., 2016) and adults alike (Breuer et al., 2020). The efficacy of such efforts can be enhanced by involving societal "influencers," e.g., elders with considerable reach and power (Veríssimo et al., 2019). Regardless, such efforts should only be done with collaborative, enthusiastic involvement from the community side and in a way that benefits local stakeholders (Berkes, 2004).

Regarding cultural importance, intergenerational change and concurrent sedentarism has been suggested to result in increased acceptance for wildlife conservation (Laverty et al., 2019). However, it may also lead to reduced physical, spiritual, or emotional contact with wildlife, e.g., by losing touch with traditional values and practices that bring humans and wildlife closer together. For example, lion killing by *moranis*, in a symbolic coming-of-age ceremony, has become rarer (Western et al., 2019) and may have reduced the importance of lions over time. This may explain the "neutral" median score lions received for cultural importance. In the NCA, the Maasai are required to live a traditional semi-nomadic lifestyle to protect wildlife habitats (Lawuo et al., 2014), which may limit shifts in the cultural importance of different carnivores. Capitalizing on the knowledge of the cultural importance of different carnivores and its predictive potential would enable authorities to influence the acceptance of different management strategies by easing or tightening current rules about lifestyles that are in place. It would therefore be prudent to collect long-term data on local scores for the cultural importance of wildlife to detect shifts over time, compare cultural importance scores between older and younger generations, and assess how scores change with different policies. It may also help to identify where and to what extent different management strategies will be accepted and be effective at limiting conflict, e.g., as with the Lion Guardians model in Kenya (Hazzah et al., 2019).

In contrast to our predictions, livestock depredation was only a significant predictor for the acceptance of relocation, and the relationship was negative. While this result may seem surprising, given that many Maasai are wholly dependent on their livestock (McCabe et al., 2014), several explanations may be valid. Firstly, with increasing livestock depredation, the predicted acceptance of relocation decreased to a point where it was strongly rejected. This may indicate that following higher rates of livestock depredation, the Maasai become wary of management strategies such as relocation which risk having the carnivores return again (McCoy and Berry, 2008). Secondly, disease and drought were much greater sources of livestock loss than livestock depredation by all three carnivores combined, which may buffer the effect of livestock depredation. It also may be partly due to the fact that the tourism industry is a source of employment for the Maasai community and may further mask the effects of livestock depredation (Homewood and Rodgers, 2004; Melita, 2014). It is also plausible that the Maasai in the NCA are accustomed to livestock depredation as an aspect of day-to-day life, as it has been unavoidable for generations. For instance, there may be an interplay between historical livestock depredation by hyenas and the negative emotions associated with them; once these long-term trends become entrenched in local perceptions, they may mask the effect of recent livestock depredation itself and instead be picked up by emotions. A similar result was found in Bangladesh, where livestock owners that were subject to the greatest perceived conflict with tigers (*Panthera tigris*) were the most tolerant of tigers; the authors posited that a greater focus on socio-psychological drivers of tolerance would have been useful to disentangle the effects of livestock depredation and other factors (Inskip et al., 2016). This lies in contrast to a study in Namibia which found that farmers tolerated carnivores the most in areas where livestock depredation was the lowest (Lindsey et al., 2013). However, the study did not assess how values or emotions that were already in place may have predicted tolerance or the acceptance of management strategies. We contend it is crucial to simultaneously consider socio-psychological factors such as emotions and cultural importance along with livestock depredation to assess which is more important as predictors of the acceptance of management strategies (Jacobsen et al., 2020). Further examination of the acceptance of other management strategies which we did not include but can also promote coexistence, such as improving livestock corrals or compensation schemes, may improve understanding of the predictive potential of livestock depredation in comparison to other factors.

It is worth recognizing that our approach—to begin by asking about livestock depredation and then going into emotions, cultural importance, and management strategies—may have introduced a bias by having respondents associating the carnivores with livestock loss. Despite this possibility, we argue that any potential effect was not severe, owing to the fact that the respondents displayed a general acceptance of no action toward the carnivores in our study, a rejection of relocation and lethal control, and views that are in accord with other studies on Maasai-carnivore relationships (Kissui, 2008; Goldman, 2011). Furthermore, livestock depredation ended up being a weak predictor, and only for one management strategy, despite being introduced first.

In summary, this study demonstrates the importance of assessing emotions and cultural importance in human-carnivore conflict studies and the importance of accounting for potential variations in acceptance of different management strategies and species. Our findings have affirmed the role of positive emotions in relation to human relationships with wildlife (Buijs and Jacobs, 2021) and confirmed the importance of considering both affective and cognitive factors (Dechner, 2021). They also question the widespread view that livestock depredation is the most important issue to focus on in human-carnivore studies. Further, we have highlighted the importance of considering the different emotions that people have toward species within the same guild—cultural and psychological factors may play a role. Specifically to the Maasai, we have underpinned the importance of different carnivores to their culture and their acceptance of different strategies, forming a basis for coexistence based on various factors. Because the effects of the factors may be direct and indirect (Teixeira et al., 2020), investigating these relationships may disentangle effects and help understand the complex processes associated with tolerance of wildlife and how human cognitions interact with ecological dimensions. In particular, it would be important to understand the interplay between the different factors in order to detect any mediating effects between predictors and their relationship with the acceptance of management strategies. Human-carnivore conflict remains a challenging and complex issue, but understanding the best predictors of the acceptance of management strategies paves the way for authorities to implement locally-accepted initiatives geared toward coexistence between people and wildlife.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are publicly available. This data can be found here: https://doi.org/10.6084/m9.figshare.14780058.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by The Tanzania Wildlife Research Institute, the Tanzania Commission for Science and Technology, and the Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research under approval number 2018-01-03. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

Conceptualization: AD, ED, MJ, TS, and OH. Methodology: AD, ED, MJ, JN, TS, and OH. Formal analysis: AD and TS. Investigation: AD and JN. Resources: JN and OH. Data curation: AD. Writing of original draft: AD, ED, TS, and OH. Review and editing of draft: AD, ED, MJ, TS, and OH. Supervision: TS and OH. Project administration: AD, JN, and OH. Funding acquisition: AD and OH. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.691975/full#supplementary-material

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Proximate Causes of Forest Degradation in the Democratic Republic of the Congo Vary in Space and Time

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Forest degradation, generally defined as a reduction in the delivery of forest ecosystem services, can have long-term impacts on biodiversity, climate, and local livelihoods. The quantification of forest degradation, its dynamics and proximate causes can help prompt early action to mitigate carbon emissions and inform relevant land use policies. The Democratic Republic of the Congo is largely forested with a relatively low deforestation rate, but anthropogenic degradation has been increasing in recent years. We assess the impact of eight independent variables related to land cover, land use, infrastructure, armed conflicts, and accessibility on forest degradation, measured by the Forest Condition (FC) index, a measure of forest degradation based on biomass history and fragmentation that ranges from 0 (completely deforested) to 100 (intact). We employ spatial panel models with fixed effects using regular 25 × 25 km units over five 3-year intervals from 2002 to 2016. The regression results suggest that the presence of swamp ecosystems, low access (defined by high travel time), and forest concessions are associated with lower forest degradation, while built up area, fire frequency, armed conflicts result in greater forest degradation. The impact of neighboring units on FC shows that all variables within the 50 km spatial neighborhood have a greater effect on FC than the on-site spatial determinants, indicating the greater influence of drivers beyond the 25 km^2 unit. In the case of protected areas, we unexpectedly find that protection in neighboring locations leads to higher forest degradation, suggesting a potential leakage effect, while protected areas in the local vicinity have a positive influence on FC. The Mann-Kendall trend statistic of occurrences of fires and conflicts over the time period and until 2020 show that significant increases in conflicts and fires are spatially divergent. Overall, our results highlight how assessing the proximate causes of forest degradation

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with spatiotemporal analysis can support targeted interventions and policies to reduce forest degradation but spillover effects of proximal drivers in neighboring areas need to be considered.

Keywords: forest degradation drivers, panel model, conservation, spatial statistics, forest condition, forest disturbance, conservation planning

INTRODUCTION

The degradation of natural forests is a serious problem with resonating impacts around the world, from significantly contributing to greenhouse gas emissions (Simula and Mansur, 2011), biodiversity loss (Foley et al., 2007), reductions in water regulation (Lele, 2009), and ultimately reducing the ability of forests to provide ecosystem services linked to food and goods which sustain local livelihoods (Lambin and Meyfroidt, 2011). Successful implementation of actions to reduce forest degradation, such as climate-relevant policies for emissions reduction and nature-based solutions requires prompt, well-informed, and appropriate actions (Griscom et al., 2017). The policy decisions based on available information, resources, socioeconomic conditions, and economic risk play important roles in how humans manage forests (Angelsen and Kaimowitz, 1999). A thorough understanding and quantification of the proximate causes and spatial determinants of the degradation, their magnitude, and spatial extent are needed to prevent degradation from eventually turning into deforestation (Griscom et al., 2020).

Deforestation is the result of forest loss or conversion to alternative land use, while degradation can fundamentally alter a forest without reducing its area or definition as a forest (Vásquez-Grandón et al., 2018). The identification of the proximate causes and spatial determinants of degradation is complicated by varied temporal time scales, dynamics, extent, definitions, and perceptions. Although deforestation and degradation can be closely correlated (Defourny et al., 2011), they differ fundamentally in terms of definition and impacts on ecosystem services. The quantification of drivers of deforestation and degradation is not only important for targeting national strategies to reduce the emissions from deforestation and degradation (REDD+), but have wide applications to sustainable development initiatives supporting local economies as well as conservation efforts seeking to reverse or slow the significant downward trends in forest cover and quality (Bernhard et al., 2020). A proper understanding of the proximate causes and determinants of degradation is essential for aligning policies with the appropriate actors (Tegegne et al., 2016), but available quantitative information on degradation drivers and how they interact at various scales is still quite limited. Degradation is often a precursor to deforestation in tropical areas (Gerwing, 2002; Vancutsem et al., 2021). This means that timely and accurate assessment of degradation risk is of utmost importance to prevent deforestation before it happens, and to improve and target mitigation activities.

The causes of forest disturbance are driven by multiple synergistic factors acting together, rather than single variables alone (Geist and Lambin, 2002; Megevand, 2013), meaning that policies and responses need to address a variety of factors and their interactions. In this study we use spatial panel regressions to assess the impact of multiple proximate causes and spatial determinants of forest degradation over time and space in the Democratic Republic of the Congo (DRC) using a novel forest condition (FC) metric which estimates a relative index of degradation from 0 (deforested) to 100 (intact; Shapiro et al., 2021). Spatial panel models are often used in the field of spatial econometrics, and assess data in spatial units over multiple time periods (Elhorst, 2010). We evaluate these patterns in the DRC, which holds the largest intact tract of tropical forest in Africa, hosting a wealth of biodiversity in a globally important carbon sink to mitigate climate change, while also supporting the livelihoods of millions of people (Molua, 2019). National rates of deforestation are relatively low, but in the last 10 years has nearly doubled to about 0.5% per year (FAO, 2020); this trend could continue with an increasing population dependent on natural resources, unregulated timber and mineral exploitation, and conflicts over these resources (Kengoum Djiegni et al., 2020). The DRC is vast, with large variations in the rates of forest loss, which are due to different demographics, threats, political frameworks, that require tailored policies and management. Unfortunately, the extent of forest degradation is still poorly understood in the DRC but can potentially result in more emissions than deforestation (Pearson et al., 2014, 2017), particularly under the high prevalence of resource-based livelihood activities, such as harvesting for fuelwood, unsustainable bushmeat hunting which affects natural forest regeneration (Harrison, 2011), and expansion of small-scale agricultural activities. The lack of understanding of the causes and determinants of forest degradation in the DRC is relevant because nearly 30% of total loss of primary forest between 2000 and 2015 was degraded before being deforested (Shapiro et al., 2016).

Direct or proximate causes of degradation have been identified as occupying five main themes: the expansion of commercial and subsistence agriculture, mining and infrastructure development, and urban expansion (Hosonuma et al., 2012). A major indirect cause of forest disturbance in the DRC is extreme poverty, which affects a majority of the population (World Bank, 2020), is closely linked to forest dependent behaviors, and is an additional contributing factor to forest degradation (Nerfa et al., 2020). This situation is compounded by political instability and an ongoing humanitarian crisis due to decades of armed conflict that pushes human activities deeper into the forests (Nackoney et al., 2014; Butsic et al., 2015; OCHA, 2021). The DRC's population is predominantly rural, with a strong reliance on the informal agricultural sector, which mostly comprises of informal slash and burn practices (Tyukavina et al., 2018; Molinario et al.,

2020) associated with increased fire frequency on managed lands, new clearings and forest edges (Morton et al., 2008; Jiang et al., 2020). The high reliance on natural resources will likely increase further due to the rapidly growing population along with urbanization; the overall population of the DRC is expected to exceed 100 million by 2035 (Tchatchou et al., 2015). We select eight variables to represent the five major direct drivers, and approximate the human impacts on DRC forests using covariates on built-up area, fire frequency, accessibility, land use, and presence of armed conflicts. We specifically choose these variables because they can be monitored over time with readily available, spatially explicit, consistent, measurable and repeatable indicators, whereas underlying variables such as the impacts of policies, socio-economic variables or underlying market forces are neither spatial in nature nor readily collected with standard approaches.

As forest degradation is dynamic, so must be the proximate causes and spatial determinants to capture the variations in time and space. Spatial econometrics techniques and their application to conservation and development enable research controlling spatial and temporal components via spatial panel data, which are a spatial cross-section of observation repeated over time (Baylis et al., 2011; Bernhard et al., 2020). The observations in a spatial panel can be correlated in time (repeated observations that may be dependent on a previous date) but also in space (neighborhood interaction; (Molinario et al., 2020). Here, we assess eight independent covariates over time within a grid of square of 25 × 25 km units. We control for fixed individual site differences and capture both time variant and time-invariant factors at unit level to isolate site-specific trends from neighboring or national trends, hence controlling for characteristics which might be auto-correlated in space and time. We evaluate the spatial panel models from 2002 to 2016 with the overall aim to provide a key understanding of the dynamic proximate causes and spatial determinants of forest disturbance to inform conservation, spatial planning, and climate mitigation initiatives. We answer two major research questions:

1. What are the spatial determinants of changes in forest condition?
2. How do these determinants interact and change over time?

METHODOLOGY

Study Area

This study assesses proximal causes of degradation in the Democratic Republic of the Congo (DRC), the largest country in the Congo Basin (**Figure 1**), which is characterized by having high forest area and low deforestation (da Fonseca et al., 2007; de Wasseige et al., 2015), with 60% forest cover and a deforestation rate of about 0.5% since 2010 (FAO, 2020). The known distribution of forest biomass and its potential carbon sinks support new economic opportunities for sustainable development under REDD+ (Xu et al., 2017). While deforestation is generally low, degradation however has been estimated to affect large areas (Shapiro et al., 2016) which are increasing over time (**Figure 2**; Shapiro et al., 2021). The forest transition model (Mather, 1992) shows that as countries develop, the related economic and population growth will likely elevate pressure on forest resources, notably intensification of agriculture and urbanization resulting in the increased threat of accelerating deforestation and forest degradation (DeFries et al., 2004; Hosonuma et al., 2012).

Data Sources

To quantify and understand human impacts on forests and the associated determinants of degradation, context and location is important. The literature regarding deforestation and forest degradation are often addressed together, citing slash-and-burn agriculture, collection of charcoal, mining and forest exploitation, infrastructure development and civil unrest, conflicts as key proximate causes in DRC (Defourny et al., 2011; Nackoney et al., 2014; Butsic et al., 2015; Tchatchou et al., 2015). In the following section, we discuss these key proximate causes of forest degradation addressed in this study which were selected to represent the major drivers of degradation via readily available data sources (**Table 1**). These are evaluated for each grid unit for each time period, which is a 3- year interval between 2002 and 2016. We then apply spatial panel regression techniques to identify the correlates for degradation and build on the concepts in published literature (Bernhard et al., 2021).

Forest Condition

Forest condition (FC; from Shapiro et al., 2021) is estimated as a relative index of forest degradation based on a gain/loss approach to above ground biomass (AGB). To create the FC index we used morphological pattern analysis (Vogt et al., 2007) on a forest extent maps to identify core, inner and outer edge and patch forests using an edge distance of 300 m. Using different forest cover maps over time we re-assess the fragmentation class of each forest ecosystem type into stable and change classes (Shapiro et al., 2016). Using the mean AGB of each fragmentation strata of each forest ecosystem type, we determine the proportion of remaining AGB of that strata and ecosystem type, where core, inner intact, and connected forest areas have an FC of 100; deforested areas have an FC = 0, and degraded or fragmented forests in between have an FC proportional to the total potential above ground biomass of intact forest. FC of all tropical dense forest area is used as the dependent variable to assess the proximate causes and spatial determinants of degradation over time. The FC metric was assessed for all dense tropical forests of the Congo Basin by Shapiro et al. (2021), and do not include the extensive dry forests. It was derived according to the unique forest ecosystem types described in Shapiro et al. (2021), from which we extract for our study area. It is estimated that there are about 27 million ha of degraded forests in DRC, with the total degraded area increasing over time (**Figure 2**).

Fire

Fires are typically infrequent in tropical forests, and most observations outside of any typical fire season have a human cause (Morton et al., 2008; Bowman et al., 2011). Anthropogenic fires occur more often in forest edges (Cochrane, 2001; Benali et al., 2017) and are a major cause of forest degradation and

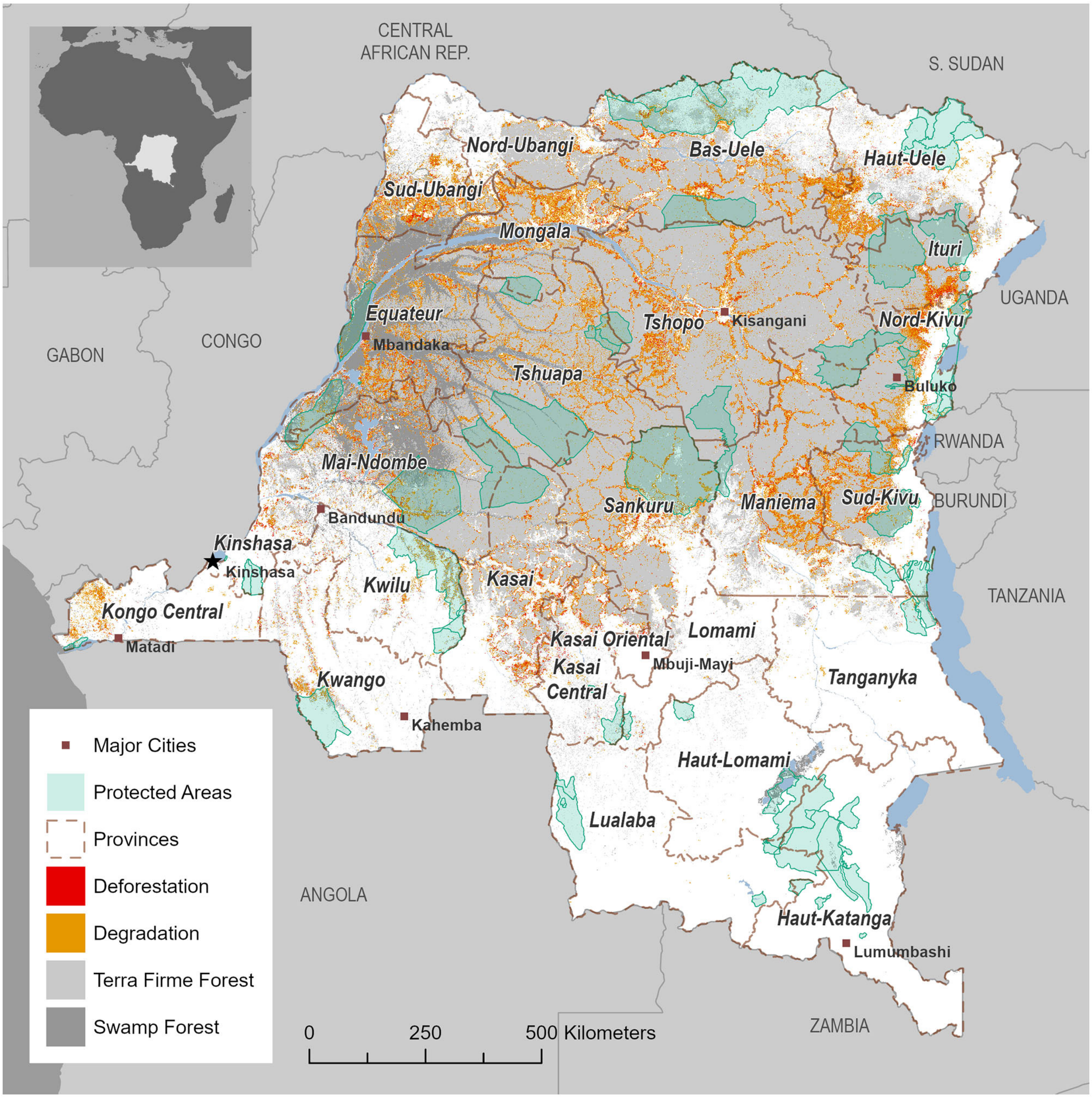

FIGURE 1 | The Democratic Republic of the Congo (DRC), with the capital Kinshasa, divided into 26 provinces, possesses over 100 million ha of tropical forest, of which about 11 million are swamp forest. Deforestation and degradation is from Shapiro et al. (2016).

deforestation in tropical biomes, which are not adapted to fire regimes and as a result experience reduced ecosystem resilience, with higher impacts on biodiversity as well as large greenhouse gas emissions (Juárez-Orozco et al., 2017; Ramo et al., 2021). These impacts can potentially increase with warming, drier climate (Siegert et al., 2001; Malhi et al., 2009). Fires, and especially multiple burns per year, are associated with agricultural expansion, especially slash and burn cultivation, which is cited as the greatest cause of forest disturbance in DRC (Tyukavina et al., 2018; Molinario et al., 2020), and is also increasing (Cochrane, 2001; Lewis et al., 2015). Fires, more importantly their frequency are therefore a crucial variable for degradation monitoring and emissions reduction interventions (Barlow et al., 2012). We use the latest Fire Information for Resource Management System (FIRMS; Giglio et al., 2016) dataset, which is the near real time active fire location product derived from the Moderate Resolution Imaging Spectrometer (MODIS) sensor thermal anomalies. We use Google Earth Engine (Gorelick et al., 2017)

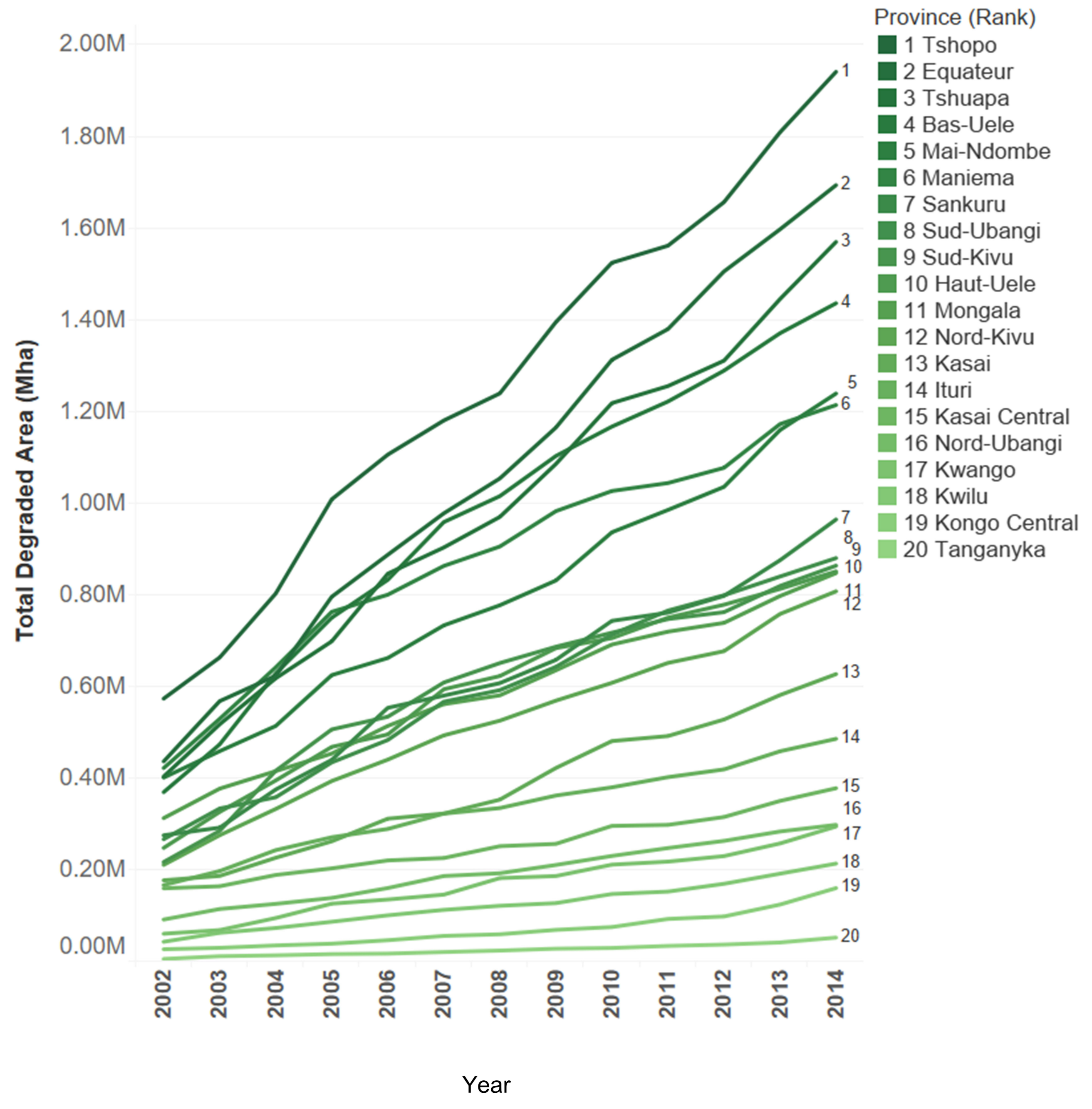

FIGURE 2 | Total degraded forest area of the 20 provinces with highest degradation rates [data from Shapiro et al. (2021)].

to sum all fire detections in each 3-year time interval. We select all fire detections with a confidence flag >30 at a resolution of 1 km. Fires are summed over all grid cells in the time interval.

Accessibility and Infrastructure

Physical access by humans into forests ecosystems is also an important driver of forest disturbance (Ferretti-Gallon and Busch, 2014). In the DRC, the means of access include both roads and rivers used to access forest areas for bushmeat, logging, and fuelwood collection, the latter being an essential resource for local communities and large cities alike and a significant cause of forest degradation (Chidumayo and Gumbo, 2013). An estimated 90% of wood harvested in the Congo Basin is destined for fuelwood, a trend exacerbated by poverty, population growth, and urbanization (Marien, 2009). Meanwhile, the extirpation of wild species by unsustainable hunting practices results in forests devoid of keystone, seed dispersing wildlife which can affect natural regeneration and resilience while also having significant

TABLE 1 | Variables evaluated for each forest grid and relevant literature.

Type	Variable	Expected effect	Spatial resolution	Temporal resolution	Data source	References
Forest degradation	Forest Condition (FC)	Dependent variable	100 m	Annual	(Giri et al., 2011; Hansen et al., 2013; Xu et al., 2017; Philippon et al., 2018)	Grantham et al., 2020; Shapiro et al., 2021
Human pressure	Total number of fires	+	1 km	Daily	MODIS Fire Data (Giglio et al., 2016)	Barlow et al., 2012; Ramo et al., 2021
	Built-up area in 2,000 and 2015 (km^2)	+	30 m	Decadal	GHS Human Population Grid, JRC (Pesaresi et al., 2016)	Corbane et al., 2017
	Total number of conflicts observed	+	Point	Daily	ACLED (Clionadh et al., 2010)	Draulans and Van Krunkelsven, 2002; Butsic et al., 2015; Negret et al., 2019
	Travel time (hours)	+	100 m	Time invariant	Data derived from slope, elevation, land cover, roads, and populated area using methods from Grantham et al. (2020)	Aguilar-Amuchastegui et al., 2014; Grantham et al., 2020
Land use	Protected areas (km^2)	–	Polygon	Annual	WWF (Pélissier et al., 2019)	Butsic et al., 2015; Leberger et al., 2020
	Forest concessions (km^2)	+	Polygon	Time invariant	World Resources Institute/ Direction Inventaire et Aménagement Forestiers (DIAF) (World Resources Institute, 2018)	Zhuravleva et al., 2013
	Mining concessions	+	Polygon	Time invariant	WRI/CAMI	Hund et al., 2013; Butsic et al., 2015
Biophysical	Swamp forest	–	50 m	Time invariant	Swamp Forest Extent (Dargie et al., 2017)	Miles et al., 2017; Dargie et al., 2019

We assign the expected effect of each independent variable.

social consequences to local human populations (Harrison, 2011; Nasi et al., 2011). We developed a travel time dataset, which is the output of a cost surface model in ArcGIS Pro version 2.7 (ESRI, 2020) derived from a source layer and a cost layer. The latter is derived from land cover, roads, rivers, elevation, and slope, and impedance as described in the development of the forest pressure index (FPI) in Grantham et al. (2020). The source layer was created from the human settlements obtained from the Global Human Settlement BUILT dataset for the year 2000 (Corbane et al., 2018), The cost surface estimates driving speed over roads and walking speed over various land cover surfaces, which are decreased with increasing slope and elevation; a navigation speed approximates travel on waterways as a function of their flow. As no temporally explicit data are available for road infrastructure, we can only develop accessibility for a single reference period of 2000, deriving the mean travel time in hours for all grid units. The BUILT dataset was also used to define the extent of built-up area per grid unit, using data for 2000 for the first four time steps and 2015 for the final time step.

Conflicts

Another determinant of degradation is armed conflict, which can have far-reaching ecological impacts (Machlis and Hanson, 2008). Violent conflicts can result in significant deforestation and degradation due to movements of refugees and internally displaced people (IDPs) into forests to escape violence (McNeely, 2003) and also adversely affects wildlife (Daskin and Pringle, 2018). Furthermore, conflicts in the region tend to be in areas of rich natural resources, such as minerals or forest; these areas are often inhabited by indigenous groups, which can result in further conflicts over land rights and acquisitions for resource extraction (Humphreys et al., 2007). The total number of conflicts recorded in DRC has been increasing in recent years, notably the violence against civilians (**Figure 3**). Conflicts in DRC are persistent in transboundary regions, which overlap with heavily forested and protected areas. For example, in the eastern DRC, conflicts have been a constant issue, especially in the Greater Virunga Landscape (GVL), which covers a network of 13 protected areas between DRC, Rwanda, and Uganda. The GVL has seen protracted conflicts, with periodic spikes over the last three decades, including ongoing armed rebel group activity based out of forests and remote areas.

We calculated the conflict variable using the Armed Conflict Location & Event Data Project (ACLED) database (Clionadh et al., 2010) which is a collection of real-time data on the locations, dates, actors, fatalities, and types of reported political violence and protest events across the world. We use the total sum of conflicts in each grid unit as our variable, and do not discern

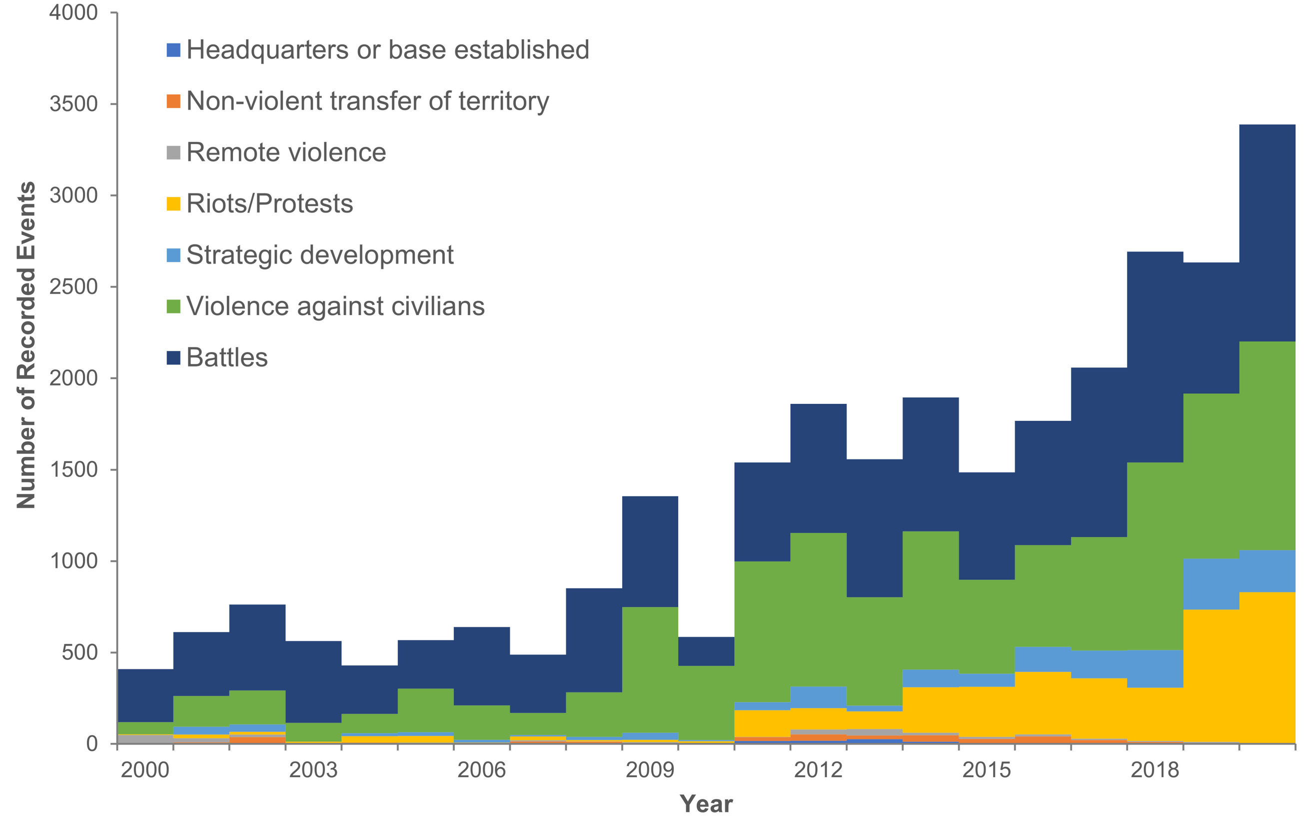

FIGURE 3 | Recorded conflict events in DRC, broken down by event type (Source: Clionadh et al., 2010).

between the number of fatalities or types of conflicts, as even non-fatal activities can have the effect of terrorizing and destabilizing local communities and their livelihood activities (Draulans and Van Krunkelsven, 2002) and the presence of protests can indicate civil unrest or political conflicts. Various rebel and armed groups use systematic and strategic sexual violence as a weapon of war (van Wieringen, 2020), increasing pressure on local resources through non-lethal threats and terror, as they depend on local communities, raid villages and fields, and force local residents to provide food, payments, or other income to armed groups (Laudati, 2013). On the other hand, some studies show that conflict could reduce or prevent deforestation by, at least temporarily, limiting private sector or extractives sector activity (Burgess et al., 2015). The armed conflicts caused by the long-term unrest in eastern DRC are therefore an important variable to consider in the assessment of the causes and determinants of forest degradation.

Land Use

The attribution of land use and its change over time is directly affecting activities on land. We use available data on protected areas, legal mining and forest concessions to assess the potential impacts from attributed land use management. The DRC is extremely rich in minerals, and efforts to extract these are exerting increasing pressure on unprotected forest and savanna ecosystems (Edwards et al., 2014). However, recent studies show the impacts on forests from industrial logging is relatively low (de Wasseige et al., 2012; Tyukavina et al., 2018). Although there has been a moratorium on forest concessions and a legal conversion process in 2002, the impact has been questionable, with extractive activities occurring regardless (Lawson, 2014). For this reason, we do not incorporate temporal information into the forest concessions as data can also be unreliable and may not be correlated with actual forestry activities. We assess total area attributed to logging concession regardless of status for each grid unit.

We source mining data directly from the DRC mining cadaster. While date information is available for some mining concessions, the information was also incomplete for many, or considered to be unreliable due to differences between different official and commercial data sources. Additionally, the timing of a particular type of legal mining license might not preclude illegal or artisanal activities, which may occur before or after the establishment or end of a legal permissions. Therefore, we do not account for temporal information of the mining concessions. We calculate total area (hectares) attributed to mining for each grid unit for this variable over the entire study period.

We incorporate protected areas, which were recently re-evaluated in DRC and include the year of establishment (Pélissier et al., 2019). Several new protected areas were established during the study period which allows us to assess their potential impacts (**Figure 4**). Protected areas downgrading, downsizing, and degazettement (PADDD) is present, but occurred mostly in the late 1950s, prior to our analysis (Forrest et al., 2014). We calculate total protected area in hectares for each grid unit and time interval.

Spatial Statistics

We estimated spatial panel regressions for the period from 2002 to 2016, separated into 3-year intervals to evaluate the impact of drivers in affecting degradation over time, spatial panel regression models were developed for the study period of 2002–2016, divided into five intervals of 3 years. Panel datasets effectively have two dimensions: a spatial dimension, with multiple temporal panels to assess effects over time (Vijayamohanan, 2016). The summary statistics of all variables is presented in **Table 2**.

The areal units were selected within the primary dense forested area of DRC, which was divided into 25 × 25 km grid squares (**Figure 5**), with data assessed over all 3-year time intervals between 2002 and 2016, resulting in 2,996 observations in each panel for a total of 14,980 observations. The decision to use equal-size grid cells as opposed to administrative boundaries was due to several reasons. First, some of the administrative boundaries changed substantially over time, in part due to instability and inconsistency in governance at both central and local government levels throughout DRC. This can adversely affect a panel model with the same units over time and, furthermore, these changes could be associated with deforestation (Alesina et al., 2019). Additionally, the availability of forest resources (timber products, bushmeat) is directly related to the amount of available forest to degrade, therefore different sized units cannot be adequately accounted for simply by normalizing area. A consistent grid avoids these pitfalls, but may lessen any potential impacts in differing governance or power structures, and therefore addresses the patterns independent of small administrative units. Given the small size of the grid in relation to other variables related to land use larger polygons such as forest concessions or protected areas are likely to cross neighbor boundaries, which could result in a source of endogeneity between units.

For each grid cell, the dependent variable, mean FC, and all independent variables (**Table 1**) were estimated for each 3-year time interval. We used zonal statistics to calculate the mean value for continuous variables, such as accessibility; for area estimates, such as mining concession area, protected area, forest concession area, built-up area, and swamp ecosystem area, we calculated the percent of the grid cell occupied by the respective variable. All temporally explicit data, such as protected area and built-up area, were calculated for the relevant time interval. A Pearson correlation matrix was assessed for all independent variables to identify multicollinearity. We assess significance at the 0.005 level using a correlation threshold of 0.5 to identify correlated variables.

Spatial Panel Regression

We evaluate spatial autocorrelation of the dependent variable through a non-parametric spatial correlogram of Moran's I using GeoDa version 1.18 (Anselin et al., 2005), where a local regression is used to evaluate correlations for all pairs of observations as a function of the distance between them (Bjørnstad and Falck, 2001). This provided the information to select the appropriate structure of the spatial neighborhood that has an influence on each observation. The spatial weights matrix is defined as a N × N matrix that identifies spatial dependence among the observations (i.e., the grid cells) across the study area.

The availability of repeated observations on the same units of a panel model allows the capture of individual-specific, time-invariant factors affecting the dependent variable in addition to unobserved effects (Baltagi, 2005). The rationale behind random effects models is that static differences across entities are presumed to have influence on the dependent variable. The random effects (RE) model therefore assumes that the unobserved time-invariant components of the model are unrelated (random) to the regressors therefore allowing the estimation of time-invariant explanatory variables (Greene, 2019). However, the assumption of no correlation between an unobserved component and the regressors is often unrealistic. This assumption is relaxed in fixed effects (FE) models that allow the unobserved random component to be related to the regressors, which causes all time-invariant explanatory variables to drop out of the analysis (Wooldridge, 2012). Both models can apply in certain situations. FEs are preferred when the interest is in assessing the impact of variables that change over time and not over observations, such as the number of conflicts and fire occurrences in our analysis. The RE models are valuable in situations where key explanatory variables are constant over time, such as bio- and geophysical variables described in our approach. We therefore apply both FE and RE models.

We apply spatial considerations to these models by adding using spatially lagged independent variables to our models. These spatial lags are the average of the neighborhood according to the spatial weights matrix without the central cell, in order to evaluate the local grid and the effect of its neighbors separately (Anselin and Rey, 2014).

We explored the different model specifications based on data constraint considerations (e.g., some spatial variables having only one reference period) and also in an effort (1) to illustrate the robustness of results to different model specifications; and (2) to provide complementary results where one model type has weaknesses. For example, fixed effects regression cannot include spatial variables without temporal variation (four out of eight independent variables). Therefore, we use the random effects to evaluate time and time invariant variables together. We describe each of the three model types through Equations 1, 2.

Random effects models incorporate parameters, which are random and uncorrelated (Equation 1).

$$y_{it} = \beta x_{it} + \alpha_i + u_{it} + \varepsilon_{it} \tag{1}$$

Where $\mathbf{y_{it}}$ is the dependent variable of entity i at time t. $\beta_\mathbf{1}$is the coefficient of variable x, the vector of independent variables, $\alpha_\mathbf{i}$is the individual specific effect potentially correlated with the independent variables, $\mathbf{u_{it}}$ is the between entity error term, and $\varepsilon_\mathbf{it}$ is the within entity error term. Random effects

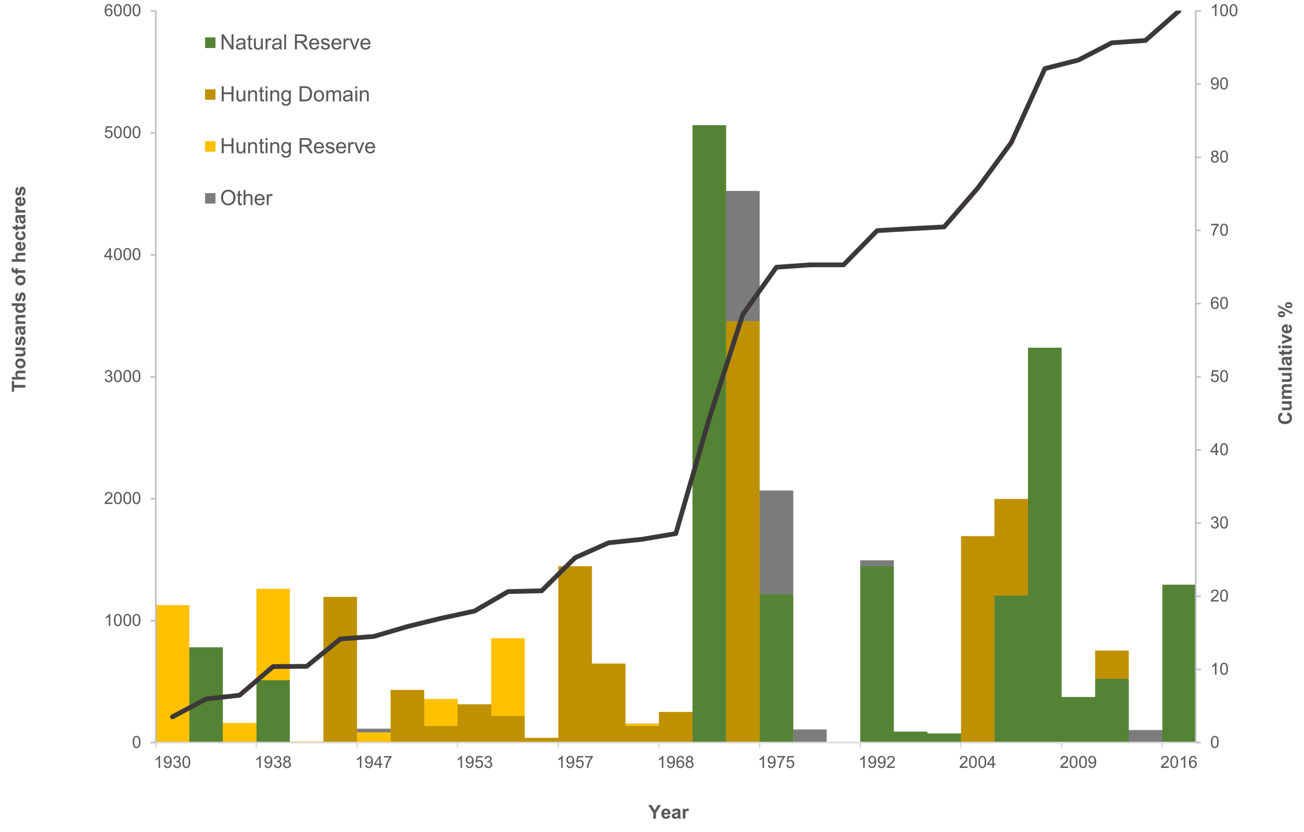

FIGURE 4 | Protected areas in DRC have been established since the 1930s, which significant increases in the 70s and early 2000s (Pélissier et al., 2019). Most protected areas are hunting reserves and domains (names are translated to English). Other category includes scientific, zoological and forestry reserves, as well as annexes.

TABLE 2 | Summary of variables.

Name	Min	Max	Mean	Std. Dev.
Forest condition (fc)	0.10905	100	62.9939	32.1467
Swamp ecosystem area (km^2)	0	621.5	37.4072	103.8042
Travel time (hours)	0.1924	57.4116	7.9027	7.6073
Forest concession area (km^2)	0	625	38.1795	127.5848
Mining concession area (km^2)	0	625	47.7687	118.7354
Protected areas (km^2)	0	625	77.3228	184.0276
Built-up area (km^2)	0	381.82	3.3940	16.4991
Total # of fires	0	40402	4371.864	5593.546
Total # of conflicts	0	322	0.8893	8.6468

models are typically fitted using generalized least squares (GLS) which is efficient and unbiased for situations with heterogeneous variance (Baltagi, 2005). Fixed effects models fix variables across observations rather than time, as some variables do not vary over time, or only have few time periods (Equation 2).

$$y_{it} = \beta_{it} * x_{it} + \alpha_i + u_{it} \tag{2}$$

Where y_{it} is the dependent variable of entity i at time t, $\alpha_i (i = 1 \ldots n)$ is the unknown intercept for each entity (n entity-specific intercepts), x_{it} represents one independent variable, and β_{it} is the coefficient for independent variable x.

We evaluate the random and fixed effects model with and without spatial lags. All regression analyses were executed in Stata (StataCorp, 2019). We assess all four models via their coefficients and significance, overall, R^2, and estimation of rho, the ratio of individual specific error variance in relation the entire error variance. We employ the Hausman statistic to select the preferred model, random effects or fixed effects.

Trend Analysis of Time Variant Drivers

Based on the outputs of the random effects panel model, we enrich the analysis by evaluating fires and conflicts over time, key dynamic determinants with high temporal resolution to highlight their impacts on forest condition in space and time. We provide two analyses to demonstrate approaches to support management efforts such as targeting fire suppression activities or where resources could be allocated to reduce armed conflicts.

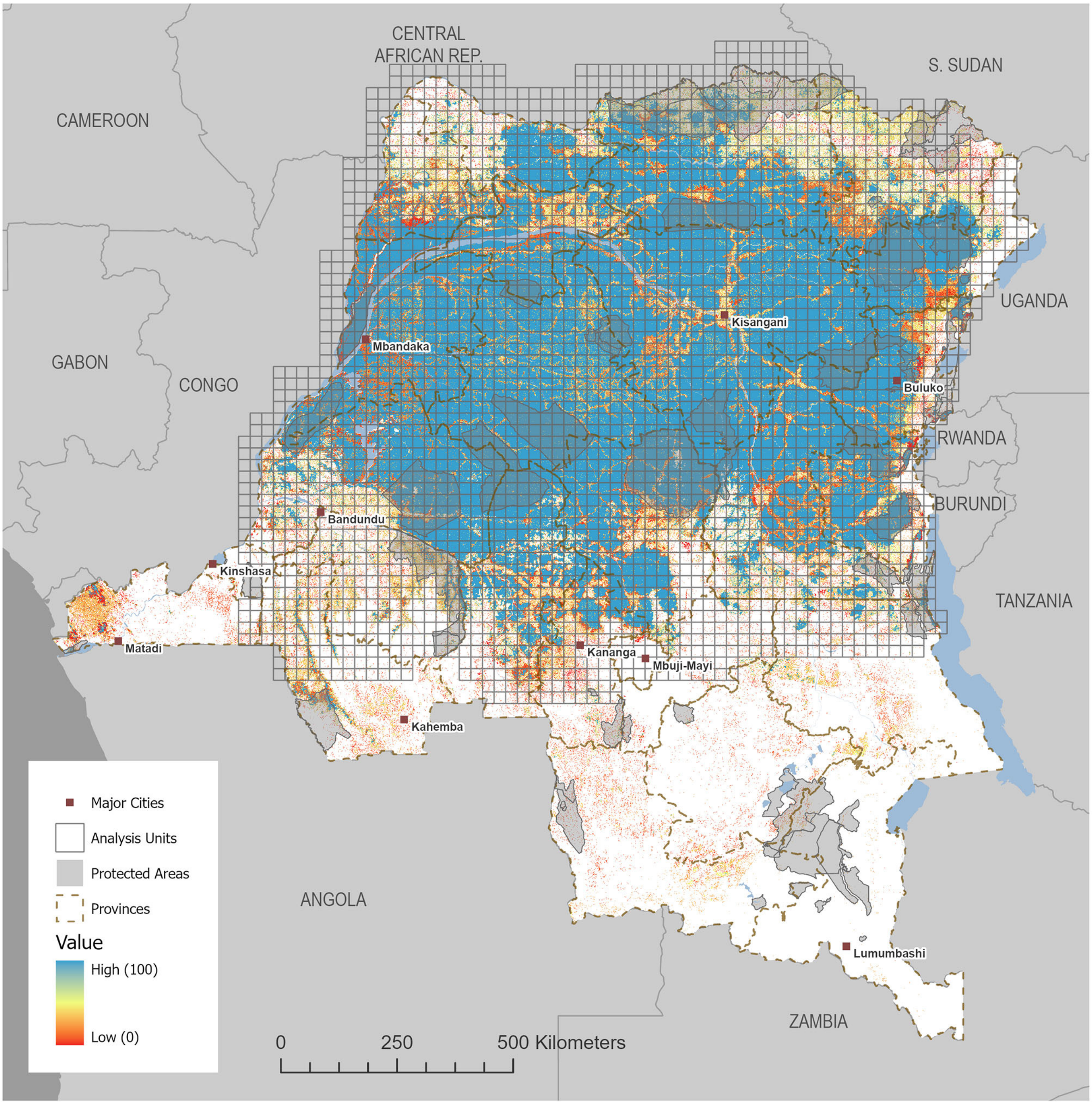

FIGURE 5 | The analysis units shown over forest condition (FC) from Shapiro et al. (2021). About 70% of DRC forests remain intact, with an FC of 100.

We assess trends over time using the Mann Kendall trend (M-K test) statistic (Mann, 1945; Kendall, 1975) to identify areas where frequency of fires and conflicts are significantly increasing or decreasing. We apply the space-time modeling tools available within ArcGIS Pro 2.7 (ESRI, 2020) using the same units as the panel data. For the case of fires, we use daily data acquired from 2002 to 2020 from FIRMS, summarized within each unit over 4 month time bins, and assess trend using the M-K test statistic. We perform the same analysis with the ACLED database of conflict locations from 2000 to 2020, applying the same temporal window of 4 months (which is selected automatically by the software based on the distribution of data in time) and using the 25 km^2 grid unit.

RESULTS

The spatial correlogram indicated that spatial autocorrelation of the dependent variable approaches zero at ∼50 km. Thus, we settled on the second order rook contiguity neighborhood as the structure for the spatial weights matrix (in analogy to a chess board, all grid cells that share a common border are considered neighbors, as well as the neighbors of the neighbors). Models using queen contiguity (common borders and common vertices) case did not significantly change model outputs. We did not detect substantial multicollinearity with all Pearson correlations below 0.4 (**Table 3**).

The results of the random and fixed effects models without and with spatial lags are presented in **Table 4**. Because we use a linear model with no interactions and FC is measured in percentage, the coefficients can effectively be interpreted as margins, meaning that for a unit increase in the independent variable, the coefficient informs the associated %change in mean FC of the unit. In all models the estimate for rho approaches one, meaning that nearly all the variance is described by differences across time, the highest rho is observed in the fixed effects model with spatial lags. The coefficient directions are mostly consistent between models, with the exception of protected areas and mining, which have opposite coefficients in the models with spatial lags. R^2 are higher for random effects models than fixed effects.

In the random effects models, a greater presence of swamp forest, higher travel time (lower accessibility) and greater coverage of forest concessions are associated with increases in mean FC. Mining concessions are negatively correlated when assessed without its spatial lag; when the lag is included the coefficient is positive, and the lag has a larger, negative coefficient indicating that mining concessions in the neighboring areas are reducing FC more than those in the local neighborhood. Protected areas have an unexpected negative effect on mean FC in models without include spatial lags, however when the spatial lag is present the locally estimated variable is positively correlated with FC while the effect of the neighborhood is negative, indicating potential displacement of disturbances. The increase in built-up area, number of fires, and conflicts all are associated with lower forest condition, along with their spatial lags which all have higher impact on FC. The % built-up variable is associated with the largest per unit decrease in FC.

For the fixed effects models, all variable coefficients are significant at the 0.05% significance level. Once again the protected variable has an opposite sign as expected, and a reverse coefficient when the spatial lag is considered. Built-up area, fires and conflicts have significant negative correlation with mean FC and built-up area has the highest per area unit effect. With the inclusion of the spatial lag, the coefficient for conflicts lower, while conflicts in the neighboring area have a stronger negative effect on FC. In the model with spatial lags, an increase in fires results in lower FC, and neighboring cells have a smaller relative impact. The total conflicts in the neighborhood have a greater influence on FC than the non-spatially lagged variable, indicating that an increase in conflicts has a further reaching effect in neighboring areas.

The Hausman test was significant at the 0.005 level, therefore we reject the null hypothesis and use the fixed effects model including spatial lags with higher goodness of fit measures for our major assessments and conclusions.

Temporal Trends of Fire and Conflict

Having addressed the importance of spatially and temporally variant determinants vs. static ones, we use the high temporal resolution of two dynamic variables to determine where they are changing over time to demonstrate the importance of time variant variables and the resulting policy implications. Conflicts and fires are the variables with the highest temporal resolution, and we determine where the greatest increases in fires and conflicts are occurring. The trends of these variables appear to be clearly spatially divergent (**Figure 6**).

Whereas, conflicts and fires were both shown to be negatively correlated with FC, we note that these variables are increasing in opposite regions of the country. Conflicts are notably present in the eastern DRC and have been increasing in the last two decades, most importantly in North and South Kivu and Ituri province overlapping with protected areas in the eastern region. We note a different pattern of changes in fire frequency, which is decreasing in these three eastern provinces, but increasing in Tshopo in the central cuvette, and Mai-Ndombe and Equateur in the western regions. Future research could explore a potential interaction between these variables, where a greater number of conflicts could be causing a reduction in fires.

DISCUSSION

The proximate causes and spatial determinants of forest disturbance and degradation have been often identified in the literature but are rarely quantitatively assessed. We provide a spatial panel analysis of drivers of FC, an index of forest degradation in the DRC using both time variant and time invariant variables to assess their relative impacts in time and space. We also assess the synergistic effects of variables and in concert with the spatial neighborhood to determine the potential impacts of neighbors. This provides important insight into the patterns and direct causes of forest disturbance, including the further reaching impacts of some drivers, the potential leakage or displacement of impacts by direct threats or land uses, and informs interventions or policies related to proximal drivers.

A greater area of swamp ecosystem could effectively be serving as a natural barrier to anthropogenic disturbance locally. However, an increased swamp area in neighboring areas may be displacing these threats. The Congo Basin peatland system is the most extensive swamp system in the world and largely forested and by nature difficult to penetrate due to peat depth (Dargie et al., 2017). There are few inhabitants directly in swamp forests. Forest clearing activities are more cost effective in *terra firme* forests, meaning most impacts in swamp ecosystems are currently limited to small scale sustainable uses (Dargie et al., 2019). Therefore, human activities are expected to be more present in areas neighboring swamp ecosystems. The addition of the spatially lagged swamp area variable to our models indicate that the natural protection of swamps is local, displaying pressure on forests in areas neighboring to swamp ecosystems. This concept of protection might not be permanent, as the effects of climate change are expected to increase accessibility and pave the way for more logging to feed increasing demand for

TABLE 3 | Pearson correlation matrix of independent variables.

	Swamp ecosystem area (km^2)	Travel time (hours)	Forest concession area (km^2)	Mining concession area (km^2)	Protected areas (km^2)	Total # of fires	Built-up area (km^2)
Swamp ecosystem area (km^2)	1						
Travel time (hours)	0.1165***	1					
Forest concession area (km^2)	0.1764***	−0.0063	1				
Mining concession area (km^2)	−0.1425***	−0.0300***	−0.1133***	1			
Protected areas (km^2)	−0.0556***	−0.3320***	−0.0101	−0.0804***	1		
Built-up area (km^2)	−0.0246***	−0.1582***	−0.0267***	0.0855***	−0.0431***	1	
Total # of fires	−0.2078***	−0.4388***	−0.1738***	−0.0885***	−0.0358***	−0.1422***	1
Total # of conflicts	−0.0323***	−0.0705***	−0.0278***	0.1125***	−0.0127	0.2029***	−0.0088

$^{***}p < 0.005$.

TABLE 4 | Results of random effects (RE), RE with lags, and fixed effects (FE), FE with lags.

	Model			
Variable	**RE**	**RE lags**	**FE**	**FE lags**
Swamp ecosystem area (km^2)	0.0347*** (0.0027)	0.0193*** (0.0063)		
Swamp ecosystem area (km^2) Spatially lagged		−0.0034 (0.0076)		
Travel time (hours)	1.913*** (0.0617)	0.6760*** (0.0771)		
Travel time (hours) Spatially lagged		1.6352*** (0.1087)		
Forest concession area (km^2)	0.0334*** (0.0019)	0.0018 (0.0031)		
Forest concession area (km^2) spatially lagged		0.0567*** (0.0049)		
Mining concession area (km^2) Spatially lagged	−0.0140*** (0.0033)	0.0019*** (0.0070)		
Mining concession area (km^2) Spatially lagged		−0.0197*** (0.0070)		
Protected areas (km^2)	−0.0066*** (0.0006)	0.0116*** (0.0015)	−0.0422** (0.0047)	0.0720*** (0.0082)
Protected areas (km^2) Spatially lagged		−0.0289*** (0.0025)		−0.1755*** (0.0112)
Built-up area (km^2)	−0.2991*** (0.0616)	−0.1239*** (0.0629)	−3.8986*** (0.1918)	−0.3038** (0.2047)
Built-up area (km^2) Spatially lagged		−0.9644*** (0.0629)		−12.0822*** (0.3761)
Total number of fires	−0.0013*** (0.00005)	−0.0006*** (0.00006)	−0.0009*** (0.00003)	−0.0005*** (0.0006)
Total number of fires Spatially lagged		−0.0009*** (0.00007)		−0.0007*** (0.00005)
Total number of conflicts	−0.0357** (0.0156)	−0.0128 (0.0143)	−0.0196*** (0.0068)	−0.0073 (0.0006)
Total number of conflicts Spatially lagged		−0.2928*** (0.0363)		−0.2231*** (0.0154)
Constant	53.0854*** (0.8470)	54.8350*** (1.0310)	69.4510*** (0.7011)	76.4417*** (0.2544)
R^2	0.5688	0.6228	0.2142	0.3057
Rho	0.9504	0.9507	0.9799	0.9995

$^{***}p < 0.005$; $^{**}p < 0.05$.

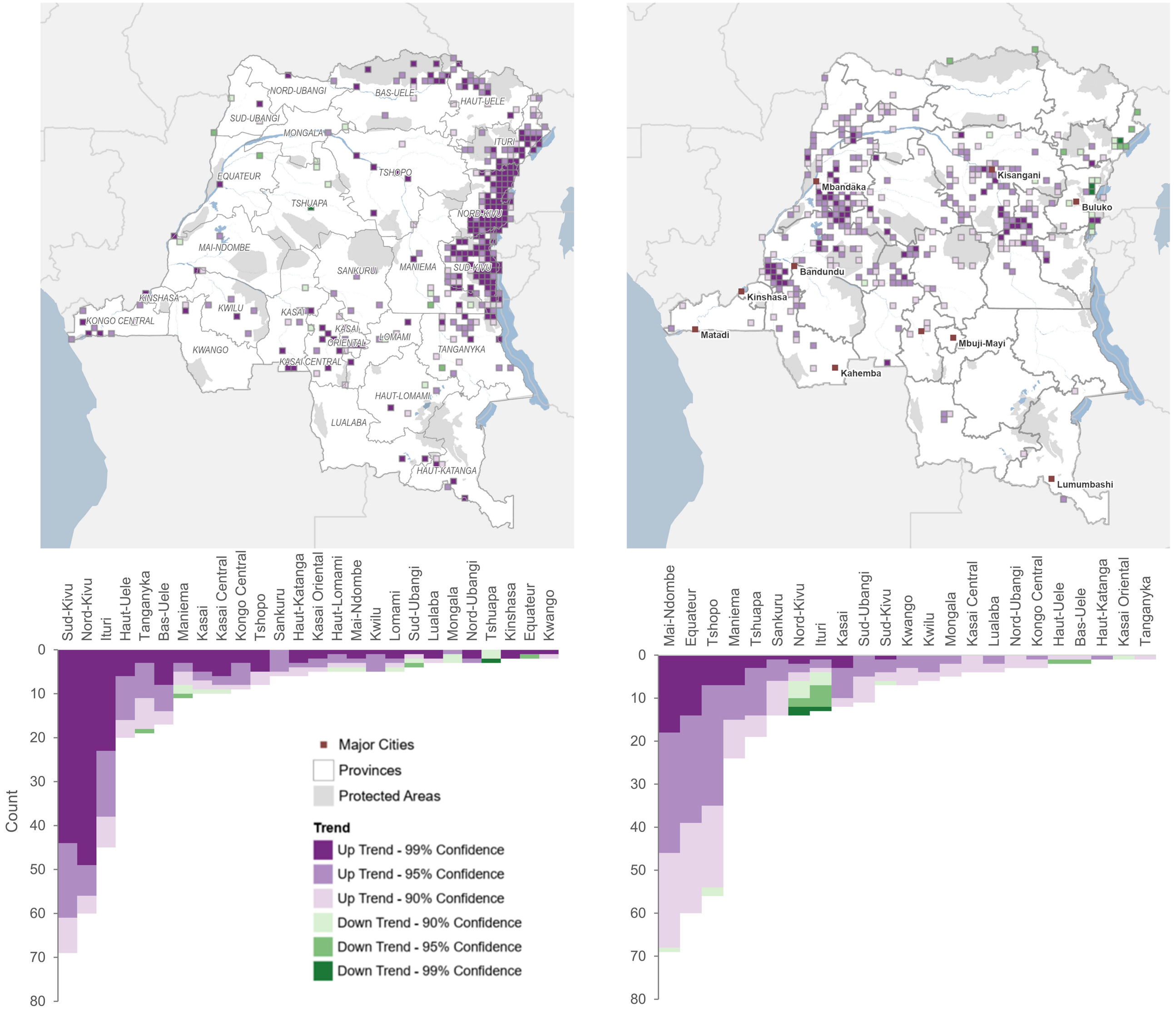

FIGURE 6 | Trends in conflicts (left) and fires (right) assessed by Mann-Kendall trend analysis.

resources. The presence of large oil and gas concessions and some forest concessions in these peatlands are raising alarms within the conservation community as these are directly threatening vast carbon reserves and extraordinary biodiversity, although these remain at the moment mostly inactive (Miles et al., 2017). A portion of these swamp forests were placed under formal protection in 2011 (Pélissier et al., 2019), which could prevent them from being exploited.

While swamp forests might afford natural protection, the assessment of formally established protected areas as a spatial determinant of FC is not as clear. Without considering the effect of the spatial neighborhood, the presence of protected areas is unexpectedly negatively correlated with FC. This could be explained by the context of protected areas in DRC. First, the establishment of protected areas in DRC were implemented to represent different ecotypes and protect major faunal population (Inogwabini et al., 2005), which means they often are located in intact, inaccessible locations, as demonstrated by the positive correlation (Pearson correlation coefficient: −0.33) of protected areas with travel time (**Table 3**). Although we have temporal data for protected areas, and several new protected areas were established in the middle of the study period (**Figure 4**) the positive effects of protection could take many more years to materialize into increased FC. Protected areas in DRC also face a difficult history, where in some locations, implementation with support of local and indigenous communities and increased militarization has limited their acceptance and effectiveness (Duffy et al., 2019). Additionally, protected areas can be targets for rebel and armed groups who seek to profit from natural resources or poaching activities and illegal trade of ivory

(Draulans and Van Krunkelsven, 2002). The Virungas National Park for example is one of the oldest parks in Africa, and remains at the center of one of the longest armed conflicts on the continent and throughout recent years has served as a base and hub for a variety of rebel groups. All of these issues are exacerbated by critical underfunding, which can significantly reduce effectiveness (Inogwabini et al., 2005). With the inclusion of the spatial neighborhood, we find a weak positive impact of protected area, with a greater negative effect from surrounding protected area. This could show that in the context of a larger area, protected areas might displace disturbances to 25–50 km beyond their borders, where they can attract development and similar activities when local communities benefit from protected areas, or use its resources, indicating a potential leakage effect (Sabuhoro et al., 2017; Bernhard et al., 2020).

Many forests remain unexploited inside forest concessions (for example swamp as described above), therefore the positive impact of timber concessions on FC is not entirely illogical. While industrial timber extraction remains a major threat to forests around the world, this pressure is actually lower in Africa (Kissinger et al., 2012; Megevand, 2013). The DRC has the lowest timber production of all Congo Basin nations, despite having the largest forest area (de Wasseige et al., 2012) which is a result of conflicts, political instability, and lack of access and transport (Tchatchou et al., 2015). There are few large clear-cutting activities, logging is primarily selective, and damage is limited to areas around logging roads which can often quickly regenerate (Zhuravleva et al., 2013). It is suggested that most logging activities in DRC are illegal (Lawson, 2014), and could therefore be outside of identified concessions, several of which are in defiance of a 2002 moratorium on new forest concessions to re-assess their legality, a factor compounded by major weaknesses in governance.

We find mining concessions to negatively correlate with FC, but when considered along with its spatial lags, the reverse correlation exists where the area of local mining concessions is positively correlated with a decrease in FC, while the spatial neighborhood is positively correlated. In the context of all forest changes observed in the region, mining is considered a rare forest disturbance driver (Tyukavina et al., 2018). Large-scale mining operations tend to be older and resulted in deforestation before the time period addressed in this study. This suggests that current mining activities are less actively causing deforestation or degradation (Putzel et al., 2011). Larger established mining concessions also tend to be associated with higher security (Hönke, 2009), which can displace artisanal or illegal extractive activities into the spatial neighborhood of our analysis. It should also be noted that this variable does not include artisanal mining, or activities which might be pushed outside concession boundaries. Unfortunately, the only available datasets for artisanal mining are not based on consistent remote sensing and are biased in terms of location and time of detection.

Most of the forest disturbance in DRC is due to small scale agricultural activities dominated by shifting cultivation, which can be difficult to discern in satellite imagery (Tyukavina et al., 2018). The travel time, built-up, and fire variables support the assessment of human activities related to agriculture as these are associated with repeated fire and ease of access (Morton et al., 2008). Our data supports the results of Molinario et al. (2020) which determine that shifting cultivation is the major cause of primary forest loss in the DRC via slash and burn activities, with strong effects of proximity to industrial activities. We identify this via the presence of larger built-up areas (roads, paths, settlements) which are associated with expansion of the rural complex, and is quantified here by reduced FC in the 25 × 25 km area. Built-up areas are indicative of greater population presence, which incurs greater demand on local resources – and per square kilometer of developed area has the largest impact on FC. However, population density plays a role, and potentially at a greater scale than the local neighborhood assessed here, although few reliable recent census data exist for DRC. For large cities, the relative influence of the large capital city is difficult to quantify, but Kinshasa, with its large population is still reliant on charcoal for energy, coupled with a large appetite for bushmeat that can impact forests well-beyond the area of our estimated spatial neighborhood, especially as more roads facilitate wider access (Behrendt et al., 2013). Larger cities might be located closer to forests that are already degraded, and easier to further disturb, while smaller urban centers could be feeding both local demand and larger urban centers (Molinario et al., 2015). The lack of detailed population data make the evaluation of human density difficult to untangle. The model results suggest that the impact of developing one square kilometer of area for human use on FC (-0.12) is 10 times larger than protecting the same area (0.01).

The presence of conflicts can affect forests in several ways, notably through higher pressure on forests for energy resources such as charcoal, increased illegal logging, mining and hunting (de Merode et al., 2007). Similar to Butsic et al. (2015), we find conflicts to be associated with forest disturbances resulting in lower FC, and the spatial neighborhood has an effect as well. This result is expected and can be explained by internal displacement of citizens fleeing unrest and threats, as is often the case in the Kivu provinces. The number of IDPs in the DRC is estimated to be over 5 million (UNHCR, 2020), and many more are known to seek refuge from armed groups in forests, resulting in increased wildlife poaching and deforestation as a result of this insecurity (Draulans and Van Krunkelsven, 2002; Nackoney et al., 2014). Peaks in violent events with increased violence against civilians occurred between 2009 and 2014 (**Figure 3**). Refugee influxes to neighboring Uganda and Rwanda also spiked in 2016/17, which correlates with the significant upward trend in conflicts in Nord Kivu (UNHCR, 2020). Unfortunately, the effects of conflicts can be long lasting on forests, whether via disturbance or the long-term effects of reduced faunal populations from overhunting of bushmeat which affect natural regeneration (Harrison, 2011; Nasi et al., 2011; Nackoney et al., 2014). The presence of armed conflicts in and around protected areas can affect their effectiveness, which is a result of the complex impact of institutions, and lack of resources (de Merode et al., 2007), indicating another potential interaction explored by Butsic et al. (2015).

Including spatially lagged elements to our models provides additional perspective on the far-reaching effects of some determinants. Higher travel time or lower accessibility of neighboring areas indicates a potential functional protection - whereby forests are protected simply by their inaccessibility by road, waterway, and land cover type. For example, an increase of 1 h of accessibility increases mean forest condition by more than 1.5%. This could speak to engaging the responsibility of forest concessionaires to limit access to newly opened logging roads, which can be more effective in limiting access than protected areas (Sheil et al., 2010) but at the same time could increase conflicts with local populations and therefore should be addressed with caution. Limited accessibility in the neighborhood might also imply that the target cell is less connected to larger cities or markets. The spatial lags of mining concessions and protected areas were shown to have the opposite impacts of the target cell. In the case of protected areas, the negative correlation, which is explained above, with a low positive coefficient of neighboring areas could bring some good news for the wider reaching impacts of protected areas.

The influence of the neighborhood is key in identifying appropriate policies or interventions and this relationship can be complex, as local decisions depend on the characteristics and processes of neighboring areas, and policies themselves can have positive or negative spillover effects (Robalino and Pfaff, 2012; Delacote et al., 2016). Considering the predominant subsistence agriculture, land-use decisions that result in forest degradation are often made at the household or community levels. Payments for ecosystem services (PES) can provide successful means to reduce impacts on forests through economic incentives, however this needs to be compatible with prevailing land tenure situations and promote participation, inclusion and compatibility with local livelihood structures (Barbier and Tesfaw, 2012). Leakage, or the spatial displacement of activities due to implementation of policies can affect overall policy success. Our study shows a strong impact of neighboring areas on local forest condition, indicating the need to consider local interactions for the strategic establishment of policies or activities (Robalino and Pfaff, 2012).

Our study period pre-dates most of the PES efforts and mitigations in DRC, notably via REDD+ projects, which enables us to establish a historical assessment of drivers and an understanding of the proximal causes and means to detect forest degradation. We cannot address every possible proximate or underlying driver, but specifically those that can be monitored over time in order to enable prediction or indicators of upcoming forest disturbance. If we consider the proposal by Combes Motel et al. (2009) to compensate countries for their deforestation efforts, while separating structural factors (essentially exogenous variables such as market forces) from enacted policies, our approach is complementary, in that it allows to determine the impact of these policies. For example, if a forest conservation activity is established, we can determine whether that activity is associated with increased forest condition, reduced development, while controlling for spillovers from neighboring areas. Yet, many of these so-called structural economic variables are difficult to measure consistently for the DRC, and there are clear elements which can potentially blur the effective establishment of PES schemes. Examples include corruption, lack of participation, leakage, political instability, de-centralized political structures and lack of adequate reporting – which are difficult to subjectively evaluate. In order for PES to be successful there needs to be a robust assessment on the quality of policies, for example, that ensure transparency, social safeguards of these institutions (Chhatre et al., 2012), and a clear evaluation of whether the policies are effective in slowing the course of deforestation. There also needs to be a clear understanding of context and current trends and the establishment of accurate reference levels (Angelsen and Wertz-Kanounnikoff, 2008).

Applying both the random and fixed models demonstrates the importance of integrating time variant variables in our assessment. The proximate causes and spatial determinants of forest disturbance are not stable in time but change along with other exogenous influences including climate, politics, or pandemics. Kengoum Djiegni et al. (2020) lament the fact that an up-to-date drivers analysis, potentially including relative impacts and spatial pattern was missing from the development of the national forest reference emissions level (FREL) in 2018. This spatial panel approach and in particular the comparison of both random and fixed effects model provides a useful mechanism to assess the relative impacts of drivers, combining both time variant and invariant datasets to assess the risk of forest degradation, which can be updated over time as new data become available. This is important to determine where specific interventions should be put in place, and prioritize the best use of limited funds.

To properly inform land use policies or interventions and to target resources we need to evaluate the covariates individually over time and space, which is particularly important in a vast country such as the DRC. We assess the trends of fires and conflicts over a time period extending beyond the statistical modeling and note that these two variables diverge spatially - there is an increased risk of forest degradation related to armed conflicts in the east, where fires are decreasing. Meanwhile fire frequency is increasing in the central cuvette and western portion of the country, potentially threatening emissions reductions programs and swamp forest ecosystems. This speaks directly to the importance of contextual information to guide use policies to drive change and spatially targeted approaches and interventions (Tegegne et al., 2016). In the example of REDD+ interventions, reduction of fires in the context of agricultural practices are a critical factor to be addressed to secure and manage forest carbon (Barlow et al., 2012). The information provided here can be used to design emissions reduction interventions related to fire that focus on high-risk areas (Holdsworth and Uhl, 1997) by promoting fire reduction or sustainable, managed or improved charcoal or biofuels for local energy needs (Megevand, 2013; Schure et al., 2014).

A number of uncertainties limit our analysis. The FC metric is dependent on accurate forest and biomass maps, which surely have a level of inherent error. The global tree cover change product used to identify loss at edges focuses on identifying tree cover loss but does not consider natural and anthropogenic regeneration, which could be occurring. New available datasets such as the Tropical Moist Forests (TMF) product from Vancutsem et al. (2021) which include both deforestation and degradation could provide opportunities for additional evaluation. Due to the nature of the tree cover loss product, the forest condition metric also includes naturally caused forest changes, although from a remote sensing perspective the causes of forest disturbance are practically impossible to separate. The increase in observed conflicts over time could also be influenced by the increase in social media and connectivity, which increases the potential information shared and reported on conflicts in recent years, more than in earlier years. We have demonstrated the importance of spatial neighborhood, but our models effectively end at the international border. Clearly, activities and varying threats in neighboring countries are going to influence Congolese forests, and these are only touched upon here. Our approach is transferable and scalable with readily available data for these identified proximate drivers and allows to contrast the impacts of land use policies: protected areas, forest concessions or development in neighboring countries or regions.

We did not include climate factors due to the coarseness of available datasets, although differences in rainfall and temperature could drive different types and trends of agricultural expansion. Next, the size of the grid unit might influence the outputs of the model. The size we selected, resulting in nearly 3,000 units, is well below the scale of the smallest administrative unit. Finally, additional variables could improve the model, including an evaluation of the threat of bushmeat hunting. The presence of certain crop types, or socio-economic variables are unfortunately difficult to spatially quantify at this scale of analysis. Spatially explicit information on poverty indices, reliance on natural energy sources, information related to diets or the structure of local economies would be very valuable to assess the impacts on forests, but is only mostly available at national scale (Bawa and Dayanandan, 1997). This could be assessed in more depth via future studies using recently-implemented national household survey approaches.

CONCLUSIONS

The proximate causes and spatial determinants of forest disturbance vary greatly in time and space, particularly in a diverse and vast country like the DRC. Therefore, to successfully safeguard forests and the people who depend on them, we need spatially targeted interventions that are informed by sub-national context. Especially considering limited financial resources for conservation, land management activities and interventions need to be implemented where they can be most successful. The increase in fire frequency in the central and western parts of the country, which are also heavily forested, should indicate the need to change where fire suppression activities are targeted. This can support the implementation of renewable energy for households or programs that reduce dependence on charcoal.

The importance of spatial neighborhoods for many spatial determinants are not only important at the local level, but also inform transboundary considerations. Multi-lateral agreements between neighboring countries to improve coordination and diplomacy, particularly in the face of moving threats is essential. Though once again, context varies. While some regions in Africa are successfully addressed by “Peace Parks,” which employ protected areas as a form of peacebuilding, their location and historical context remains important. While peace tourism might be fruitful in some areas, the realities in the eastern DRC are more complicated and currently muddled by increased militarization to protect tourists (Trogisch and Fletcher, 2020). Before we achieve both forest conservation and socioeconomic development goals for forest adjacent communities, a drastic reduction in conflicts and better security is needed. While complicated, conservation peace-building should not be rules out. This spatio-temporal approach can be replicated at various scales or extents for transboundary decision support systems to the support the implementation of these kinds of interventions.

Finally, it is clear that forest disturbances change in dynamic fashion. The COVID-19 pandemic has demonstrated that all populations, especially those on the margins of poverty, are vulnerable to global events. The trends observed in DRC show little sign of relenting, exacerbated by increases in violent events. It is increasingly clear that humans rely on nature for survival and basic needs, it is important to provide intact and resilient ecosystems to allow communities, including the impoverished to overcome more future climate and economic perturbations.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

AS: conceptualization, data curation, methodology, formal analysis, writing original draft, writing review and editing, and visualization. KB: conceptualization, methodology, writing original draft, and writing review and editing. SZ and DM: methodology and writing review and editing. Rd’A: writing review and editing. NA-A: conceptualization and writing review and editing. All authors contributed to the article and approved the submitted version.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.690562/full#supplementary-material

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Experimental Evidence on the Impact of Payments and Property Rights on Forest User Decisions

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Clearing forests for swidden agriculture, despite providing food to millions of farmers in the tropics, can be a major driver of deforestation. Payments for ecosystem services schemes can help stop swidden agriculture-induced forest loss by rewarding forest users for maintaining forests. Clear and secure property rights are a key prerequisite for the success of these payment schemes. In this study, we use a novel iterative and dynamic game in Madagascar and Kenya to examine farmer responses to individual and communal rights to forestlands, with and without financial incentives, in the context of swidden agricultural landscapes. We find that farmer pro conservation behaviour, defined by the propensity to keep forests or fallows on their lands, as well as the effects of land tenure and conservation incentive treatments on such behaviour, differ across the two contexts. The average percentages of land left forest/fallow in the game are 65 and 35% in Kenya and Madagascar, respectively. Individual ownership significantly improves decisions to preserve forests or leave land fallow in Madagascar but has no significant effect in Kenya. Also, the effect of the individual tenure treatment varies across education and wealth levels in Madagascar. Subsidy increases farmers' willingness to support conservation interests in both countries, but its effect is four times greater in Kenya. We find no interaction effects of the two treatments in either country. We conclude that the effectiveness of financial incentives for conservation and tenure reform in preserving forestland vary significantly across contexts. We show how interactive games can help develop a more targeted and practical approach to environmental policy.

Keywords: interactive game, swidden agriculture, payments for ecosystem services, property rights, forest land tenure, forest conservation, Madagascar, Kenya

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INTRODUCTION

Nature conservation is coming increasingly into conflict with human livelihoods (Redpath et al., 2013). In the tropics, large forest areas are being converted to agriculture by shifting cultivation, also known as swidden agriculture (Fox et al., 2000). While other macro-economic or distant factors such as migration and remote market demand can cause forest loss (Meyfroidt et al., 2013; Cairns, 2015), swidden agriculture has long been considered a major driver of deforestation and biodiversity loss (Zabel et al., 2019). However, swidden agriculture provides subsistence for millions of people across the developing world (Van Vliet et al., 2012) and covers roughly 280 million hectares worldwide, including both cultivated fields and fallows (Heinimann et al., 2017). Market-based economic instruments such as payments for ecosystem services (PES) schemes offer potential for reducing swidden agriculture-induced forest loss while improving local people's livelihoods (Namirembe et al., 2014; Wunder, 2015). PES programmes are based on rewarding forest users for maintaining or increasing the provision of ecosystem services (Noordwijk et al., 2012).

Clear and secure property rights are a key prerequisite for the success of PES schemes, as they determine who is eligible to benefit and how contracts can be legally enforced (Swallow and Meinzen-Dick, 2009; Corbera et al., 2020). In many tropical countries, governments have de jure ownership of forestlands (Kelly and Peluso, 2015). However, state ownership is often weakly enforced in practise or is locally contested (Unruh, 2008; Rakotonarivo et al., 2018). While much can be learned from reviews on the importance of various contextual, design, and implementation features on the effectiveness of PES schemes (e.g., Börner et al., 2017; Snilsveit et al., 2019; Wunder et al., 2020), evidence is missing for how the effectiveness of PES in incentivising pro-conservation behaviour might vary between land tenure systems such as communal and individual ownership of forestlands. Yet, pilot or real-world interventions to address this knowledge gap would be difficult to implement because of practical costs and ethical concerns. In this study, we develop a novel interactive and dynamic game to investigate the effects of payments and different types of property rights on forest-user behaviour in the context of swidden agricultural landscapes in Madagascar and Kenya.

Games can extend more traditional survey approaches by testing the impact of policy interventions that may not yet have analogues in past experience and would be difficult or expensive to test in reality (Redpath et al., 2018). This is the case in many African contexts where well-defined forest tenure regimes such as individual and communal forest ownership are largely missing, and where forest tenure is contested and unclear, and forest users are not landowners (Rights and Resources Initiative, 2018; Sunderlin et al., 2018; Miller et al., 2021). While we were not able to include such de facto contested tenure situations in our experimental game design, our study examined the influence of individual and communal property rights to forestlands on forest user behaviour and thus, provides valuable insights on the influence of potential tenure reform policies on conservation outcomes. In addition, experimental games allowed us to vary property rights regimes exogenously while holding other factors constant, which is challenging in observational, quasi-experimental studies.

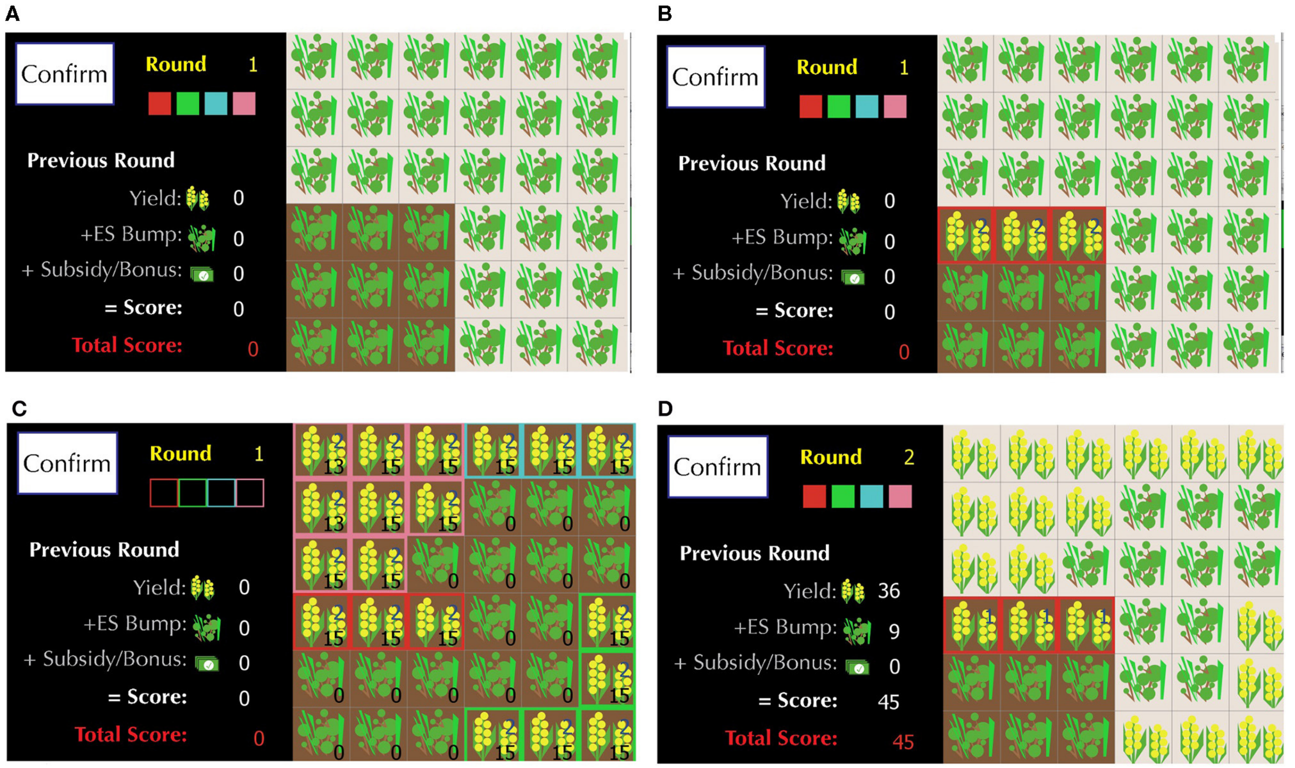
Games have been used to study individual or group coordination strategies and facilitate change processes and social learning in complex socio-ecological contexts (e.g., Bodonirina et al., 2018; Celio et al., 2019; Speelman et al., 2019; Andreotti et al., 2020; Garcìa-Barrios et al., 2020). In other settings, games have been used to investigate the effectiveness of alternative payment structures in encouraging pro-conservation behaviour in the context of forest resources (e.g., Travers et al., 2011; Narloch et al., 2012; Kaczan et al., 2017; Salk et al., 2017; Andersson et al., 2018; Gatiso et al., 2018). These studies are useful for exploring how conservation incentives are best delivered (e.g., to groups or individuals), but they offer limited insights into the potential impacts of communal or individual ownership over forestlands on farmer behaviour. The traditional pen and paper approach used in most of these games also limits their potential to model ecologically relevant temporal and spatial dynamics of the resources, particularly at the landscape level (Janssen et al., 2014). This might limit their ability to attribute the observed behavioural patterns to the experimental interventions (Cardenas et al., 2009).

We used a novel game to test how alternative policy interventions affect farmer pro-conservation behaviour. We conducted the games in Madagascar and Kenya, two countries which have varying degrees of reliance on swidden agriculture as described in the study context section. The Netlogo framework (Wilensky, 1999) allowed us to include both temporal and spatial dynamics in the games, which significantly increased realism and famers' engagement (Rakotonarivo et al., 2021a,b). We specifically aimed to address the following questions: (i) How do communal or individual rights affect farmer decisions to farm or keep forests or fallows in the games? (ii) Do financial incentives affect rural farmers' willingness to keep forests or fallows? (iii) Do the effects of the tenure and financial incentive treatments vary across different wealth, education and community trust levels? (iv) How do treatment effects vary across the two contexts, Madagascar and Kenya?

MATERIALS AND METHODS

Game Design

The game—Sharedspace—was framed around farmer decisions in swidden agricultural landscape and played on tablet computers linked via a mobile hotspot. It is part of a family of games developed using the NetLogo modelling platform to examine conflicts among people, resources, and wildlife that includes NonCropShare, a coordination game for insect-based ecosystem services (Bell et al., 2016), and GooseBump, a coordination game for resolution to human-wildlife and conservation conflicts (Rakotonarivo et al., 2021a,b). In the game, four farmers make land use decisions on a 6 × 6 grid-cell digital farming landscape. Each participant has an equal share of the land in the game, a total of nine cells each. On each cell, the farmer can decide to (i) conserve the forest (or fallow) or (ii) farm it for their private benefits (**Figures 1**, **2**). Each interactive game session consists of 7–12 rounds analogous to agricultural years where participants make decisions and have the option to communicate with other players between game sessions about any aspects of the game, including their choices, and beliefs about the optimal strategy. The number of rounds was randomised to prevent participants from anticipating the conclusion of a game session. In each round, participants decide whether to farm the cells or keep them as forest or fallow. Each grid cell was framed as "forest" at the



A

Round 1

Previous Round

Yield: 0

+ES Bump: 0

+ Subsidy/Bonus: 0

= Score: 0

Total Score: 0

B

Round 1

Previous Round

Yield: 0

+ES Bump: 0

+ Subsidy/Bonus: 0

= Score: 0

Total Score: 0

C

Round 1

Previous Round

Yield: 0

+ES Bump: 0

+ Subsidy/Bonus: 0

= Score: 0

Total Score: 0

D

Round 2

Previous Round

Yield: 36

+ES Bump: 9

+ Subsidy/Bonus: 0

= Score: 45

Total Score: 45

FIGURE 1 | Visual repress entation of the farming landscape in the individual right treatments, players are colour-coded, **(A)** the bottom left corner is the active player's 3 × 3 grid at the start of round 1; **(B)** the active player farmed three cells (the red coloured cells), the black numbers in the red coloured cells are the remaining number of farming cycles with high yield; **(C)** Game screen of the active player after all four players have made decisions at the end of round 1, the decisions taken by the other players are also visible (the green, blue, and pink cells are farmed by the three other players); **(D)** game screen of the active player at the start of round 2, the scores of the active player in previous round is shown in the left-hand side of the panel.

start of each game and "fallow" once it has been farmed for the first time.

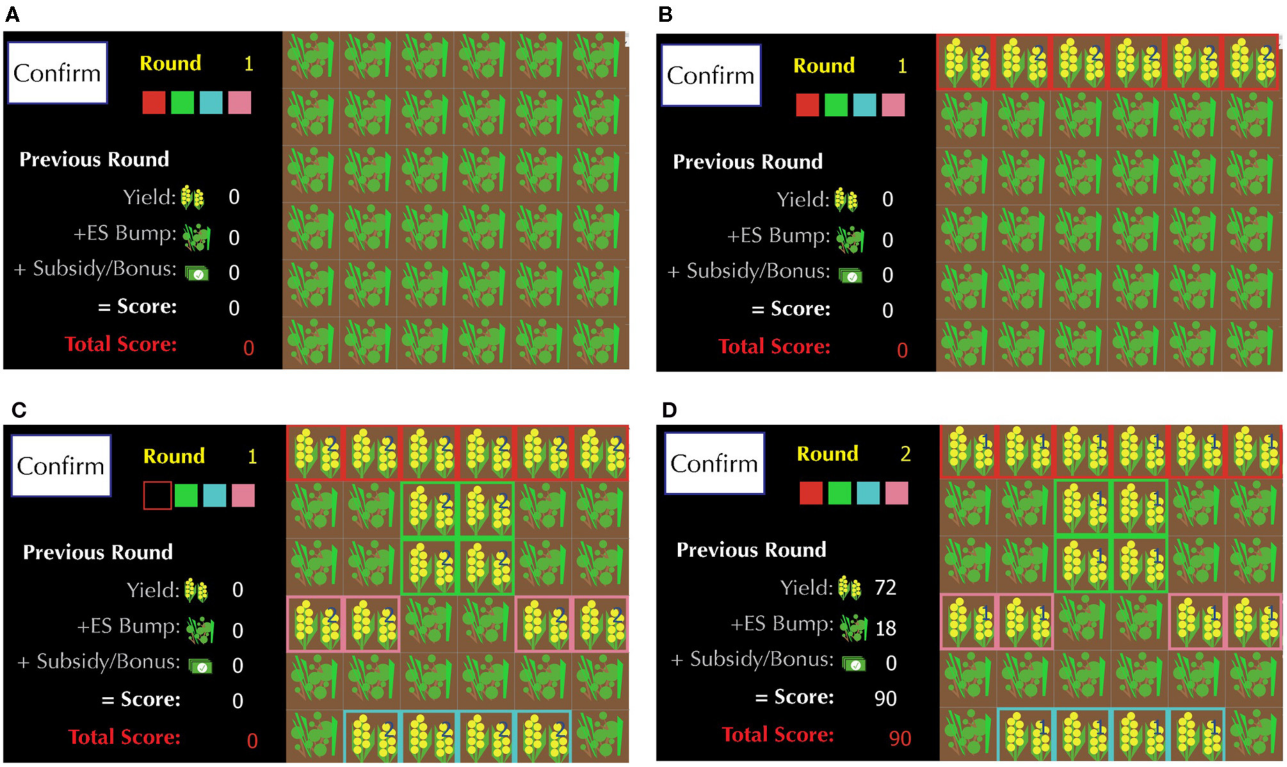
Farming the cell brings some yields, while keeping the forest or fallowing the cell boosts crop yields to neighbouring farmed cells through ecosystem service provision (e.g., pollination, soil restoration, watershed protection, landslide prevention) (**Table 1**). To reflect this, a forest/fallow cell increases the yield of all farmed cells within a radius of two cells by 1. These effects can spill over from one farmer to another. Since a fallow land yields the same ecosystem services as a fully intact forest, they were referred to as forest/fallow hereafter.

Returns from farming depend on the conditions of the lands. Farming gives a payoff of 12 when the farmed land is in good condition and 10 when it is not. If participants farm the same forest/fallow cell for two consecutive rounds, the land becomes depleted and the yield drops to the lower level in the following round. If participants continue farming the land of lower quality, the yield remains at the lower level. Fallowing the land for at least two consecutive rounds returns the yield to the higher level, and the soil fertility is restored (**Table 1**). The game is therefore temporally and spatially dynamic; the state of a cell in any given round is dependent on decisions taken in previous rounds, and the ecosystem's service provision depends on concurrent decisions on nearby cells. The maximum output for a farmed square from ecosystem services benefits is capped at 15 for a good quality land and 12 for a low-quality land. At the start of each session, all land is in good condition and leads to a high yield if farmed (**Table 1**).

In some of the treatments, a subsidy of x is given for every cell of forest/fallow in the landscape, where xx randomly takes aon random value of 4, 8, or 12 with equal probability in a game. Summing across squares under their control, participants' overall scores are calculated in each round as,

$$\text{Score} = \Sigma_{n=1}^{9}\text{Yield} + \Sigma_{n=1}^{9}\text{Ecosystem services} + \Sigma_{n=1}^{9}\text{Subsidy} \qquad (1)$$

To ensure sufficient realism and motivation for play, our treatments incorporated spatial dynamics (ecosystem services spilling over from forest or fallow lands to neighbouring farms). We also allow for the decisions of current rounds to potentially affect payoffs in future rounds. These game dynamics make it impossible to find closed form solutions for optimal play. However, it is possible to derive analytical solutions for simplified conditions (e.g., a single round of game play). The game parameters (**Table 1**) were specified to reflect a plausible range



A

Round 1

Previous Round
Yield: 0
+ES Bump: 0
+ Subsidy/Bonus: 0
= Score: 0
Total Score: 0

B

Round 1

Previous Round
Yield: 0
+ES Bump: 0
+ Subsidy/Bonus: 0
= Score: 0
Total Score: 0

C

Round 1

Previous Round
Yield: 0
+ES Bump: 0
+ Subsidy/Bonus: 0
= Score: 0
Total Score: 0

D

Round 2

Previous Round
Yield: 72
+ES Bump: 18
+ Subsidy/Bonus: 0
= Score: 90
Total Score: 90

FIGURE 2 | Visual representation of the farming landscape in the common right treatments, players are colour coded, **(A)** game screen of the active player at the start of the game; the player can farm any cells in the landscape (up to nine); **(B)** the active player farmed six cells (the red coloured cells in the first row of the grid); **(C)** game screen of the active player after all four players have made decisions at the end of round 1, the decisions taken by the other players are also visible, the green, blue and pink cells are farmed by the three other players; **(D)** game screen of the active player at the start of round 2, the scores of the active player in previous round is shown in the left-hand side of the panel.

TABLE 1 | Game parameters.

	Player choice (cell level)		
	Forest or Fallow	**Farm**	
			
		High yield*	**Low yield****
Yield	0	12	10
Neighbourhood effect	0	+1 for all neighbouring forest/forest/fallow cells (in a radius of two cells around the cell), up to 15	+1 for all neighbouring forest/fallow cells (in a radius of two cells around the cell), up to 12
Subsidy	x [4,8,12]***	None	None

At the start of each session, the yield on all cells is at the high level if the land is farmed.

***Yield drops to the lower level in any given round if the cell is farmed in the two previous rounds. It recovers the higher level after two consecutive rounds of fallowing.*

****In the subsidy treatment, a subsidy of X points is awarded for each forest or fallow cell, where X is an integer taking one of three values [4, 8, 12]. The value is randomly assigned at the start of each game session.*

of potential costs and benefit scenarios under these simplified conditions (for instance, for a single game round, farming all landscape cells yields the highest payoff regardless of the decisions of other players; however, a cooperative strategy of fallowing a single cell can result in a total higher total payoff for players than if all players farm all of their cells, despite being vulnerable to defection from the higher payoff strategy of farming all cells). We have provided a detailed explanation of the theory underlying our game design in Appendix A in **Supplementary Material**. While such theoretical predictions were useful for calibrating the game parameters, our analyses do not aim to test specific game theoretic predictions, but instead focus on how farmers respond to policy interventions and how these responses vary across different sub-groups.

Experimental Design and Data Collection

We used a within-subject design; each game session consists of one practise session (3 rounds) followed by four different game treatments played in random order in each game session. The four game treatments form a 2 × 2 design of (i) Subsidy vs. no subsidy, (ii) individual vs. communal property rights. Communication between participants was permitted in all the sessions as this mirrors the condition in which real-life incentive schemes operate. All elements of the game were explained at the start, including the randomly drawn subsidy values. The participants were all sitting in a circle and could easily talk to each other. The fallowing history and high/low yield status were visible on screen and could be tracked by participants.

In the individual property rights treatments, each participant is endowed with nine forest patches at the start of each game (3 × 3 grid-cell section of the 6 × 6 grid-cell agricultural landscape) (**Figure 1**). In each game round, participants choose whether or not to farm each cell. All four players make decisions in parallel every round. The round ends when all players have confirmed their choices. Participants can farm *or* forest/fallow cells as desired in all subsequent rounds. The scores (total points earned) are calculated for each cell on the choices made in and around the cell. At the end of each round, every participant can see decisions made by all participants in the landscape and what yields were achieved in each cell. When a subsidy is added, a randomly assigned flat subsidy is privately offered to each of the participant forest/fallow lands.

Under communal property rights, all four participants can access any cells in the agricultural landscape (**Figure 2**), this can mimic situations where farmers collectively own and manage forested lands. In each round, each participant can farm a maximum of nine cells, as in the individual rights treatment. In each game round, participants make simultaneous decisions, and the round ends when all four players have confirmed. Participants' identity is colour coded, so players can see each other's decisions during the round. A cell that is farmed by one participant can no longer be farmed by another participant (cells are allocated on a first come first serve basis during the round). Participants can choose to farm the same cells in subsequent rounds or move to other cells (in which case the cell becomes available to other players). When a subsidy is introduced, a randomly assigned flat subsidy is collectively offered for all forest/fallow lands at the landscape scale, the total value of the subsidy is then shared equally by all four participants.

We conducted our study in Madagascar and Kenya, two countries which have varying degrees of reliance on swidden agriculture (see section below on study context). We selected four villages near the Mangabe protected area in eastern Madagascar, and two villages adjacent to Mount Kenya National park and forest reserve in Kenya (**Figure 3**). We purposely selected villages near protected areas because of their specific features: participants in these settings live near protected forest resources; they have experiences of conservation restrictions, yet many of them are still highly dependent on swidden agriculture. These forest communities are also among the poorest in Madagascar and in Kenya.

In each of the study villages, we first compiled a full list of households residing in the village using key-informant interviews, ensuring isolated households and hamlets were also included. We then randomly sampled 75% from each list allowing for substitution if the selected household was not present in the villages at the time of the study or was not willing to participate. In total, we administered the games to 272 participants in Madagascar (68 groups of four participants) and 100 participants in Kenya (25 groups of four participants). Only one representative per household, the one who makes most agricultural decisions, was invited to participate in the games. Participants were compensated ∼1 day of local labour wage (2.5 and 3.5 USD in Madagascar and Kenya, respectively) for their time, plus a performance bonus based on their game play, 0.25 USD per 75 points earned in one of the games drawn randomly at the end of the session; this bonus ranged from 0.5 to 2.5 USD. The entire process lasted 60 to 120 min.

The game design and protocol (see **Supplementary Material**) were carefully piloted in nearby villages prior to implementation. We also conducted a follow-up survey with each participant after they had participated in the game. The survey included socio-economic characteristics such as age, gender, education, wealth levels, land holdings and community trust attitudes. After we finished administering the games in each village, we also facilitated a group debriefing session in which most participants attended. The aim of the debriefing was to explore respondents' rationales for their game decisions and relate their experiences from playing the games with their real-life experiences of forest conservation and farming practises. The research ethics committee of the University of Stirling approved this study; we told participants that results would be presented in aggregate form and would not be linked to their identity or villages. We gained verbal informed consent from all participants before implementing the games.

Study Context

Madagascar's protected areas have expanded from 3.1% of the terrestrial surface area (1.8 million hectares) in 2003 to ∼12% by 2010 (Corson, 2014; Gardner et al., 2018). Despite this expansion, deforestation continues at an alarming rate (Vieilledent et al., 2018) and is driven primarily by swidden agriculture (Urech et al., 2015; Zaehringer et al., 2015). The vast majority of local communities still rely on swidden agriculture to sustain their livelihoods (*idem*) and transitions to more intensive or sustainable agricultural practises throughout the island are yet to happen (Scales, 2014; Llopis et al., 2019).

In Kenya, as in many Sub-Saharan Africa countries, agriculture fuels the foundation of the economy and mostly consists of smallholder farmers (McCord et al., 2015). In Kenya, the traditional agricultural system based on swidden agriculture has become less common (Heinimann et al., 2017) and has over the years been replaced by more intensive small-scale agriculture

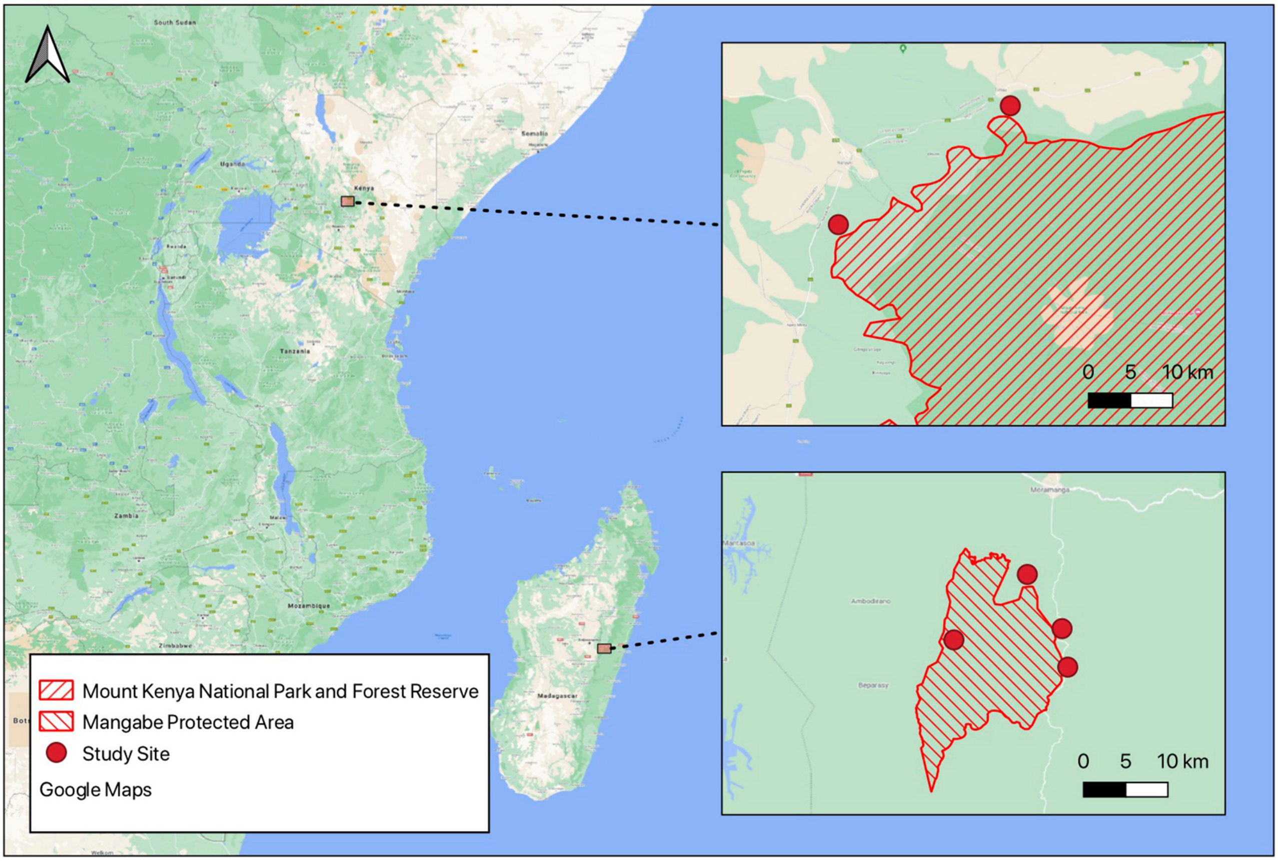


FIGURE 3 | Study sites (four villages near the Mangabe protected area in eastern Madagascar, and two villages adjacent to Mount Kenya National park in Kenya).

(Eckert et al., 2017). However, in the wake of population increase in Kenya, more land is put under cultivation to meet the food demand (Eckert et al., 2017). Forest conversion to agricultural lands (especially subsistence) in Sub-Saharan Africa is a popular practise, and Kenya is not exempted.

Decentralisation processes or the transfer of management rights to local communities were initiated in both Madagascar and Kenya in the 1990s and have led to the establishment of community-based forest management or forestry associations (Ferguson et al., 2014; Chomba et al., 2015). All participants surveyed in this study were members of such community associations. In theory, communities' rights in these associations are limited to management, only governments have a vested right to legally own forestlands in both countries. Therefore, the individual and communal property rights treatments investigated in this study (in which local people enjoy a full bundle of rights over forestlands, including ownership, exclusion and alienation rights) (Schlager and Ostrom, 1992) are hypothetical treatments. We explained to our study participants that in our game scenarios, they own the forestlands and have full freedom of choice over their use. We also emphasised our independence from government authorities and ran lengthy warm-up sessions to desensitise the issue of forest clearing for swidden agriculture and ensure participants fully understood the rules of the game.

Data Analysis

Our main outcome variable is the average percentage of cells left forest/fallow (average number of forest/fallow cells × 100/9), defined at the individual player level. This variable represents game level data summed over the rounds within each game treatment. Rounds 9 to 12 were dropped to avoid end game effects. The dataset is panel in nature because the randomly assigned treatment varies across but not within games and individuals are observed at different points in time (as in a within-subject design). We estimate average treatment effects by regressing participant decisions to keep forests or fallow their lands on the treatment variables. The individual treatment is represented by a binary variable for whether or not participants have individual ownership of forestlands. For the subsidy treatment, the analysis considers both binary (whether or not a subsidy is given) and discrete random variables (subsidy rate per forest/fallow cell, taking the value of 0, 4, 8, or 12).

We estimate a fixed effect panel data model on the pooled round-level data, separately for each country, and then test the significance of the estimated treatment effects on mean fallowing (or forested cells) (equation 2) (Woolridge, 2010). Fixed effect is a panel data model, which is useful when the outcome variable, mean fallowing, depends on explanatory variables, which are not observable but correlated with the observed explanatory variables

(Woolridge, 2010). They thus allow the time-invariant observed and unobserved variables (i.e., variables that don't vary across treatments such as participants' demographics) to correlate with the error term. As data points from the same group are not independent from one another, we cluster the standard errors at the group-game level to allow for correlations between the group-specific error components. We also test for the interaction between individual rights and subsidy treatments.

$$Y_{it} = \lambda + a_1 R_{it} + a_2 S_{it} + a_3 R_{it} S_{it} + \beta_1 R_{it} X_{it} + \beta_2 S_{it} X_{it} + \beta_3 R_{it} S_{it} X_{it} + \alpha_i + \varepsilon_{it} \quad (2)$$

i: participant
t: round
Y: average percentage of cells left forest/fallow (outcome)
λ: intercept
R: property right (individual or communal)
S: subsidy
X: participant characteristic (age, gender, education, wealth, land size, or community trust)
$a_1, a_2, a_3, \beta_1, \beta_2, \beta_3$: scalar coefficients
α: fixed effects (unobserved time-invariant variables)
ε: Time-varying error.

To assess how different subgroups might react to the treatments, we interact the two treatments with the specific variables of interest: education, wealth, and community interpersonal trust (this was specified as a three-way interaction between the two treatments, individual rights and subsidy and individual characteristics). Community trust is a numeric variable representing the weighted factor scores from three survey measures of trust among local communities (**Table 2**, **Supplementary Figure 3**). The wealth variable is the first principal component vector of a range of household wealth indicators (such as household assets, livestock, food security, extracted from a principal component analysis (PCA) using the psych package and promax rotation (Revelle, 2018) (**Supplementary Table 1**, **Supplementary Figure 1**). We hypothesised that subsidy would provide poorer participants with the much-needed short term resources to forego swidden agriculture (Nyein and Shinya, 2016; Dressler et al., 2017) and that higher educated participants would be more able to invest in off-farm activities and hence more likely to be responsive to financial incentives (by being less reliant on swidden agriculture and instead opting for more forest/fallow lands) (Van Vliet et al., 2013). We also expected that participants who have higher levels of trust toward other community members would be more likely to keep forest/fallow under communal ownership. This is because community members with increased interpersonal trust are more likely to comply with institutional arrangements for management of land and forests at the community level (Cramb et al., 2009). The controls include socio-economic variables such as age, gender, and lands under swidden agricultural systems.

All of the explanatory variables were standardised (expressed as z-scores), with the exception of the treatments and gender, to enable the comparison of magnitudes of estimated coefficients within models. We attempted to identify differences across the two countries and what factors might have contributed to those differences by comparing regression estimates across countries. The fixed effect models were conducted in STATA 16.0 and all other analyses (such as PCA) in R version 4.0.2 (R Core Team, 2020).

RESULTS

Participant Characteristics

The control variables and the variables hypothesised to be associated with the treatment effects are summarised in **Table 2**. Significant differences are observed in the socio-economic characteristics of participants across the two countries. The average age of participants was 49 in Kenya and 35 in Madagascar. The number of official schooling years of the Kenya sample was three times higher than that of Madagascar (**Table 2**). Participants were 70% male in Madagascar, while gender was more balanced in Kenya (47% male). PCA of ten measures of wealth resulted in the first two principal components explaining 44% of the variation and revealed that the Kenya sample had much higher average wealth levels (**Supplementary Table 1**, **Supplementary Figure 1**). Participants in Kenya were much more food secure; they perceived that they had a variety of food and enough to eat for almost 12 months for the past year (vs. only 6 months in Madagascar) (**Supplementary Table 1**). The first axis of the PCA, which was used in the fixed effect model, was strongly correlated with measures of food security and livestock. Almost all the game participants relied on agriculture as their primary sources of income (98 and 100% in Madagascar and Kenya, respectively). Twenty two percentage of the total sample in Kenya also had other sources of income such as livestock and small businesses vs. 55% in Madagascar (such as small trades, charcoal making, wild food harvesting). Proxies for community trust were high (>53%) in both countries (**Supplementary Figure 3**).

The average size of lands cultivated by each participant household was 0.39 and 0.97 hectares in Kenya and Madagascar, respectively. The lands cultivated by the Malagasy sample consisted mostly of swidden agriculture plots on hillsides, created originally from forest clearings. However, lands used by most Kenyan participants were under agroforestry practises, which consist of intercropping perennial and annual food crops, also known as the shamba system.

Treatment Effects and Their Variations Across Subgroups

Participants in Kenya kept significantly more forests/fallows on their lands (**Figure 4**, **Supplementary Figure 2**). The average percentage of forest/fallow lands across all rounds and games were 65 and 35% in Kenya and Madagascar, respectively. Individual ownership significantly increased decisions to keep forest/fallow by 12 percentage points in Madagascar but had no significant effect in Kenya (models 1 and 2, **Table 3**). Subsidies also had slightly different effects on participant decisions in each of the two countries, significantly raising decisions to keep forest/fallow in Kenya by 9 percentage points and only by 2 percentage points in Madagascar. Decisions to keep forest/fallow did not significantly change across rounds. However, in Madagascar, decisions to fallow decreased with

TABLE 2 | Descriptive statistics of predictor variables included in the models.

Variables	**Description**		**Summaries**	
		Country	**Kenya ($n = 100$)**	**Madagascar ($n = 272$)**
Age	Numeric variable indicating the age of the participant	Mean	49.52	35.82
		SD	12.79	13.71
		Min	22	18
		Max	79	75
Education	Numeric variable indicating the years of official schooling of the participant	Mean	9	3.213
		SD	2.543	3.049
		Min	0	0
		Max	15	12
Gender (Male)	Binary variable indicating whether the participant was male	%	47%	70%
Wealth component 1	Numeric variable representing the first principal component score from 10 measures of wealth and explaining 30% of the total variation (**Supplementary Table 1** and **Supplementary Figure 1**)	Mean	−0.55	1.50
		SD	0.40	0.40
		Min	0.63	−1.26
		Max	2.47	1.11
Off-farm income	Binary variable indicating whether the participant household has other sources of income than	%	22%	55%
Land size	Numeric variable measuring the land size cultivated by the household agriculture in the past agricultural year (measured in local units and converted in acres)—The value in Madagascar are proxies for areas used in swidden agriculture	Mean	0.97	2.41
		SD	0.86	4.61
		Min	0	0
		Max	5	27.1
Community trust index	Numeric variable representing the weighted factor scores from three measures of trust among local communities; figure Sx; Cronbach's alpha* = 0.48, the one-factor solution explained 48% of the total variance (this table and **Supplementary Figure 3**)	Mean	−0.003	0.010
		SD	0.97	0.75
		Min	−2.22	−2.5
		Max	1.15	1.15

rounds in three of the four treatment conditions (**Figure 4**). This effect was most pronounced under communal ownership; fallowing decisions were as high as 40% at the start of the game and decreased by half by round 3 (**Figure 4**). This was particularly the case when subsidy was also introduced under communal rights (**Supplementary Figure 2**). These results are robust to alternative specifications of subsidy as a continuous (models 2 and 4, **Table 3**) or categorical variable (**Supplementary Table 3**). We find no interaction effects of the two treatments in either country.

To examine how different subgroups react to the treatments and try to explain the differences in observed outcomes across the two different samples, we interacted the treatments with three variables of interest: education, wealth, and community interpersonal trust. Contrary to our expectations, we found no association between the effect of subsidy and wealth or education in either country (models 5 and 6, **Table 3**). These results persisted even when subsidy was specified as a continuous variable (models 7 and 8, **Table 3**). Instead, we found that in Madagascar, education level and wealth affected the effectiveness of the individual property right treatments in encouraging fallowing decisions (**Supplementary Figure 5**). A one standard deviation increase in education is associated with an increase in fallowing of 3.3 percentage points under individual ownership: this amounts to almost 10 % of the community ownership reference level. On the other hand, the individual right treatment was less likely to lead to increased decisions to keep forest/fallow among wealthier participants; a one standard deviation increase in wealth levels is associated with a decrease in fallowing of 1.6 percentage points under individual ownership (compared to communal rights) (model 5, **Table 3**). These effects were not robust to the alternative specification in which the subsidy is specified as a continuous variable (model 7, **Table 3**). Participants with larger swidden agriculture plots in Madagascar (as represented by the variable "land size", **Table 2**) were more likely to keep forest/fallow in the individual right treatments (2.3% increase which is robust to alternative specification) (model 5, **Table 3**).

We did not find any association between the property rights treatment and community trust level in either of the two countries. In Kenya, we did not observe any associations between the treatment effects and any of the socio-economic characteristics, except the off-farm income (model 8, **Table 3** where subsidy was specified as a continuous variable). The subsidy was more effective at encouraging decisions to keep forest/fallow among participants who had other sources of income than agriculture (1.26% increase).

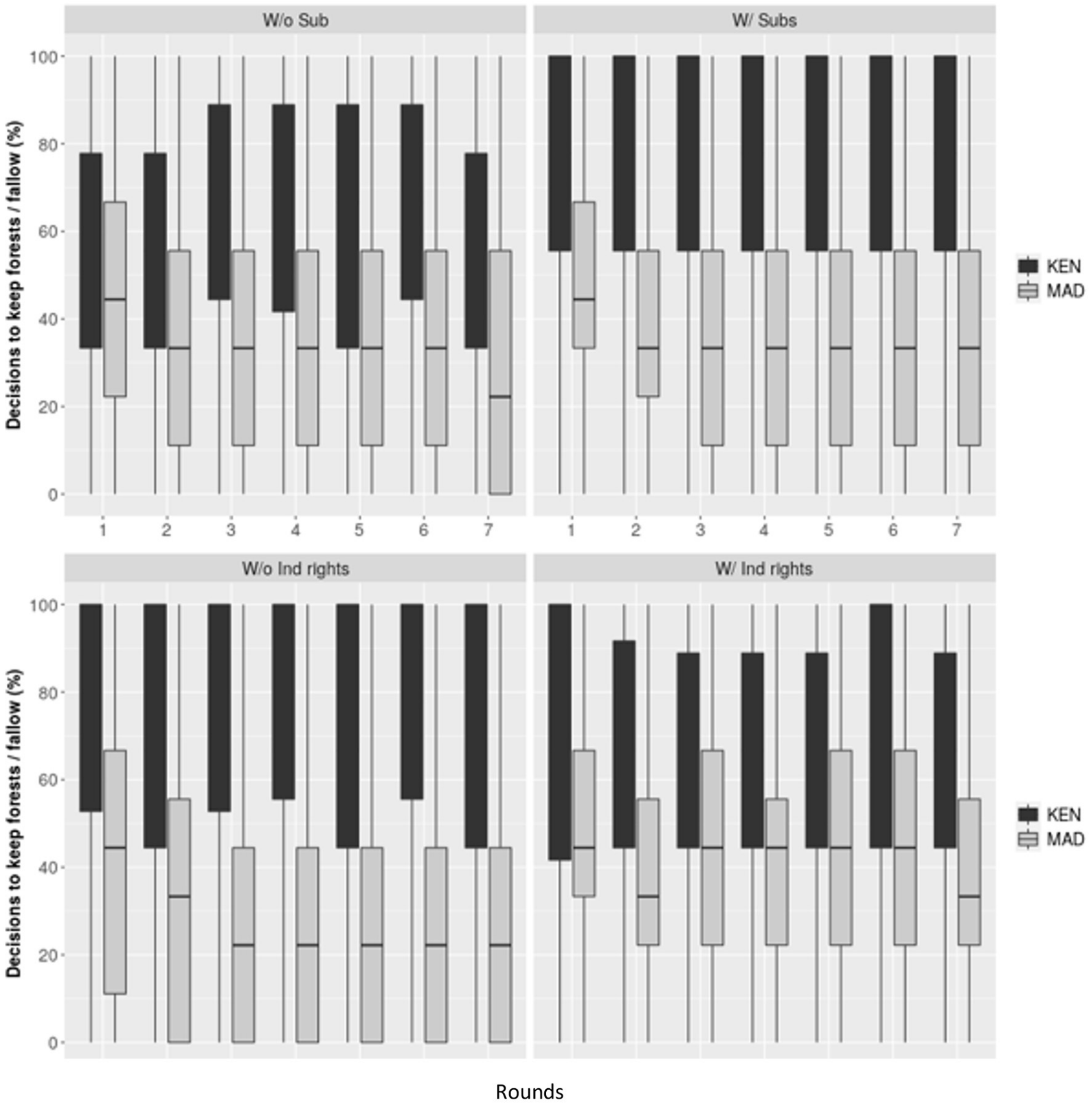


FIGURE 4 | Distribution of mean observed percentages of decisions to keep forest/fallow in the treatments and rounds (Subsidy takes a value of 1 if there is subsidy, 0 otherwise, and same with individual rights) across households and groups. The median marks the midpoint of the data and is shown by the line that divides the box into two parts. The box represents the middle 50% of percentages of decisions to keep forest/fallow.

DISCUSSION

Our study examines farmer responses to financial incentives and property rights to forestlands using a temporally and spatially dynamic interactive game in Madagascar and Kenya. We find that farmer proconservation behaviour (which we define as farmer propensity to keep forest or fallow lands) as well as the effects of land tenure and fallowing subsidy treatment vary considerably across the two contexts. Participants in the Kenyan sample were twice as willing on average to forego farming on their lands as players in the Malagasy sample. Though our experiment was not designed to fully disentangle the differences in game outcomes across the two countries, we discuss a few possible causes using responses to the follow up survey and insights from the literature and the community debriefings.

The first set of possibilities lie in the stark contrasts in wealth and swidden agricultural practises across the two countries. In Kenya, agroforestry practises have been partially shaped by a government-led plantation establishment and livelihood improvement scheme (PELIS). This scheme has been highly effective in improving food security and income among community members (Witcomb and Dorward, 2009). Since these agroforestry systems are practised on forested plots which are generally very fertile, levels of surplus output and extra income tend to be relatively high (Kagombe and Gitonga, 2005). However, farmers in eastern Madagascar mostly

TABLE 3 | Estimates from the fixed effect panel data model showing the effects of the treatments on individual participant decisions to keep forest/fallow and their variations across different subgroups.

	Treatments only (subsidy binary)		**Treatments only (subsidy continuous)**		**Treatments and other covariates (subsidy binary)**		**Treatments and other covariates (subsidy continuous)**	
	M/car (1)	**Kenya (2)**	**M/car (3)**	**Kenya (4)**	**M/car (5)**	**Kenya (6)**	**M/car (7)**	**Kenya (8)**
Ind_Rights	12.255***	−4.032	12.483***	−5.214	11.251***	−2.983	11.284***	−4.977
	(1.117)	(2.806)	(1.138)	(2.53)	(2.019)	(3.827)	(1.78)	(3.66)
Subsidy	2.533**	9.222***	0.317***	0.908**	5.254**	9.43**	0.575**	0.826*
	(0.985)	(2.852)	(0.103)	(0.355)	(2.274)	(3.845)	(0.244)	(0.435)
Ind_Rights*Subsidy	0.951	2.222	0.059	0.551	−0.846	−0.385	−0.095	0.365
	(1.04)	(3.233)	(0.122)	(0.342)	(3.076)	(4.453)	(0.325)	(0.456)
Ind_Rights*Age					−0.948	1.716	−1.005	2.107
					(0.911)	(2.147)	(1.026)	(1.999)
Subsidy*Age					1.341	−0.546	0.162*	−0.023
					(0.851)	(2.139)	(0.093)	(0.294)
Ind_Rights*Subsidy* Age					−1.1	0.854	−0.122	0.015
					(0.911)	(2.423)	(0.108)	(0.312)
Ind_Rights*Male					2.67	−2.65	2.361	−2.122
					(1.97)	(3.37)	(1.909)	(3.45)
Subsidy* Male					−2.83	−2.861	−0.308	−0.576
					(2.16)	(4.052)	(0.26)	(0.543)
Ind_Rights*Subsidy* Male					0.423	8.002	0.117	1.041
					(2.733)	(4.931)	(0.319)	(0.615)
Ind_Rights*Education					3.352***	−0.216	3.143***	−0.007
					(1.045)	(2.106)	(0.984)	(1.839)
Subsidy*Education					0.811	0.742	0.067	0.102
					(1.096)	(1.316)	(0.12)	(0.192)
Ind_Rights*Subsidy* Education					−0.078	2.044	0.047	0.152
					(1.19)	(2.27)	(0.134)	(0.237)
Ind_Rights*Wealth					−1.618*	0.136	−1.381	0.77
					(0.811)	(1.858)	(0.879)	(1.815)
Subsidy*Wealth					0.491	0.187	0.082	0.092
					(0.934)	(2.453)	(0.105)	(0.297)
Ind_Rights*Subsidy* Wealth					0.039	1.101	−0.051	0
					(0.903)	(2.658)	(0.101)	(0.285)
Ind_Rights*Land size					2.30***	−1.88	2.21***	−2.382
					(0.751)	(2.749)	(0.791)	(2.626)
Subsidy* Land size					0.84	3.073	0.01	0.329
					(1.193)	(2.045)	(0.125)	(0.2)
Ind_Rights*Subsidy* Land size					−1.407	−1.204	−0.139	−0.109
					(0.98)	(3.102)	(0.110)	(0.321)
Ind_Rights*Community trust					0.545	−2.871	0.453	−3.009
					(0.832)	(3.125)	(0.843)	(2.857)
Subsidy*Community trust					0.876	−2.57	0.106	−0.234
					(0.823)	(1.581)	(0.091)	(0.223)
Ind_Rights*Subsidy*Com-munity trust					−1.109	3.554	−0.114	0.505
					(1.071)	(2.335)	(0.117)	(0.305)
Ind_Rights*Off farm_ income trust					−1.582	0.91	−0.973	2.595
					(1.956)	(5.222)	(1.954)	(4.871)

(Continued)

TABLE 3 | Continued

	Treatments only (subsidy binary)		**Treatments only (subsidy continuous)**		**Treatments and other covariates (subsidy binary)**		**Treatments and other covariates (subsidy continuous)**	
	M/car (1)	**Kenya (2)**	**M/car (3)**	**Kenya (4)**	**M/car (5)**	**Kenya (6)**	**M/car (7)**	**Kenya (8)**
Subsidy*Off farm income					−1.331	5.168	−0.068	1.268**
					(2.044)	(5.352)	(0.211)	(0.606)
Ind_Rights*Subsidy*Off farm income					2.72	−5.244	0.16	−1.159
					(2.384)	(6.433)	(0.271)	(0.714)
Mean (ind_rights = 0)	29.09	67.15	29.09	67.15	29.09	67.15	29.09	67.15
Mean (Subsidy = 0)	33.95	60.52	33.95	60.52	33.95	60.52	33.95	60.52
Constant	27.83***	63.375***	27.763***	63.375***	27.83***	62.54***	27.779***	63.554***
	(0.705)	(1.517)	(0.688)	(1.517)	(0.665)	(1.56)	(0.652)	(1.435)
Observations	1,088	400	1,088	400	1,088	400	1,088	400
R-squared	0.341	0.187	0.342	0.187	0.38	0.209	0.379	0.244

*Subsidy is modelled both as a binary variable (models 1, 2, 5, and 6) and as a continuous variable (models 3, 4, 7, and 8). The treatments are the only explanatory variables in models 1, 2, 3, and 4, while the treatments and other treatment-fixed variables are included in models 5, 6, 7, and 8 in interaction terms. Data were pooled across rounds within each game treatment. Standard errors are in parentheses, ***$p < 0.01$, **$p < 0.05$, *$p < 0.1$.*

rely on swidden agriculture with very low use of agricultural inputs, chemical fertilisers and improved seed varieties (Harvey et al., 2014). Most Malagasy farmers receive little to no technical assistance in crop production and rely on rudimentary technological approaches (Styger et al., 2007). These differences in farming practises across the two contexts are reflected in their different wealth levels, with the Kenyan sample being better off both with respect to technological assets and food security (**Supplementary Figure 1**). However, we note that these wealth measures were only proxies of rural income and do not fully account for rural livelihoods and environmental income (Angelsen et al., 2014).

Differences in conservation enforcement levels might have also contributed to the differences in forest/fallow decisions in the games across the two contexts. In the follow-up survey, all the Kenyan participants unanimously reported that the risks of being fined would deter them from clearing forests for agriculture, vs. 80% of the Malagasy participants. Although clearing forests for swidden agriculture is banned in Madagascar, enforcement on the ground is often very weak, and corruption and non-compliance are salient features of forest conservation in many rural areas (Gore et al., 2016). In these contexts, clearing forestland for agriculture often gives farmers land rights (Angelsen, 1999; Rakotonarivo et al., 2017). More rapid forest clearance, as observed among the Malagasy sample, becomes an investment to the farmer and is a right establishment strategy.

The individual rights treatment had no effect on Kenya participants' decisions but led to better conservation outcomes compared to the communal right treatment in Madagascar. While community members in Madagascar are entitled to decide how forest resources can be used and the corresponding benefits shared, these benefits are often in practise very vulnerable to elite capture (Poudyal et al., 2016). These elite captures often result in participants being much less inclined to follow community conservation rules and engage in less sustainable agricultural practises. These fears of biassed benefits toward the better socially connected community members were reflected in the survey responses; 42% of the Malagasy sample reported having low and very low trust toward the leaders and decision-making members of community forestry associations (**Supplementary Figure 4**). Community leaders can play a critical role in aligning community members' practises with the provisions of community-level institutions (Corbera et al., 2020). If they are not trusted by a large share of community members, they might fail to nurture the collective actions and social norms that have been associated with enhanced forest conservation under communal rights (Ostrom and Hess, 2008).

The literature suggests mixed evidence on the impact of property rights on environmental outcomes. While a comparative study found that indigenous communities management significantly reduced deforestation and forest carbon emissions in Bolivia, Brazil and Colombia (Blackman and Veit, 2018), a metanalysis suggests that community management and land tenure security were not consistently associated with either less or more deforestation (Busch and Ferretti-Gallon, 2017). The evidence is even less clear on the effectiveness of PES under individual and communal rights to forests. PES resulted in positive environmental outcomes among individual forest-owning households in Uganda (Jayachandran et al., 2017) and Costa Rica (Arriagada et al., 2012). PES can be equally effective when built upon communal tenure rights such as community based-forest management (Brouwer et al., 2011; Baylis et al., 2012). The absence of interaction effects between our two policy options might be explained by the large effect of the individual property rights and financial incentives on participants' decisions in Madagascar and in Kenya, respectively.

In-migration and the community inability to prevent forest clearance by migrants were also reported as a potential explanation for the lower pro-conservation behaviour observed in the communally owned treatment in Madagascar. The debriefing suggested that migrants move to the forest frontier mostly to access new lands. As new migrants increase the number of people sharing the return from the common resources, participants perceived that their rights were more secure under individual ownership. Individuals who belong to a cooperative do not also perceive a direct link between their personal contributions and benefits. Migrants, who are also often better educated, do not often recognise the legitimacy of communal management rights. This often results in less secure property rights that lead potential users to engage in conflicts so as to gain control over forestlands through clearance. These patterns have also been observed elsewhere in Madagascar (Jones et al., 2018).

Interestingly, we found that in Madagascar, the positive effect of the individual tenure treatment in encouraging pro-conservation behaviour was significantly greater among better educated and wealthier participants. This might pose risks for equity if the privatisation of forest resources mostly benefits the elites, or the power and resource holders (Benjaminsen et al., 2009). We also found that participants with larger swidden agriculture plots in Madagascar were more likely to keep forest/fallow in the individual right treatments. This is most likely because they can afford to rotate between various plots and keep more forests or fallow lands (Styger et al., 2007).

In Kenya, the absence of a significant effect of the property right treatment on participants' decisions to keep forest/fallow are puzzling, as we did not observe any associations between the treatment effects and the participants' characteristics. The results might stem from the irrelevance of tenure security among the Kenyan sample who exclusively use public gazetted lands under the control of the Kenyan forest services for a limited number of years, with no prospect of rights transfer to forest users. Unlike the Malagasy sample, participants in Kenya showed relatively high levels of trust both toward the community forest associations leaders and the Kenyan forest service (**Supplementary Figure 4**). The Kenya participants also felt that the current government forest strategy balances forest conservation and rural development, mostly through the PELIS scheme which allows community members to practise agroforestry in government-owned degraded lands. Participants also perceived additional livelihood benefits from these schemes, such as fuelwood and access to pasture. This was in stark contrast to farmers' perceptions of conservation organisations in Madagascar, whose restrictions on forest use and access were felt to have severely constrained local livelihoods (**Supplementary Figure 4**) (Gore et al., 2016).

The subsidy increased farmers' willingness to support conservation interests in both countries, but its effect was considerably greater in Kenya. These results are congruent with previous studies showing the role of payments in incentivising forest conservation (Cárdenas, 2017; Sims and Alix-Garcia, 2017). The differences in the effect sizes of subsidy across the two contexts are not immediately clear, as the two samples differ in many socio-economic factors, including land ownership, farm holding size, education, wealth levels, and levels of trust toward governments and conservation agencies, which may affect people's attitudes toward the payments. These results might also be explained by unobservable factors beyond what the surveys and experiments were able to capture. As participants received both the show-up fee and a second payout that was tied to their performance in the games, this might have introduced some real stakes that may be associated with varying wealth levels across the two countries.

Another explanation for the different findings across countries lies in possible differences in the administration of the games. This is unlikely, since we used the same game instructions, and all enumerators were trained by the same person (lead author). We cannot rule out potential differences in understanding the game rules across the two countries which could be associated with different education levels. The use of the same game protocol, practise rounds, and visual handouts should have helped reduce these confounding factors.

As in all game-based studies, the external validity of our results (the extent to which the game decisions reflect what participants would do in real life) is difficult to assess (Jackson, 2012). Our game did not allow more detailed incorporation of the complex socio-ecological context and the study of social interactions as is common in serious boardgame studies (e.g., Celio et al., 2019; Speelman et al., 2019; Andreotti et al., 2020). Adding more complexity would risk both the tractability of the analysis and player engagement. In addition, the game features, which are stylised representations of the swidden agricultural systems, might not match participants' characterisations of these elements. In particular, the communal and individual property rights tested in our game design are new in both contexts, i.e., none of the participants have directly experienced such tenure reforms (see study section). Contested and unclear property rights is an issue in many tropical forest countries (Rights and Resources Initiative, 2018; Robinson et al., 2018; Sunderlin et al., 2018). The experimental games we developed in this paper were thus useful in testing the effectiveness of such interventions, which would otherwise be very costly and difficult to test at reality scale.

Despite the hypothetical nature of these interventions, understanding of the game rules and the interventions was generally high across the two countries and was greatly enhanced by the practise rounds, and additional explanations provided by the facilitators (OSR and AK who are both native speakers of Madagascar and Kenya, respectively). Surveys confirmed that participants seriously thought of the consequences of their choices and took into account real-life contexts (such as immigration, elite capture, low trust toward community leaders as evidenced by the debriefings) in their game decisions. In addition, a follow up question asking participants about their main goal in the games further suggested that 185 (68%) and 97 (97%) participants in Madagascar and Kenya, respectively, aimed to maximise their utility by playing as in real life (**Supplementary Figure 6**).

Although our game settings were necessarily simplified, they were perceived by most participants as a safe and useful decision-support tool to voice their preferences. The incorporation of the temporal and spatial dimension also enhanced realism and helped uncover nuances that are invisible to conventional tools such as questionnaire surveys (Murnighan and Wang, 2016). For instance, most participants alluded to the importance of ecosystem services provided by the forests and fallow lands in the debriefing meetings (such as microclimate and protection against soil erosion) and the influence that these ecosystem services had on their decisions.

The differences in forest/fallow decisions in the context of the games and in the real-life contexts across the two countries also show that the games can provide a lens into real world choices. Games are best understood as one perspective within a body of knowledge on forest user behaviour and how they are affected by factors of interest such as property rights or incentives, rather than having specific real-world patterns against which they must be validated (Camerer, 2015). Our results provide important insights on the influence of PES and communal and individual property rights on forest user decisions in contexts where forest tenure is unclear and contested. We draw upon the group debriefing and the follow-up survey to contextualise our results.

While we had to simplify the property right treatments in our experimental game design and were not able to include a baseline reference of weak and insecure tenure, our study sheds light on the influence of individual and communal property rights to forestlands in PES schemes. We argue that if PES programmes are developed in contexts of weak state enforcement and unclear rights to forests, their effectiveness might be seriously compromised (e.g., Robinson et al., 2014; Paudel et al., 2015; Riggs et al., 2016; Horning, 2018; Corbera et al., 2020). The majority of effective PES to date have been implemented in countries where the institutional framework is well-defined and where land is individually owned (Pagiola, 2008; Karsenty et al., 2014; Myers et al., 2018; Sunderlin et al., 2018). Designing PES in situations of weak institutions is challenging, yet these contexts are dominant features of biodiversity hotspots where threats to ecosystem services are the highest (Chomitz et al., 2007) and where conservation actions are viewed as most urgent (Mittermeier et al., 2011).

In conclusion, we used a dynamic interactive game framed around farmer land-use decisions to examine farmer responses to two new policy options, financial incentives under individual and communal forest ownership. We found that their effectiveness in preserving forestland varied across contexts; the individual right treatment had no effect on participant decisions in Kenya, but in Madagascar, it led to much better conservation outcomes than the communal rights treatment. The incentives increased farmers' willingness to support conservation interests in both countries, but its effect was four times greater in Kenya. Such mixed relationships between property rights and forest conservation outcomes have also been reported in other contexts (Robinson et al., 2014; Busch and Ferretti-Gallon, 2017; Blackman and Veit, 2018). In contexts such as Madagascar, with strong reliance on swidden agriculture and a de facto open access regime, giving local communities individual property rights to forestlands on its own might be effective at incentivising conservation. However, where people feel relatively secure about their rights, and where people have adapted to stronger enforcement and transitioned from swidden agricultural practises, tenure reforms might be inefficient. In these contexts, subsidies can play a major role in encouraging proconservation behaviour. There is no panacea; no single set of institutions generates better outcomes for the resource and for the users under all conditions. We show how interactive games can help develop a more targeted and practical approach to environmental policy in a given context.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://reshare.ukdataservice.ac.uk/854068/.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the ethical review committee of the University of Stirling (GUEP286). Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

OSR, AB, and AD conceived the ideas and designed the games. OSR, AB, AD, JR, and NB provided important inputs on the research design. OSR and AK collected the data. OSR analysed the data with inputs from BD and RAR. OSR led the writing of the manuscript. All authors have contributed critically to the drafts and have given final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.661987/full#supplementary-material

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Conflict of Interest: JR is the executive director of the association Madagasikara Voakajy which manages Mangabe protected area, one of our study areas.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.