IMPACTS OF HABITAT TRANSFORMATION ON SPECIES, BIODIVERSITY AND ECOSYSTEMS IN ASIA

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EDITORIAL
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Editorial: Impacts of Habitat Transformation on Species, Biodiversity and Ecosystems in Asia

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Keywords: biodiversity loss, conservation, habitat transformation, ecosystem health, urbanization

Editorial on the Research Topic

Impacts of Habitat Transformation on Species, Biodiversity and Ecosystems in Asia

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PRESENT AND FUTURE OF BIODIVERSITY IN ASIA

Asia is a land of contrasts. This is the largest and most populated continent of the world, it is where urbanization is increasing at the highest rate (Seto et al., 2012). At the same time, it is extremely biodiverse (Myers et al., 2000), so that promoting harmonious human-wildlife coexistence is complex. This complexity is not recent. Ancient civilizations populating this area have left a lasting impact on its nature (Ellis et al., 2021), and recent impacts add to these historical effects. This issue is acknowledged by governments across Asia, who have recently developed numerous initiatives to protect their biodiversity (Ghosh-Harihar et al., 2019; Wu et al., 2019). Yet, despite increasing regional conservation efforts, not all species will make it. For instance, millions-year old species are still being led to extinction (Zhang et al., 2020). In a recent positive development, the United Nations' Convention for Biodiversity (COP-15) will set a 30% threshold of protected areas of terrestrial land (Zhu et al., 2021). But, to achieve such an ambitious biodiversity conservation goal, urgent action is needed.

This Research Topic aimed to assess the impacts that human-driven habitat transformation has on species, biodiversity, and ecosystems in Asia, and to envision ways in which these impacts can be minimized. Moreover, our intention was to bring together research works from around Asia (and the rest of the world) which address this issue. We gathered papers authored by researchers from 8 countries, i.e., India, China, Singapore, Australia, Pakistan, Brunei, Sri Lanka, and United States. We are convinced that collaboration among Asian nations is an essential condition for any meaningful biodiversity conservation targets to be achieved (Chen et al., 2019; Bawa et al., 2020). We are also convinced that biodiversity conservation should develop interdisciplinary approaches outside the boundaries of traditional academic disciplines, and that it should be science that addresses people's and nature's needs (Kremen and Merenlender, 2018). This collection of 12 papers is our humble contribution to achieve these conservation targets in Asia.

IMPACTS AND SOLUTIONS

Due to the broad and ambitious goal of this Research Topic, its papers are heterogeneous in their scopes and aims. In this volume, you will find works focusing on landscape ecology, ecological restoration, human-wildlife conflict, and investigating animal behavior in response to habitat transformation.

Human infrastructure construction is a key driver of biodiversity loss. For instance, hydropower stations are very impactful infrastructures that can profoundly disrupt ecosystem dynamics (Anderson et al., 2015). Here, we are presenting two studies examining the consequences of hydropower station construction for ecosystem dynamics in upstream systems. For instance, using the Lancang River (also known as the Mekong River) Valley (SW China) as a case study, Liu S. et al. showed that forest connectivity decreased after the construction of the station, particularly upstream, in small forest patches and in large patches in the edge of the study area. In another study, Jelil et al. illustrated mammal persistence in upstream riparian forests at Koyna Reservoir (W India) 55 years after the construction of a hydropower station. They show that ungulates were particularly abundant close to the river body, that small body-sized ungulates had higher extinction risk, and that distance to the river was the main factor explaining species detection.

Also from a landscape ecology perspective, Wang et al. quantitatively examined landscape change patterns in the Yancheng National Nature Reserve in the coast of East China to show that newly built artificial landscapes (such as farmland and aquaculture ponds) grew at the expense of natural habitats, and report an overall steep increase in the surface of these human-made landscapes. Landscape structure plays a fundamental role in shaping biodiversity patterns (Tscharntke et al., 2012). Wu et al. showed that flowering ground cover and the proportion of semi-natural habitats correlated positively with wild bee abundance and diversity, which in turn had a positive impact in apple orchards in the Northern China Plain. Interestingly, in tropical rainforest buffer zones of Sri Lanka, Hanle et al. showed that traditional small-holder tree gardens harbored greater abundance of species of high conservation interest than forest fragments or tea plots. This study is a nice example of how traditional farmlands managed by indigenous peoples can harbor almost as much biodiversity as natural habitats (Bhagwat and Rutte, 2006; Ranganathan et al., 2008).

From landscape to local scales, plant species play a fundamental role in animal conservation and this can be true even for invasive species, which can have in certain instances neutral and positive effects on animal species (Houlahan and Findlay, 2004; Szigeti et al., 2020). Jain et al. showed that tropical butterfly populations of Singapore were highly dependent on non-native host plants. Yet, invasive plants also have well-known negative effects and can disrupt ecosystem functioning (Simberloff et al., 2013). Two additional studies in this collection focused on plant ecology. Chen et al. tested several hypotheses that could explain patterns of exotic plant invasions in natural reserves of China and found that human activities are the main facilitators of these invasion processes. Hayyat et al. conducted a study in Pakistan showing the potential for plant restoration in quarry sites using limestone quarry waste to promote the growth of two woody Angiosperm species.

Another key aspect of wildlife conservation in our region is to investigate ways to promote dispersal of large mammals and ameliorate conflicts with humans (Goswami and Vasudev, 2017). Liu X. et al. investigated potential dispersal routes of giant pandas in a key distribution area in China and provided recommendations to favor this natural process. Tripathy et al. performed a comprehensive spatial analysis of human-elephant conflict in Keonjhar (E India), an area where 345 people have been killed by elephants between 2001 and 2018, to ensure that mitigation efforts are directed to priority areas.

Finally, Sung et al. investigated population trends of wintering waterbirds in the Deep Bay area (S China), a wetland of international importance over a 20-year span, showing that larger species strongly dependent on the Yellow Sea and breeding in Southern Siberia experienced steeper declines, while Liang et al. provided insights on individual niche variation across habitat transformation gradients of birds and frogs. This last study highlights how important is to better understand biodiversity responses to habitat transformation, such as how species forage and select territories in human dominated habitats.

COP-15: BUILDING AN ECOLOGICAL CIVILIZATION

The years 2021 and 2022 will be crucial for biodiversity conservation across countries in the world, as the United Nations' Convention for Biodiversity (COP-15) on-site meeting is scheduled to take place in October, 2021 in Kunming, Yunnan (SW China). As an area where our lack of knowledge of the effects of human-driven habitat transformation is laid bare, Asia has large areas of intense human concentration and has experienced rapid changes. Therefore, we believe this collection of works serves as an example of how landscape ecology and biodiversity conservation have progressed in Asia in recent decades. This is crucial as Asian countries continue to grow, both economically and population wise, which has the potential to impact its extremely diverse ecosystems. From a broader perspective, it seems clear that the events taking place in this continent will strongly determine the future of our shared Earth—for both people and biodiversity.

AUTHOR CONTRIBUTIONS

EP-N wrote a first draft. All authors contributed to the article and approved the submitted version.

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How to Become a Generalist Species? Individual Niche Variation Across Habitat Transformation Gradients

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Species in transformed habitats, frequently labeled as environmental generalists, tend to show broader niches than species in natural habitats. However, how population niche expansion translates into changes in the niches of individual organisms remains unclear, particularly in the context of habitat transformation. Niche expansion could be a product of individuals having broader niches, greater distances among individuals' niches, or a combination of both processes. This would challenge the traditional conceptions on niche dynamics, which emphasize the role played by individual specialization (IS). Here, using stable isotopes, we computed total niche width (TNW), its within- and between-individual components (WIC and BIC), and IS (the ratio WIC/TNW), in 13 populations of 6 bird species and 8 populations of 3 frog species in natural and transformed habitats. We confirmed that species had broader niche width in transformed than in natural habitats, yet population niche expansion across habitats was mainly a product of increased distance between individuals. Within each habitat type, increases in TNW were linked to increases in WIC for all habitat types, while relationships between TNW and BIC were found in transformed but not in natural habitats. Hence, both increased individual niche width and increased distance among individuals were apparent within habitats, particularly in transformed ones, where increases in WIC dominated. Neither across or within habitats was niche expansion associated with increasing IS. Therefore, our results overturn traditional conceptions associated with the niche variation hypothesis and illustrate that niche expansion is not invariably associated with increased IS, because the distance between individual's niches (BIC) can increase, as well as the breadth of those niches (WIC).

Keywords: habitat transformation, individual specialization, niche variation hypothesis, urbanization, stable isotopes

INTRODUCTION

Habitat transformation is one of the main drivers of biodiversity loss (Newbold et al., 2015). This loss is not neutral in that predominantly specialized species – those requiring particular habitat or food resources – are disproportionately lost, while environmental generalists – those with less selective habitat or dietary needs – become dominant (Flynn et al., 2009; Ducatez et al., 2018; Sol et al., 2020). A consequence of this process is that species in transformed habitats display broader niches than species in natural habitats (Bonier et al., 2007; Clavel et al., 2011; Coogan et al., 2018; Pagani-Núñez et al., 2019; Palacio, 2019). It is unclear however how this process of population niche expansion translates into the niches of the individual organisms.

Total niche width (TNW) of a population is composed by the sum of its within-individual component (WIC) and between-individual component (BIC) (Roughgarden, 1972, 1974), while individual specialization (IS) is computed as the ratio between WIC and TNW (Bolnick et al., 2003; Araújo et al., 2011), and increases as this ratio decreases. Traditionally, the niche variation hypothesis (NVH) predicts that TNW is positively correlated with IS (Van Valen, 1965), meaning that increases in TNW are mostly associated with increasing IS (Cachera et al., 2017; Maldonado et al., 2017). This is because when TNW increases, IS is likely to increase too, simply because TNW would increase at a higher rate than WIC. This seems a realistic assumption, as generalist populations are often composed of individuals only using a subset of the total population niche (Araújo et al., 2011; Layman et al., 2015; Pagani-Núñez et al., 2015).

Many studies, however, have cricitized and/or found no support to the NVH (e.g., Simberloff et al., 2000; Meiri et al., 2005). This suggests that population niche expansion could be achieved through different mechanisms than an increase in IS, such as changes in other components of individuals' niches or a population's niche structure. As stated above, when a population niche expands (TNW increases), the value of the ratio WIC/TNW decreases automatically, as long as WIC does not necessarily change, or at least that it increases less than TNW and thus the main increase is in BIC (because TNW = BIC + WIC). We suggest here that if TNW increases the components of TNW likely increase too, yet this process of niche expansion could be achieved in many different ways (either BIC, WIC or both may increase). It is thus fundamental to consider how changes in these different niche components shape patterns of niche expansion, and habitat transformation gradients offer an excellent scenario to test these ideas.

Increases in both WIC and BIC are likely to occur across transformation gradients. Assuming that population size stays constant, this process of niche expansion at the population level (i.e., increasing TNW) could be reflected at the individual level through three main avenues: increasing WIC, increasing BIC, or increasing both WIC and BIC (**Figure 1**). Several extrinsic and intrinsic factors could facilitate this process. For instance, habitat heterogeneity could promote greater BIC –less overlap among individuals (Darimont et al., 2009; Newsome et al., 2015). Conversely, innovativeness could promote greater WIC –larger individual niches (Sol et al., 2013; Ducatez et al., 2015). Furthermore, these processes may also be apparent within habitats –particularly transformed ones– as WIC and BIC may increase with increasing population niches.

In this study, we assessed the role played by different niche components (WIC, BIC and the ratio WIC/TNW) in explaining patterns of niche expansion across habitat transformation gradients. We did this using six bird and three frog species inhabiting natural, rural and urban habitats in China, which harbors tremendous biodiversity yet is currently experiencing a vast process of habitat transformation driven particularly by urbanization (Seto et al., 2011; Liu et al., 2018). Birds and frogs strongly respond to habitat transformation and human activities, and are commonly used as models to investigate this issues (McKinney, 2008; Herrera-Montes and Aide, 2011). Furthermore, there is a wealth of research using stable isotopes to answer different questions about these two taxa (e.g., Inger and Bearhop, 2008; Araújo et al., 2009; Smith et al., 2017). While birds and frogs certainly are different (frogs would be less mobile and to some extent more specialized than birds, at least in relation to habitat use, due to their dependency from water) (e.g., Dayananda et al., 2017), we confirmed the consistency of our hypotheses by pooling together data from both taxa. To compute niche characteristics we used stable isotopes, which has become a common technique to quantify trophic niche (Layman et al., 2012; Figgener et al., 2019). First, we asked if species had broader niches in transformed than in natural habitats, and determined whether differences in WIC, BIC and the ratio WIC/TNW existed across natural, rural and urban habitats. Second, we assessed the relationships between these niche components and TNW within habitats. In doing so, we were able to determine which of these individual niche components was most important in explaining population niche expansion (**Figure 1**).

MATERIALS AND METHODS

Study Locations and Species

We passively sampled passerines from November 2015 to April 2017 using mist nets in six locations in Guangxi Zhuang Autonomous Region and Yunnan Province (southwest China), and frogs during July–August 2018, actively capturing them in six locations in Gansu and Shaanxi Provinces (northwest China) (**Figure 2** and **Supplementary Material 1**). We categorized our study locations as urban, rural and natural habitats, according to land-use gradients and the level of anthropogenic disturbance (cf. Newbold et al., 2015). Natural habitats were relatively undisturbed and protected forested areas, rural habitats were predominantly agricultural areas or managed forests with low human population density, and urban habitats were human-dominated areas inside cities (Liang et al., 2018; Pagani-Núñez et al., 2019; **Figure 2**). Six common passerines in the area included the Rufous-capped Babbler *Stachyris ruficeps*, the Gray-checked Fulvetta *Alcippe morrisonia*, the Common Tailorbird *Orthotomus sutorius*, the Red-whisked Bulbul *Pycnonotus jocosus*, the Red-billed Leiothrix *Leiothrix lutea* and the Scaly-breasted Munia *Lonchura punctulata*. Frogs belonged to three species of the genus *Feirana* (Swelled-vented Frog *F. quadranus*, Taihangshan

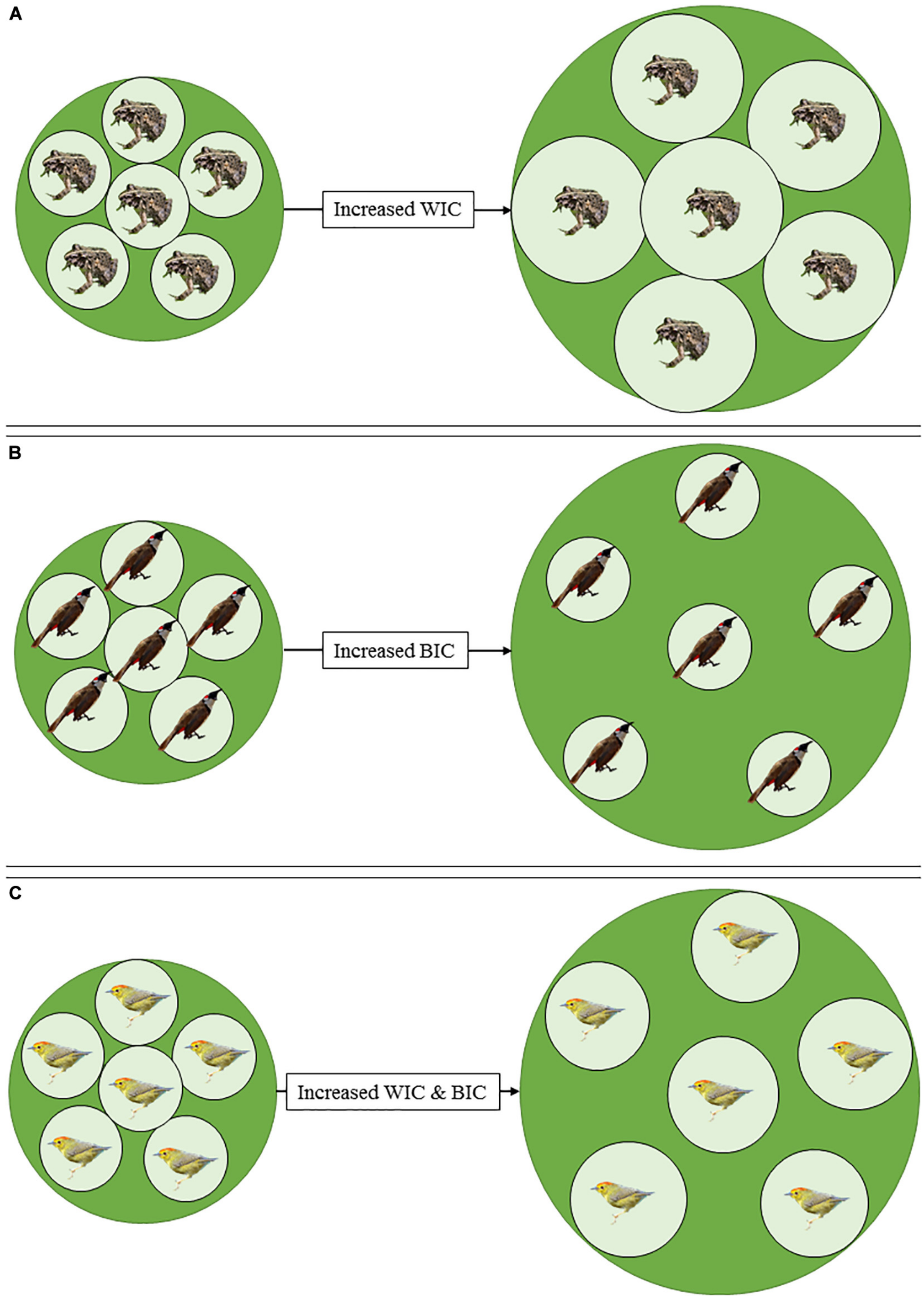

FIGURE 1 | Conceptual illustration of population-level niche expansion resulting from different individual-level niche changes. When population size remains constant, population niche expansion could be achieved through: **(A)** increased within-individual niche component (WIC), **(B)** increased between-individual niche component (BIC), or **(C)** a combination of both processes. Note that increases in individual specialization (IS = WIC/TNW) may or may not be achieved in all these scenarios.

Swelled-vented Frog *F. taihangnica* and Kangxian Swelled-vented Frog *F. kangxianensis*) (**Figure 3**; Fei et al., 2009; Yang et al., 2011). For birds, we sampled a large number of individuals and species (see Pagani-Núñez et al., 2019). We focused, however, on six common species that were present in several habitats and limited sample size to 10 individuals per species (**Figure 3**). We did this by randomly selecting up to 10 individuals per species for stable isotope analysis. In doing so, we were able to use

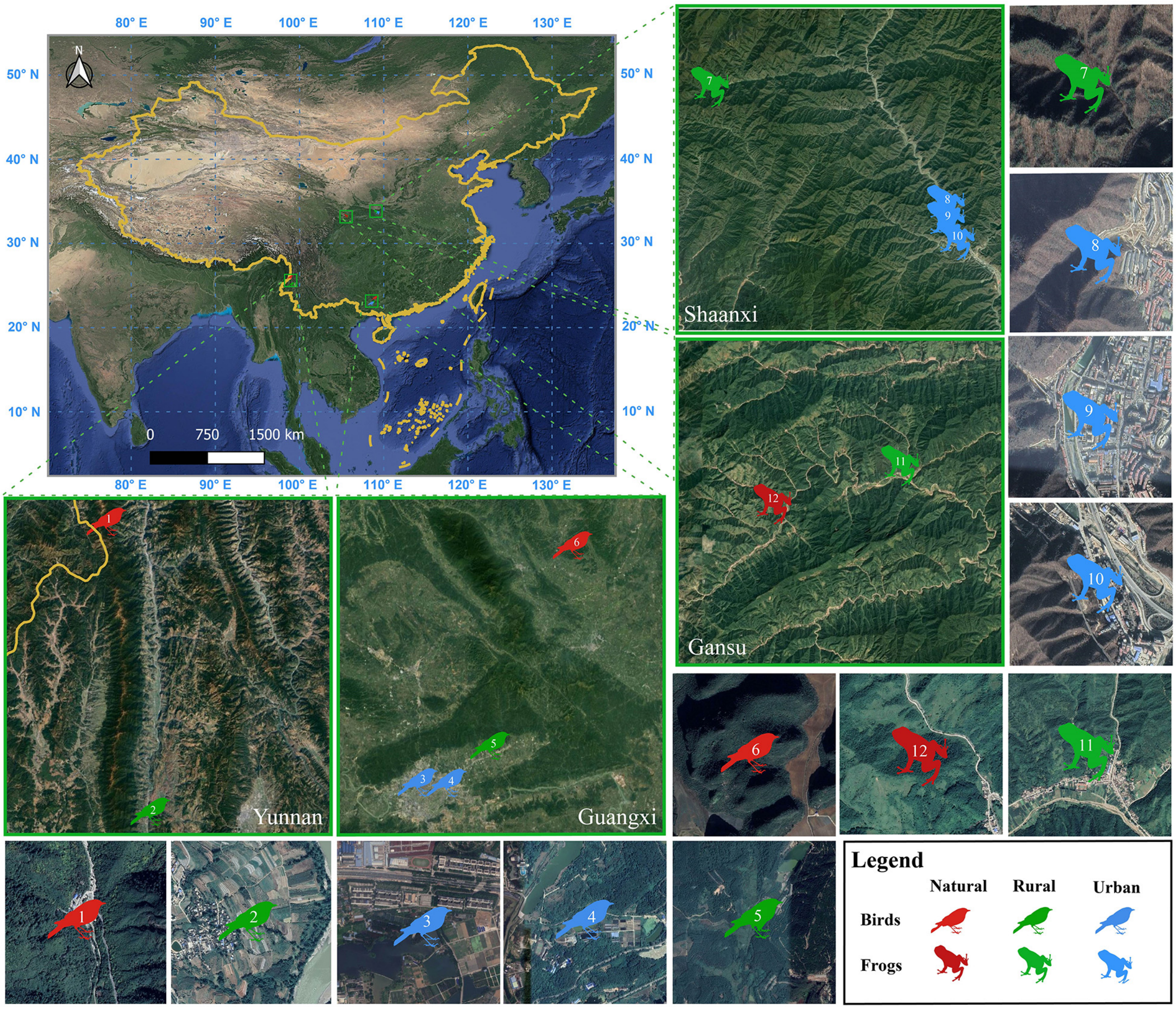

FIGURE 2 | Map showing our study locations in Guangxi Zhuang Autonomous Region and Yunnan Province (southwest China), and Gansu and Shaanxi Provinces (northwest China). Left top panel shows a general map of the People's Republic of China. The four larger squares illustrate the distance among study locations and their general aspect. The smaller squares provide a closer look of these study locations.

a similar number of individuals per species to compute niche characteristics. For frogs, since sample size per species was rather similar but lower in total than for birds, we did not set any sample size threshold. In the end, we used 176 individuals (118 birds and 58 frogs) from 21 populations (**Supplementary Material 2**).

Sampling Procedures

After birds were extracted from the mist net, we measured body mass using an electronic balance with an accuracy of 0.01 g. We then collected the second secondary feather (P8) of the right wing and the claw tip of the largest claw from the right leg. All individuals were banded before being released and we only included data from the first capture.

We searched for frogs shortly after sunset in and around water bodies using flashlights. For each captured adult, we measured body mass to the nearest 0.01 g with an electronic balance. After euthanasia, we clipped the fourth toe for molecular identification and collagen extraction. We also collected the muscle tissue from hind limbs, washed the muscles with distilled water and stored them in 2 ml tubes. All the samples were kept in cold conditions in the field and then stored at −20°C in the laboratory. After sampling, the adult frogs were placed in 4% buffered formalin and the voucher specimens were deposited in the Herpetological Museum of the Chengdu Institute of Biology (CIB), Chinese Academy of Sciences (CAS). These procedures are part of a long-term line of research focused on the ecology and evolution of *Feirana* frogs (e.g., Hu and Jiang, 2018; Wang et al., 2019; Huang et al., 2020), and are a common practice in other stable isotope studies on this taxon (e.g., Araújo et al., 2009). For frog species identification, we integratedly referred to morphological characteristics, and geographic and genetic information (Hu and Jiang, 2018; Wang et al., 2019; Huang et al., 2020).

All animal handling and processing were in accordance with the Law of the People's Republic of China on the Protection of

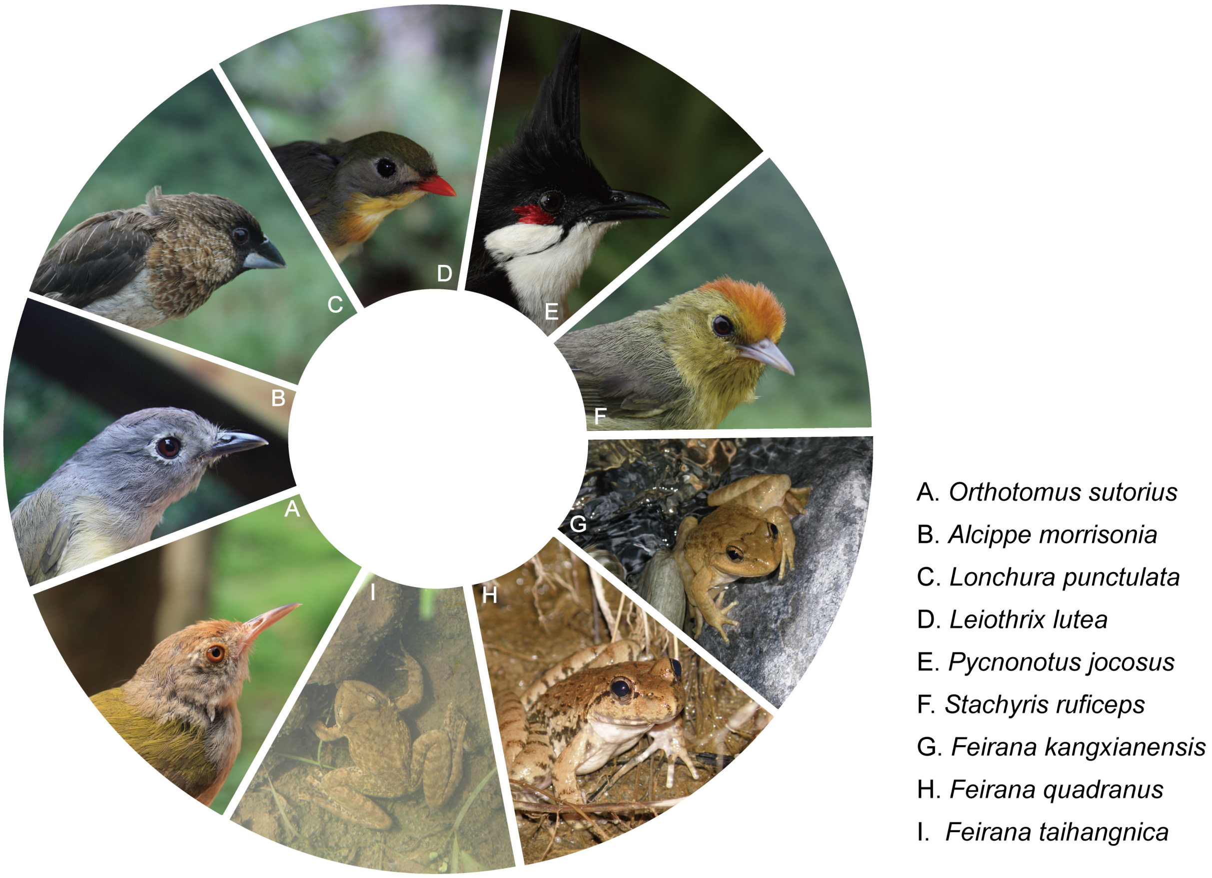

FIGURE 3 | Study species including six common passerines from southwest China (Common Tailorbird *Orthotomus sutorius*, Gray-checked Fulvetta *Alcippe morrisonia*, Scaly-breasted Munia *Lonchura punctulata*, Red-billed *Leiothrix Leiothrix lutea*, Red-whiskered Bulbul *Pycnonotus jocosus*, and Rufous-capped Babbler *Stachyris ruficeps*) and three frog species from northwest China (Kangxian Swelled-vented Frog *Feirana kangxianensis*, Swelled-vented Frog *F. quadranus* and Taihangshan Swelled-vented Frog *F. taihangnica*).

Wildlife and approved by the Guangxi Forestry Bureau and the Animal Care Committee of CIB, CAS.

Tissues and Niches

Nitrogen stable isotope ratios (δ^{15}N) are commonly used to estimate species' trophic level (Boecklen et al., 2011; Layman et al., 2012). We focused only on this element because we were particularly interested in linking our finding to individuals' and species diets. Using different tissues it is possible to determine individual specialization because different tissues reflect individuals' diets across different temporal scales (Vander Zanden et al., 2015; Bond et al., 2016; Maldonado et al., 2017). Thus, we were able to compute intra-individual niche variation using δ^{15}N values of two easy-to-obtain tissues.

We collected feathers and claws (birds) and muscle and bone collagen samples (frogs) to compute niche characteristics because these tissues provide information on niche use at two different temporal scales for each individual. Feathers correspond to a specific temporal window during summer molt, while claws correspond to the previous weeks to months prior to sample collection (Bearhop et al., 2003; Hahn et al., 2014; Vander Zanden et al., 2015; Bond et al., 2016). We collected these samples continuously across our study period so that they represent diets across a broad temporal scale. Similarly, muscle tissue would reflect niche use in a time window of weeks prior to sample collection, while bone collagen tissue would reflect a broader time span across individuals' development (Vander Zanden et al., 2015; Matsubayashi et al., 2017).

Thus, we used δ^{15}N values from two different tissues from each individual as the continuous data input about niche use to calculate TNW, WIC, BIC and WIC/TNW for each species per location. WIC/TNW ranges from 0 (individuals use completely different resources, i.e., display high IS) to 1 (individuals use the full range of the population niche, i.e., display low IS). In our sample, WIC ranged between 0.04 and 1.13, BIC between 0.05 and 1.62, and TNW between 0.15 and 2.53 (**Supplementary Material 2**).

Stable Isotope Analysis

Claws and feathers from birds were cleaned from surface contaminants using NaOH (0.25 mol/L), and then were air-dried for at least 12 h. We included approximately 0.35 mg

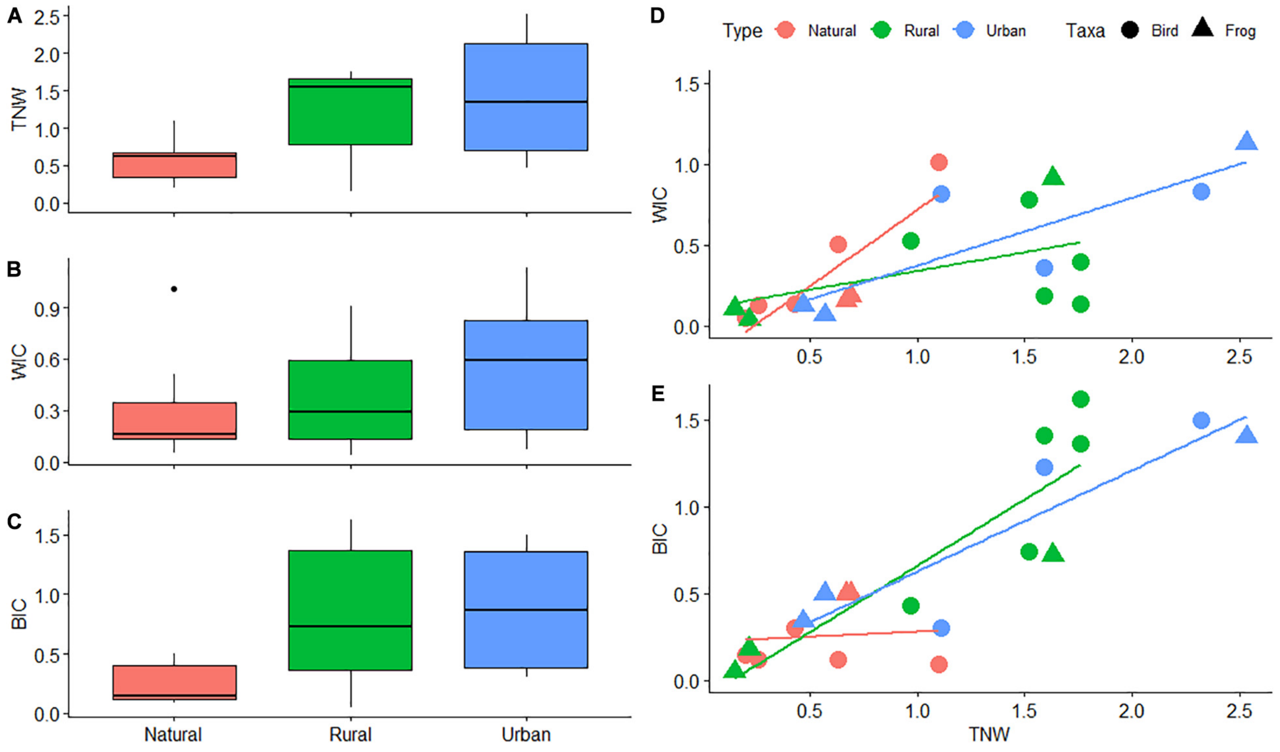

FIGURE 4 | Differences in niche components and their relationshisp across and within habitats. **(A)** Differences in Total (i.e., population) Niche Width (TNW; *y*-axis) between natural, rural and urban habitats (*x*-axis). **(B)** Differences in the Within-Individuals niche Component (WIC; *y*-axis) between natural, rural and urban habitats (*x*-axis). **(C)** Differences in the Between-Individuals niche Component (BIC; *y*-axis) between natural, rural and urban habitats (*x*-axis). **(D)** Linear relationships between the Within-Individuals niche Component (WIC; *y*-axis) and TNW (x-axis) in natural, rural and urban habitats. **(E)** Linear relationships between the BIC (*y*-axis) and TNW (*x*-axis) in natural, rural and urban habitats.

of feather tips and claws of each individual into separate tin cups, which were loaded for $\delta^{15}N$ analyses. We used a Flash 2000 HT elemental analyzer coupled via ConFlo IV Universal Continuous Flow Interface (Thermo Scientific) to a Thermo Scientific DELTA V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany). We conducted stable isotope analyses for this taxon in the Stable Isotope Laboratory of the College of Forestry at Guangxi University (Nanning, S China). Toe clips from frogs were demineralized for 24 h in 0.5 M HCl, rinsed twice with deionized water. Next, the samples were treated with 0.1 M NaOH for 12 h and washed twice with deionized water. We immersed the bones in a methanol:chloroform mixture (2:1, vol:vol) for about 24 h, then thoroughly rinsed and heated in deionized water at 90°C for about 12 h. Bone collagen and muscle tissues from frogs were freeze-dried for 36 h to constant weight, grounded to a fine powder and analyzed at the Public Center of Experimental Technology in CIB, CAS. We used a vario isotope cube elemental analyzer (vario ISOTOPE cube, Elementar, Germany) interfaced to an isotope ratio mass spectrometer (IsoPrime100, Isoprime, United Kingdom).

For both taxa, stable isotope ratios were expressed as parts per thousand (‰) using the equation as follow: $\delta^{15}N$ (‰) = [(Rsample/Rstandard)-1] × 1000, where *Rsample* and *Rstandard* are the $^{15}N/^{14}N$ ratios of sample and standard, respectively. The standard was atmospheric nitrogen (AIR N_2) and measurement precision was 0.25%.

Statistical Analysis

Using a linear mixed-effects model, we first tested whether TNW was larger in rural and urban habitats than in natural ones. TNW was our response variable, and habitat type (natural, rural or urban), taxa (bird or frog) and species' average body mass were our predictors. We included body mass as it may have played a relevant role in shaping niche community structure and due to the differences between the studied taxa (Vergnon et al., 2009). Study location (**Supplementary Material 1**) and species (**Figure 3** and **Supplementary Material 2**) were the random factors. Using the same statistical approach, we were interested in determining whether differences in BIC, WIC and IS (the ratio WIC/TNW) existed among habitat types (in parallel to differences in TNW). Thus, we constructed three different models with the same predictors and random variables yet subsequently using BIC, WIC and IS as response variables.

Second, we were interested in assessing the relationships between the different niche components (BIC, WIC and IS) and TNW across habitat types. To do this, we constructed a set of models subsequently using niche characteristics as response variables (BIC, WIC and IS). Taxa, body mass and the interaction between TNW and habitat type were the predictors, and study

TABLE 1 | Differences in niche characteristics between habitats.

TNW				
***Fixed effects**	**Estimate**	**SE**	***t***	***P***
Intercept	1.44	0.37	3.85	< 0.01
Natural – Rural	0.34	0.33	1.02	0.31
Natural – Urban	**0.95**	**0.37**	**2.57**	**0.01**
Rural – Urban	0.61	0.33	1.85	0.06
Taxa	0.72	0.57	1.26	0.21
Body mass	**−0.04**	**0.02**	**−2.54**	**0.01**
***Random effects**	**Variance**	**SD**		
Location	0.06	0.24		
Species	0.16	0.41		
Residual	0.19	0.44		

WIC				
***Fixed effects**	**Estimate**	**SE**	**t**	**P**
Intercept	−0.84	0.59	−1.43	0.15
Natural – Rural	0.17	0.62	0.28	0.78
Natural – Urban	0.81	0.65	1.26	0.21
Rural – Urban	0.64	0.61	1.05	0.29
Taxa	−0.07	0.74	−0.10	0.92
Body mass	−0.03	0.02	−1.35	0.18
***Random effects**	**Variance**	**SD**		
Location	0.30	0.55		
Species	< 0.01	<0.01		
Residual	0.74	0.86		

BIC				
***Fixed effects**	**Estimate**	**SE**	**t**	**P**
Intercept	0.67	0.31	2.20	0.03
Natural – Rural	0.37	0.30	1.27	0.21
Natural – Urban	0.60	0.32	1.89	0.06
Rural – Urban	0.23	0.29	0.79	0.43
Taxa	0.17	0.44	0.38	0.70
Body mass	−0.02	0.01	−1.28	0.20
***Random effects**	**Variance**	**SD**		
Location	0.07	0.26		
Species	0.07	0.26		
Residual	0.12	0.35		

IS (WIC/TNW)				
***Fixed effects**	**Estimate**	**SE**	**t**	**P**
Intercept	0.61	0.16	3.73	< 0.01
Natural – Rural	−0.10	0.18	−0.55	0.58
Natural – Urban	−0.06	0.18	−0.33	0.74
Rural – Urban	0.04	0.17	0.23	0.82
Taxa	0.02	0.20	0.10	0.92
Body mass	−0.01	0.01	−1.11	0.27
***Random effects**	**Variance**	**SD**		
Location	0.04	0.21		
Species	<0.01	0.05		
Residual	0.02	0.16		

Results from a set of linear mixed-effects models using Total Niche Width (TNW), its Within-Individual (WIC) and Between-Individual (BIC) Components, and Individual Specialization (IS = WIC/TNW) in 21 populations of birds and frogs as response variables. The predictors were habitat type (natural, rural or urban), taxa (birds or frogs) and body mass (g). Location (see ***Supplementary Material 1****) and species (see* ***Supplementary Material 2****) were random factors. Significant effects are marked in bold letters. WIC values were log-transformed to approximate normality.*

location and species were the random factors. Habitat type factor had three levels (natural, rural and urban), so that we dummy coded these factors and repeated the analysis using a different level as reference to ascertain all the possible combinations (e.g., natural vs. rural, rural vs. urban and natural vs. urban). Furthermore, there was considerable altitudinal variation among locations, and in spite that we have previously recorded negligible altitudinal effects on species' niche characteristics (Pagani-Núñez et al., 2019), we assessed whether it impacted individual level metrics. We recorded no significant effects of altitude on niche characteristics, so we excluded this variable from the final models (TNW: $P = 0.37$, WIC: 0.11, BIC: 0.81, IS: 0.21, data not shown).

We visually examined qqplots to confirm that model residuals were normally distributed. From the first set of models assessing differences in niche characteristics across habitat types, we found that the one using WIC as dependent variable did not fit this criterion. Thus, we repeated this model using log-transformed WIC values to approximate normality. We computed niche characteristics using the function WTcMC from the RInSp package (Zaccarelli et al., 2013) and constructed the linear mixed-effects models using the package lme4 v1.1-23 (Bates et al., 2015). All analyses were performed in R software v3.6.1 (R Core Team, 2017).

RESULTS

Differences in TNW, WIC, BIC, and IS Across Habitat Types

We found that frog and bird urban populations had larger TNWs than natural populations (**Figure 4A** and **Table 1**). Urban populations showed a non-significant tendency to display larger TNW than rural populations, while rural and natural populations showed no apparent differences in TNW (**Table 1**). We also found that TNW correlated negatively with body mass. Bird and frog populations did not show significant differences in WIC across habitat types (**Figure 4B** and **Table 1**). WIC and body mass were uncorrelated (**Table 1**).

Between-individual component of bird and frog urban populations showed a non-significant tendency to be larger than that of natural populations (**Figure 4C** and **Table 1**), while rural populations did not show significant differences with natural or urban populations. BIC and body mass were uncorrelated (**Table 1**).

We did not record any significant effect of habitat type or body mass on IS (WIC/TNW) (**Table 1**). Taxa showed no significant effects on niche characteristics (**Table 1**).

Relationships Between TNW and WIC, BIC and IS Within Habitat Types

Within-individual component and TNW correlated positively in natural, rural and urban populations, the former showing the steepest curve (**Figure 4D** and **Table 2**). BIC showed a different pattern. BIC and TNW showed a strong positive correlation in both urban and rural populations but not in natural populations (**Figure 4E**). Finally, IS and TNW were uncorrelated across habitats (**Table 2**). Taxa and body mass showed no significant effects on these models (**Table 2**).

DISCUSSION

In this study, we illustrate how increases in population niche width (TNW) in birds and frogs showing different patterns across and within habitats. Within habitats, increases in TNW were a product of both increased niches within individuals (WIC), namely increased individual niche width, and increased distance between individuals (BIC), namely reduced overlap among individuals. These processes occurred simultaneously, thus, supporting our third hypothesis on individual niche dynamics across habitat transformation gradients (**Figure 1**). These positive relationships between TNW, WIC and BIC were rather persistent within habitats, with the exception of the relationship between TNW and BIC, which was not significant in natural habitats. Conversely, across habitats, although TNW increased markedly, we recorded no differences in WIC and only a weak tendency of BIC to increase from natural to urban habitats. Individual specialization (IS) showed no significant relationships with TNW across or within habitats. Hence, our results highlight how increases in TNW can be achieved by a combination of individual and population level niche changes, and is not invariably associated with an increase in IS.

Differences in Niche Characteristics Across Habitat Types

We found that species' niche expansion from natural to transformed habitats, namely increased TNW, did not necessarily imply dramatic changes in both WIC and BIC. While we did record markedly larger TNW in urban than in natural habitats, differences in WIC were negligible and species only showed a non-significant tendency to have larger BIC between these two habitat types. Many studies using different approaches have reported similar patterns of niche expansion across habitat transformation gradients (Bonier et al., 2007; Devictor et al., 2008a; Callaghan et al., 2019; Pagani-Núñez et al., 2019; Palacio, 2019), yet no study had thoroughly addressed how this pattern is a result of changes in different niche characteristics at the individual level. Our study is original in showing this pattern of trophic specialization within species, while previous studies analyzing changes in specialization mostly focused on interspecific comparisons in habitat use (Julliard et al., 2006; Devictor et al., 2008b; Rivas-Salvador et al., 2019). Nevertheless,

TABLE 2 | Relationships among niche characteristics within habitats.

		WIC		
***Fixed effects**	**Estimate**	**SE**	**t**	**P**
Intercept	0.05	0.23	0.21	0.84
TNW: Natural	**0.62**	**0.26**	**2.42**	**0.02**
TNW: Rural	**0.31**	**0.13**	**2.42**	**0.02**
TNW: Urban	**0.41**	**0.11**	**3.91**	**< 0.01**
Taxa	0.08	0.24	0.34	0.73
Body mass	0.00	0.01	−0.44	0.66
***Random effects**	**Variance**	**SD**		
Location	0.02	0.15		
Species	0.02	0.13		
Residual	0.05	0.21		
		BIC		
***Fixed effects**	**Estimate**	**SE**	**t**	**P**
Intercept	−0.05	0.23	−0.21	0.84
TNW: Natural	0.38	0.26	1.47	0.14
TNW: Rural	**0.69**	**0.13**	**5.32**	**< 0.01**
TNW: Urban	**0.59**	**0.11**	**5.61**	**< 0.01**
Taxa	−0.09	0.24	−0.38	0.71
Body mass	<0.01	0.01	0.47	0.64
***Random effects**	**Variance**	**SD**		
Location	0.02	0.14		
Species	0.02	0.12		
Residual	0.05	0.22		
		IS (WIC/TNW)		
***Fixed effects**	**Estimate**	**SE**	**t**	**P**
Intercept	0.60	0.18	3.38	<0.01
TNW: Natural	0.14	0.23	0.63	0.53
TNW: Rural	−0.12	0.10	−1.25	0.21
TNW: Urban	−0.02	0.09	−0.20	0.84
Taxa	−0.02	0.19	−0.09	0.93
Body mass	−0.01	0.01	−1.12	0.26
***Random effects**	**Variance**	**SD**		
Location	0.04	0.20		
Species	<0.01	0.05		
Residual	0.02	0.15		

Results from a set of linear mixed-effects models using the Within-Individual (WIC) and Between-Individual (BIC) niche components, and Individual Specialization (IS = WIC/TNW) in 21 populations of birds and frogs as response variables. The predictors were the interaction between Total Niche Width (TNW) and habitat type (natural, rural or urban), taxa (birds or frogs) and body mass (g). Location (see ***Supplementary Material 1****) and species (see* ***Supplementary Material 2****) were random factors. Significant effects are marked in bold letters.*

having a clear idea of what happens to individuals is fundamental to avoid biased estimations of species- or population-level estimation of isotopic niches (Flaherty and Ben-David, 2010).

Larger TNWs could be a product of urban individuals showing high behavioral innovativeness typical of generalist species (Ducatez et al., 2015; Sol et al., 2016; Griffin et al., 2017), having broad available empty niches (Sanz-Aguilar et al., 2015; Yurkowski et al., 2016; Balme et al., 2019), or a combination of both processes. However, since BIC increased more than WIC across the transformation gradients, our results suggest therefore that habitat heterogeneity would be the main facilitator of niche expansion –promoting lower overlap among individuals within each species (Darimont et al., 2009; Newsome et al., 2015). We cannot discard that changes in aggressiveness toward conspecifics across habitats may have influenced BIC values too.

Differences in the Relationships Between Niche Characteristics Within Habitat Types

We recorded different relationships among niche characteristics within habitat types. A positive relationship between TNW and WIC was apparent in natural, rural and urban habitats. We also recorded strong positive relationships between TNW and BIC in rural and urban habitats, but not in natural habitats. Both WIC and BIC facilitated niche expansion (**Figure 1**), and our results showed that increased distance among individuals, i.e., BICs or decreased inter-individual niche overlap, was only possible in transformed habitats, where population niches (TNWs) were large enough to allow this process to occur, supporting the idea that increasing habitat heterogeneity may have facilitated niche expansion across the transformation gradient.

In contrast with previous studies using a diverse array of statistical approaches (Newsome et al., 2015; Navarro et al., 2017; Murray et al., 2018), we recorded no significant relationships between TNW expansion and individual specialization (IS). Traditionally, the niche variation hypothesis suggests that increases in niche width (TNW in our case) are mainly achieved as a main consequence of a parallel increase in IS (Ebenman and Nilsson, 1982; Dayan and Simberloff, 1994; Bolnick et al., 2007; Cachera et al., 2017; Maldonado et al., 2017). Conversely, our study suggests that WIC, and especially BIC, are predominantly associated with increases in TNW. We recorded this pattern using two rather different taxonomic groups, birds and frogs, which suggests that this fashion may be common throughout vertebrates.

CONCLUSION

Generally, research investigating the consequences of habitat transformation for niche characteristics of species and populations (and, therefore, community assemblage dynamics) focus on broad scale processes (Darimont et al., 2009; Quevedo et al., 2009; Newbold et al., 2018; Sol et al., 2020). Thus, it remains unclear how individuals respond to these changes at finer scales. In other words, environmental generalists have broad niches and are able to colonize many habitat types but, so far, it was unclear how their individual niches were configured (Ducatez et al., 2018). Our research is important in linking population-level niche processes to individual-level niche characteristics. Although we may acknowledge that our sample size was rather limited and we were pooling different taxa (birds and frogs), our findings overturn traditional conceptions on the mechanisms and consequences of niche expansion, illustrating diverse ways in which it can be achieved. Further research could ascertain to what extent individual-level niche characteristics of transformed habitats are a consequence of individuals being generally more innovative and thus exploiting a broad variety of food and habitat resources or whether they merely reflect a particular habitat structure that enables individuals having broad niches without overlapping with conspecifics (Ducatez et al., 2015).

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 below: NCBI (https://www.ncbi.nlm.nih.gov/) MT940544-MT940569 (26 16S sequences) and MT941534-MT941565 (32 ND2 sequences).

ETHICS STATEMENT

The animal study was reviewed and approved by Animal Care Committee of CIB, CAS and Guangxi Forestry Bureau.

AUTHOR CONTRIBUTIONS

EP-N, YL, JH, DL, SY, and EG conceived and designed the study. EP-N, CH, DL, and SY performed the study and collected the data with assistance from YL, JH, and WL. EP-N, SY, and DL analyzed the data and wrote the draft of the manuscript with input from all authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.597450/full#supplementary-material

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Multi-Scale Ecological Connectivity Dynamics Associated With Hydropower Station: A Case Study in the Lancang River Valley

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Dam construction is a major threat to terrestrial ecological processes that exhibit spatial variation. As an effective indicator of species movements at large scales, the dynamics of forest landscape connectivity for the dispersal abilities of local species such as primates both upstream and downstream of the Manwan hydropower station were compared in three periods: before, during, and after dam construction (in 1974, 1988, and 2004, respectively). The equivalent connected area (ECA) index which was modified from the probability of connectivity (PC) index based on the graph theory was applied in this study. We used this method to analyze the spatial and temporal changes in the overall forest landscape connectivity due to dam construction. The results showed that forest connectivity decreased after dam construction. The forest connectivity upstream was much greater than that downstream in 1974 but was lower in 1988 and 2004. The importance of connectivity increased with increasing dispersal distance. Only 8, 12, and 18% of forest patches of small area exhibited changes in 1974, 1988, and 2004, respectively. Most of the large habitat patches (i.e., those with dECA values >50%) remained stable, and the greatest patch changes were found at a dispersal distance of 400 m in all three periods. These large forest patch changes often occurred near the boundary of the study area. The Betweenness Centrality indicator, which identifies patches as stepping stones while accounting for ecological processes and biological flows at a larger scale, indicated that some habitat patches near Manwan Dam acted as stepping stones in maintaining the forest connectivity. Furthermore, rank correlations between the forest patch area and the three dPC ($_{intra}$,$_{flux}$,$_{connector}$) fractions indicated that the dPC$_{flux}$ indicator can be used to measure the prioritization of habitat patches.

Keywords: forest landscape connectivity, patch prioritization, spatiotemporal difference, Manwan dam, Lancang River

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INTRODUCTION

Dams are considered one of the most important human disturbances to river basins. Although they provide many economic benefits, their negative effects on ecological processes and habitats cannot be ignored (Bombino et al., 2006). After the impoundment of a dam, spatial differences occur in landscape pattern and related connectivity between the upstream and downstream stretches of a river. As dam construction continues, the connectivity of natural habitat patches is disrupted and fragmented, and vegetation is submerged by the impounded water (Gordon and Meentemeyer, 2006). Previous studies showed that trophic and community interactions were affected by river structure and position (Anderson and Hayes, 2018). Moreover, the declining sizes of forest patches and the lack of habitat continuity can lead to landscape fragmentation, connectivity reduction and habitat loss (Fahrig, 2003). Therefore, it is essential to measure the impacts of spatial changes of habitats and habitat connectivity to preserve biodiversity and understand the ecological effects of dam construction.

Landscape connectivity is composed of two different facets, including structural connectivity and functional connectivity (Baguette and Van Dyck, 2007). Structural connectivity refers to the level at which two landscape elements or habitat patches are physically connected. Functional connectivity can be defined as the degree to which the landscape impedes the dispersal movements of populations across habitat patches (Taylor et al., 1993; Saura and Pascual-Hortal, 2007). Landscape connectivity has been linked to various ecological processes, such as nitrogen cycling, decomposition, pollination, seed dispersal, and animal migration (Forman and Deblinger, 2000; Minor and Urban, 2008; Nichols et al., 2008). Improved connectivity can facilitate the ecological flow of materials and resources (Bélisle, 2005). Also, connectivity shapes diversity patterns at different levels (Carrara et al., 2012). The alteration of natural links between patches affects community composition and population persistence (Fagan, 2002; Carrara et al., 2014; Ma et al., 2020). Landscape connectivity depends not only on the area and patterns of habitats but also on the habitat affinities and dispersal abilities of species (Galpern et al., 2010). It has frequently been argued that the ecological effects of dam construction depend on the relatedness of habitats and the various ecological processes that determine the survival of local species (Laita et al., 2010). As information on most species' dispersal movements is limited, researchers usually focus on potential functional connectivity in estimating connectivity. This is because potential connectivity makes use of assumed dispersal distance thresholds estimated from the limited data on actual dispersal abilities and the physical attributes of the landscape, and it can be used to predict the degree of connectivity of landscapes with respect to a particular species (Diaz-Varela et al., 2009).

With increasing recognition of the importance of landscape connectivity and habitat availability, a series of landscape connectivity metrics based on graph theory and related network frameworks have been developed to model the spatial patterns of habitats and the dispersal behavior of rare species (Pascual-Hortal and Saura, 2006, 2007; Zetterberg et al., 2010; Saura et al., 2011). Graph theory considers that the network consists of a set of nodes and a set of links connecting different nodes. In ecological applications, a node typically represents a habitat patch and a link typically represents dispersal. Conefor Sensinode software is a tool for combining data on the habitat patch distributions and habitat availability of landscape patches (Saura and Torné, 2009). The equivalent connected area (ECA) index, modified from the probability of connectivity (PC) index, can be used to quantify spatial pattern changes in the quantity of habitats within landscapes and monitor their potential impacts on landscape connectivity variation. ECA (PC) is convenient for measuring the dynamics of functional connectivity of habitat areas in a landscape (Saura et al., 2011). ECA is measured as that property of the landscape that determines the amount of available habitat within it (Saura et al., 2011). Moreover, to identify the key habitat patches in a landscape network and stepping stone effects, the PC index can be divided into three separate fractions including dPC_{flux}, dPC_{intra}, and $dPC_{connector}$ which quantify dispersal flux through the links, interpatch connectivity, and contribution of patch or connection to the connectivity, respectively (Saura and Rubio, 2010). These three metrics are based on the same concept and are measured in the same units, so they are easily computed and compared within a framework. Additionally, several topological indicators can be used to identify conservation priorities regarding the quantification of important landscape elements (such as habitat patches and stepping stones) (Lander et al., 2010). For example, measurements of centrality characteristics are degree centrality, closeness centrality, betweenness centrality (BC), eigenvalue centrality, subgraph centrality, and the Harary index (Baranyi et al., 2011). Integrating the ECA index and centrality characteristics to depict the habitat importance is necessary for conservation.

Manwan Dam is a typical gorge dam in the middle and lower reaches of the Mekong River in Yunnan Province (He et al., 2004). In recent years, the landscape pattern dynamics arising in response to the construction of the Manwan Dam have been extensively studied. Some researchers have noted that the land use structure changed markedly during and after dam construction and forest as the main habitat decreased its area and experienced intense fragmentation due to farmland transformation (Zhao et al., 2010; Yang et al., 2013). Landscape pattern and dynamics analysis has also revealed forest fragmentation in the reservoir basin (Zhao et al., 2012). Although many sensitive structural indicators have been used to assess landscape patterns and the interaction between human activity and the natural landscape (Zhang et al., 2010), ecological processes have not been taken into accounted in the assessment of ecological effects of dam construction. Previous studies that have addressed the ecological processes occurring in the reservoir ecosystem have concentrated on inner river processes, such as runoff and deposition (Zhao et al., 2012), and few studies have attempted to analyze the fragmented landscape and its effects on the terrestrial species dispersal in reservoir basin ecosystems. Therefore, studies of the landscape connectivity dynamics in the upstream and downstream reaches of Manwan Dam are needed.

In this study, we focused on the landscape connectivity dynamics upstream and downstream of the Manwan hydropower station both before and after the construction of Manwan Dam. The objectives of this study were to (1) analyze the spatial patterns and overall connectivity changes of forest patches in 1974, 1988, and 2004; (2) compare differences in landscape connectivity between the upstream and downstream reaches based on dECA at the patch level; and (3) evaluate the relative importance of the three functional indexes PC_{flux}, dPC_{intra}, and $dPC_{connector}$ in estimating dispersal distances and measure the prioritization of habitat patches in the Manwan habitat network.

MATERIALS AND METHODS

Study Area

The Manwan hydropower station is located near Manwan town in the middle reach of Lancang River in Yunnan Province. It began operation in June 1993, and it is the first multimillion-kilowatt hydropower station to operate along the Lancang River, with an installed capacity of 125 × 10^4 kW (Feng et al., 2000). After the dam began operation, the size of the reservoir increased to more than twice its the original size, and it currently averages 337.1 m in width and occupies an area of 23.6 km^2 (Zhou et al., 2008). It is 148 m long, 132 m in height and has a backwater area of 70 km (Liu et al., 2006). The climate of Manwan basin is subtropical, and the forest types are broadleaf and coniferous; species include *Bon bax ceiba*, *Cycloba lanopsis*, *Lithocarpus* spp., *Lauraceae* spp., and *Pinus kesiya var langbianensis* (Zhou et al., 2010). According to the landscape effect range in Manwan dam as derived from buffer analysis (Zhao et al., 2010), the study area was selected as the 0–10 km buffer zone (distance from the Manwan dam site) in the river watershed (**Figure 1**).

Data Sources

The original land cover data for the area of the Manwan hydropower station were interpreted from Landsat Multi Spectral Scanner (MSS) and Landsat Thematic Mapper (TM) images. These land use data were obtained from the Data Center for Resources and Environmental Sciences, Chinese Academy of Sciences (Zhao et al., 2012). MSS images were utilized as the primary data for creating the land use maps of 1974. In addition, a map of Yunnan land-use types in 1975 (scale of 1:100,000) obtained from the Yunnan Department of Land and Resource served as a reference map for the classification and accuracy evaluation of the MSS images. Two TM images were interpreted as land use maps for 1988 and 2004, and a vegetation map (scale of 1:100,000 in 1991) obtained from the Yunnan Forest Bureau was used as a reference for the classification and accuracy evaluation of the TM images. The TM and MSS images were classified using a supervised maximum likelihood classification approach, and the results were revised as necessary based on visual interpretations and ground survey data. One hundred and two ground control points (Global Positioning System) were compared with the images, and the overall classification accuracies of these images were identified as 83.3, 83.9, and 83.6% in 1974, 1988, and 2004, respectively. The land use maps were classified into forest, grassland, shrubland, farmland, construction land, and water.

Landscape Connectivity Evaluation [Equivalent Connected Area (ECA) Index]

Based on the concept of habitat availability, the ECA, modified from the PC, is defined as the size of a single habitat patch that would provide the same value of PC metric as the actual habitat pattern in the landscape (Saura et al., 2011). Generally, the ECA can be considered as the EC (equivalent connectivity) whenever patch habitat quality or population size is used as the node attribute (Saura et al., 2011). The ECA index is computed as the square root of the numerator of the PC index, and the expression is as follows:

$$ECA = \sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^{*}} \tag{1}$$

Where a_i and a_j are the areas of resource patches i and j, respectively, and p_{ij}^{*} is the maximum product probability of

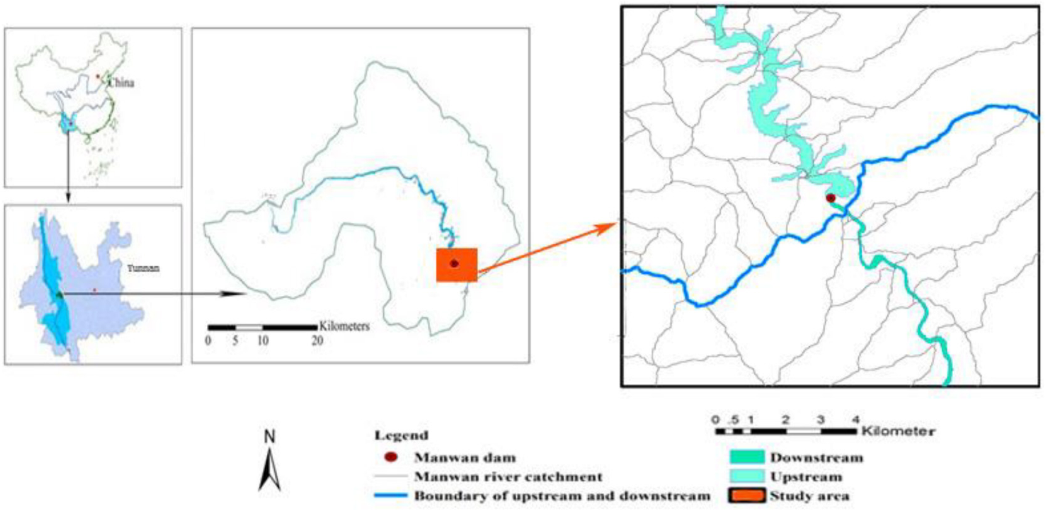

FIGURE 1 | Location of the study area.

the overall probable paths between patches i and j (including single step paths). The product probability of a path is the product of all of the p_{ij} values for all of the connections in a habitat patch (Saura et al., 2011). The formula of p_{ij} is given by:

$$p_{ij} = e^{-k \cdot d_{ij}} \tag{2}$$

Where p_{ij} is the direct dispersal probability, which reflects the strength of each link; d_{ij} is the effective (minimum cost) distance between patches i and j (in meters); and k is a species-specific constant (automatic index) that matches the function to the probability distance values (Pascual-Hortal and Saura, 2007; Saura et al., 2011). Here, the p_{ij} value was characterized by a negative exponential as a function of the inter-patch effective distances selected in our study (Bunn et al., 2000; Saura et al., 2011).

The ECA metric of Conefor Sensinode software was strongly correlated with the ecological processes within the habitat patches, which requires that the dispersal abilities of local species be accounted for in the evaluation of functional connectivity. In the present study, the capabilities of the forest dwelling species were considered in the scenario analysis in the ECA model. Researchers have observed that most seeds travel only a few tens of meters to a hundred meters through habitat patches. In addition, researchers from Yunnan University reported that 135 mammals and some other endemic animals (such as *Macaca nemestrina, Presbytis phayrei,* and *Eothenomys* spp.) only occur in the Lancang River valley (He et al., 2004). Moreover, according to the dispersal ability information from previous studies, most mammals in the study area can only travel short distances of less than 1,000 m to another habitat patch (Sutherland et al., 2000; Bowman et al., 2002; Johst et al., 2002; Wang et al., 2010). Therefore, in the present study, we evaluated four different dispersal distances (d = 200, 400, 600, 800 m) in the ECA model. In addition, due to the same dispersal probability (p_{ij}) of the occurrence of a random event among the habitat patches, the p_{ij} value was set to 0.5 for these four dispersal distance thresholds (Pascual-Hortal and Saura, 2007; Saura et al., 2011).

Importance Evaluation of Landscape Connectivity

The ranking of habitat patches by their contributions to overall landscape connectivity and habitat availability can be computed from the dECA values (Saura et al., 2011). The index is described as the difference in the ECA value before and after changes in spatial pattern (i.e., loss of habitat patches), and it describes the proportional importance of connectivity for each habitat patch. A higher dECA value indicates greater habitat importance in increasing landscape connectivity for forest patches (Saura et al., 2011). In addition, the percentage of the total habitat area (dA) was computed.

All of the ECA and other connectivity indicators were calculated using Conefor Sensinode software 2.6 (Saura and Torné, 2009).

The Three Distinct Fractions of dPC

The dPC values can be divided into three fractions that reflect different ways in which a particular habitat patch can contribute to entire overall landscape connectivity and availability in the landscape. The formula is as follows:

$$dPC = dPC_{intra} + dPC_{flux} + dPC_{connector} \tag{3}$$

Where dPC$_{intra}$ is the contribution of a habitat patch in terms of interpatch connectivity; it describes how a patch may be connected to other patches and relates to available habitat area or other patch attribute of availability. It is independent of patch connections to other patches thus even if it is isolated dPCintra will not change (Saura and Rubio, 2010). dPC$_{flux}$ is associated with the area-weighted dispersal flux through the links of an individual patch to or from other patches in the landscape. This fraction depends on the patch area and its position within the landscape network. dPC$_{connector}$ is the contribution of patch or connection to the connectivity between other habitat patches, as a connecting element or stepping stone between them. In the landscape network, the topological position of a patch or connection in the landscape network will affect the dPC$_{connector}$ value (Saura and Rubio, 2010). The intra, flux, and connector fractions yield information on the importance of a patch in a landscape network, and they measured most of the variability in habitat patch priorities.

Betweenness Centrality

The network centrality of habitat patches can be measured by the BC indicator. BC based on the PC index is denoted BC (PC). It describes a habitat patch in which the shortest paths (based on topological distance) between all pairs of patches in the landscape are calculated and the number of times those paths cross each node are counted (Bodin and Saura, 2010). BC (PC) improves on the classical BC metrics measured in the Conefor model (Bodin and Saura, 2010). In addition to the PC (intra, flux and connector) fractions, BC (PC) can be considered as a "fourth fraction" of PC metrics, as it is measured in the same units and within the same analytical framework. The BC index may be effective for identifying patches as stepping stones when taking into account biological flows at a larger scale. Unlike the connector fraction of the PC metrics, BC do not estimate the impacts of a patch removal in terms of connectivity loss. We used the topological indicators dPC$_{connector}$ and BC (PC) characterize different properties of the habitat network of Manwan Dam.

Statistical Analysis

Correlation analysis were conducted using the non-parametric Kendall's tau_b rank test of correlation coefficients (Arndt, 1999). To reveal the effectiveness of different indexes, correlations were investigated between the three dPC fractions (dPC_{intra}, dPC_{flux}, and $dPC_{connector}$), between the total dPC value and the three dPC fractions. Further, to understand how the patch size affect the connectivity, the correlation between habitat patch area and three dPC fractions were also investigated. This analysis was conducted using SPSS software (Norušis, 1993).

RESULTS

Forest Fragmentation and Total Landscape Connectivity Changes From 1974 to 2004

At the landscape level, the forest connectivity, as measured by the ECA values, successively decreased from 1974 to 2004, particularly after dam construction. The functional connectivity before dam construction was highest in 1974, likely due to the numerous forest patches of large area. With the fragmentation of the forest after dam construction and impoundment, the overall connectivity values of ECA were lower than before dam construction in 1974 (**Table 1**). However, the overall connectivity increased slightly with the increase in dispersal distances from 200 to 800 m.

As indicated by the total ECA values, there was considerable spatial variation in forest connectivity between the upstream and downstream areas of the dam in 1974, 1988, and 2004 (**Figure 2**). Under the four dispersal distance thresholds, the forest connectivity upstream of Manwan Dam was much greater than downstream before the dam construction, and the lowest ECA value reached 0.4. In 1988 and 2004, the total connectivity of ECA values upstream was lower than that downstream. Alterations in connectivity due to dam construction primarily occurred downstream of Manwan Dam, and the lowest ECA value upstream was observed in 2004, after dam construction. However, with increasing dispersal distance from 200 to 800 m, a slight overall increase in forest connectivity was observed around Manwan dam, with the highest values observed at 800 m.

TABLE 1 | Total ECA values in the Manwan forest landscape (1974–2004).

Total ECA value (10^8) (m^4)	200 m	400 m	600 m	800 m
1974	1.42	1.51	1.54	1.56
1988	1.14	1.07	1.25	1.27
2004	1.07	1.17	1.21	1.23

The Dynamics of the Importance of Key Patches in Relation to Connectivity at the Patch Scale

The dynamics of patch importance of functional connectivity at the patch scale are described by the dECA values in **Figure 3**. In 1974, the importance of forest connectivity in forest patches at the edges of the study area changed most at dispersal distances of 400 and 800 m (ranging from 20 to 50%). Only 8% of forest patches exhibited significant changes in connectivity under the four dispersal distances. The average dECA values for all of the forest patches ranged from 54% at a dispersal distance of 200 m to 66% at 800 m, values greater than the average dA value of 51%.

In 1988, approximately 12% of forest patches exhibited obvious changes in connectivity under the four dispersal distances, with dECA values greater than 20%. The greatest change in forest connectivity was observed at the dispersal distance of 400 m, upstream of the dam. The average dECA values for all of the forest patches ranged from 41% at a dispersal distance of 200 m to 49% for the 800 m distance, values greater than the mean dA value of 39%.

In 2004, approximately 18% of forest patches had importance level changes in connectivity under the four movement distances. The greatest change in forest connectivity downstream occurred at the dispersal distance of 800 m, with a dECA value greater than 50%. The average dECA values for all of the forest patches ranged from 45% at a distance of 200 m to 52% at 800 m, values higher than the average dA value of 35%.

Due to changes in spatial pattern between 1974 and 2004, the overall forest landscape connectivity increased at the patch level. The dECA values indicated a slight increase in the importance of connectivity on forest patches under the four

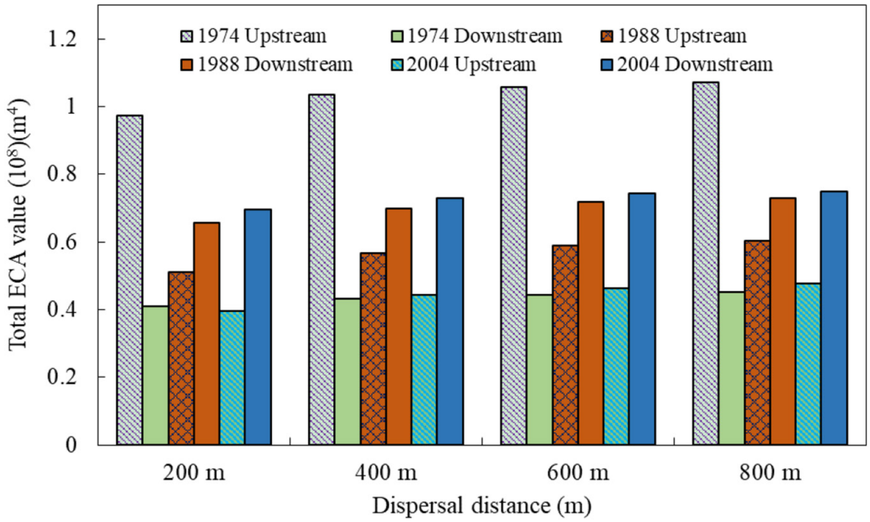

FIGURE 2 | Spatial differences in total landscape connectivity as measured by the ECA index (1974–2004).

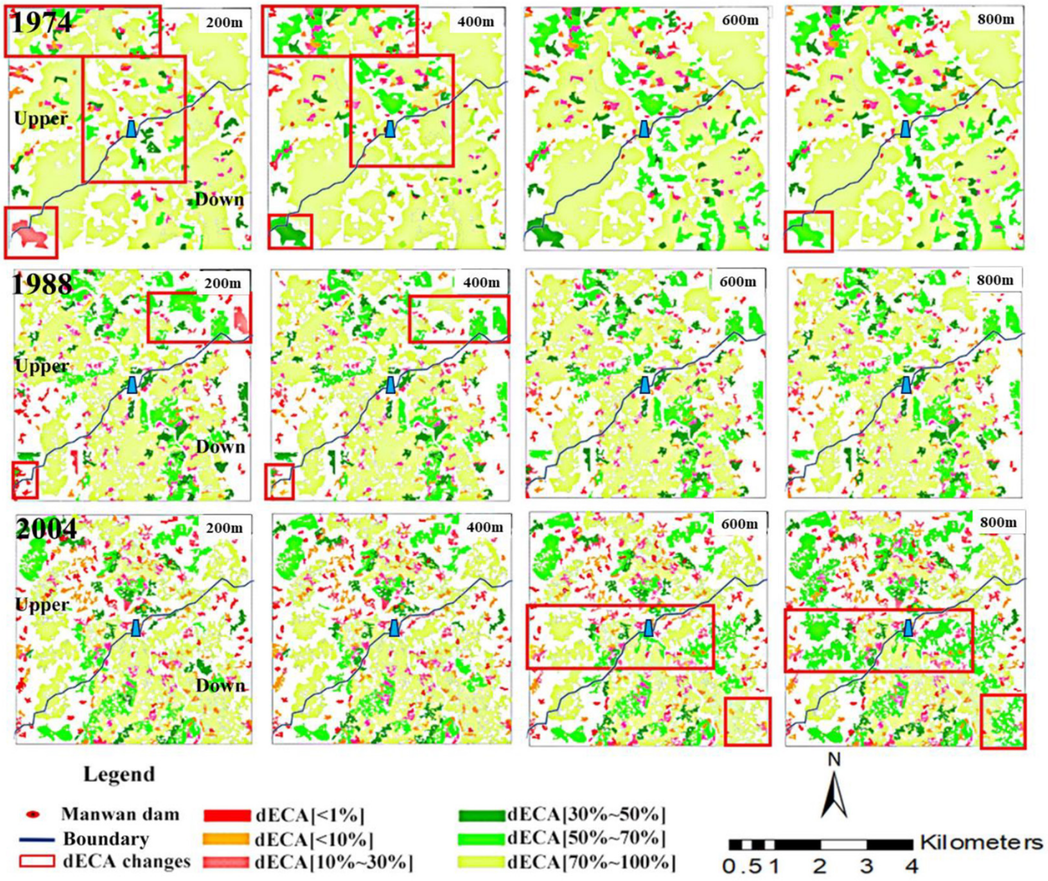

FIGURE 3 | Connectivity changes in the Manwan forest patches under four different dispersal distances in 1974, 1988, and 2004, as measured by the dECA index.

dispersal distances in all three periods (**Figure 3**). At the patch level, the degree of connectivity was stable for most of the large habitat patches, with dECA values in excess of 50% under the four dispersal distances. In each of the three periods, dECA tended to increase slightly with the increase in dispersal distance. The most important forest patches were those with the largest patch areas. The greatest individual changes were found in edge forest patches of small and medium area; these key forest patches were located primarily near the boundary of the study area.

Change in the Three dPC Fractions and Correlations With Forest Patch Area

Correlations between dPC and its different fractions (intra, flux, and connector) are illustrated in **Figure 4**. Similar trends in rank correlation were observed between dPC and both habitat area and dPC$_{flux}$. The rank correlations of dPC$_{flux}$ and patch area increased steadily with dispersal distance, particularly at 600 and 800 m. The tau_b correlation coefficients of dPC and dPC$_{flux}$ were high at both 200 and 800 m, with the lowest coefficient values ranging from 0.82 to 0.85 and the highest values approaching 1 (0.92 and 0.95). In accordance with the dPC$_{flux}$ fraction, for the longer dispersal distances, the key forest patches were generally related to the largest habitat patches. This is because these large forest patches are more likely to be inter-connected; the P^{*}_{ij} value often approached 1 for large habitat patches. The flux features of different habitat patches were primarily influenced by patch area.

Independent of the dispersal distance, the dPC$_{intra}$ value had a strong rank correlation (tau_b = 1) with patch area (**Figure 4**). This fraction did not change with dispersal distance. This fraction indicates that forest patches with the largest habitat area have the highest importance for connectivity.

The dPC$_{connector}$ fraction evaluates landscape pattern and was not in accordance with the area-based prioritization. The rank correlation coefficients of dPC$_{connector}$ and patch area remained low relative to other three indicators. With increasing dispersal distance, the tau_b values were stable at 0.29, except at 400 m, with a value of 0.31.

Similar increasing trends were observed among the correlations between dPC and dPC$_{flux}$, dPC$_{flux}$ and dPC$_{connector}$ (**Figure 5**). As their tau_b values are near 1, the prioritization of habitat patches can be measured with the dPC and dPC$_{flux}$ indicators. The coefficient correlations were lower at 200 and 400 m and higher at 600 and 800 m. The rank correlations of dPC and dPC$_{connector}$ were lower than those of other two indices, with the lowest values occurring at 200 and 400 m. The results also indicated that dPC$_{connector}$ is an

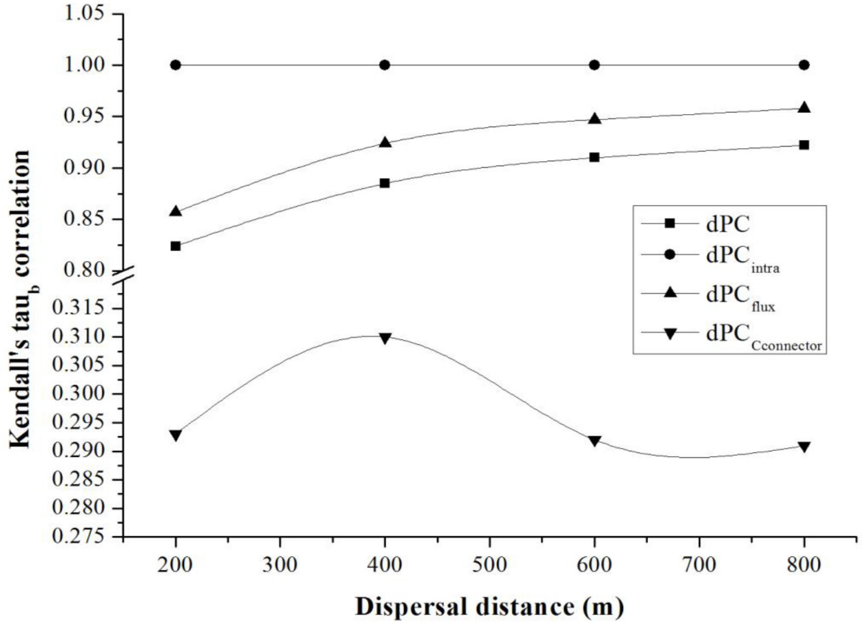

FIGURE 4 | Kendall's rank correlations (*tau*$_b$) between the patch importance indices (dPC, dPC$_{flux}$, dPC$_{intra}$, dPC$_{connector}$,) and patch area with increasing dispersal distance.

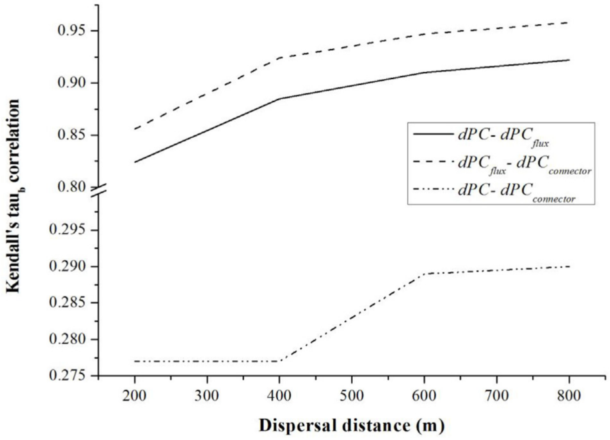

FIGURE 5 | Kendall's rank correlations (*tau*$_b$) between *dPC*, *dPC*$_{flux}$, and *dPC*$_{connector}$, at different dispersal distances.

effective metric for measuring landscape connectivity in habitat patches.

The Three Fractions of dPC and BC as Indicators of the Importance of Key Habitat Patches

In emphasizing the prioritizing of habitat patches, our results identified some differences between BC (PC) and dPC$_{connector}$. Links or ecological corridors can only contribute through dPC$_{connector}$, not through dPC$_{intra}$ or dPC$_{flux}$. Although the calculation of dPC$_{connector}$ for a certain patch is independent of the patch attributes, it does consider patch area in the operational process.

In the present study, our results suggested that obvious changes to stepping stone patches occurred at both the maximum dispersal distance of 800 m and the minimum dispersal distance of 200 m (**Figure 6**). We consider the BC index and dPC$_{connector}$ as the most effective metrics for identifying key habitat patches as stepping stones in the landscape. These key stepping stones between large habitat patches characterize the flux and total habitat area in the landscape near Manwan Dam.

Although the BC (PC) metric does not directly measure the overall connectivity of the entire landscape, it is a topological indicator that only considered the habitat patch position at the patch scale. The BC indicator suggested that some larger area habitat patches near Manwan Dam were significant in maintaining the forest connectivity of the networks in the Manwan reservoir ecosystem (**Figure 6**). This indicator revealed the degree to which the shortest paths for dispersal between other habitat patches pass through a given habitat patch. However, the patch area or habitat quality of that particular patch that is connected through the shortest path was not taken into account.

DISCUSSION

The Influence of Dam Construction on Landscape Pattern and Ecological Processes

In the post-dam era, landscape dynamics take place over time due to many driving factors, mainly anthropogenic alterations

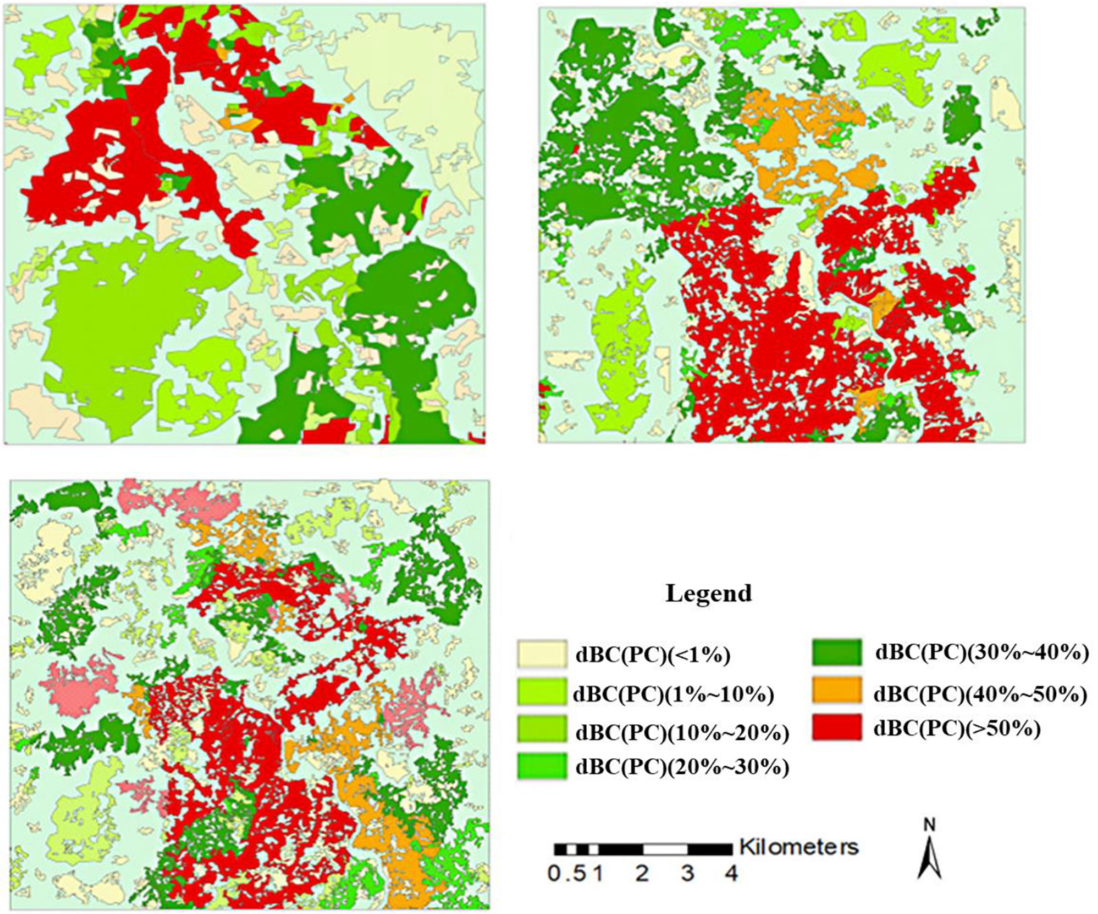

FIGURE 6 | Dynamics of the Betweenness Centrality BC (PC) index in the three periods.

near dams. Variation in landscape distributions, which alter landscape connectivity and habitat availability, may be the result of dam construction, the extension of road networks, agricultural activities, economic development, and immigration (Safner et al., 2011).

Many researchers have focused on landscape dynamics due to dam construction and evaluation of the natural landscape at different spatial and temporal scales (Zhou et al., 2010; Zhao et al., 2012). Previous studies showed that the reservoir impoundment have significant effects on land use in the Manwan reservoir basin (Zhao et al., 2010). Due to the high level of anthropogenic disturbance in this region, dam construction can not only degrade river connectivity but also inhibit adjacent landscape processes in the river basin (Zhao et al., 2012). Our results indicated that landscape dynamics and fragmented watersheds influenced the connectivity of the adjacent landscape, particularly in 2004 (after the construction and impoundment of Manwan Dam). These results emphasize that functional landscape connectivity varies with dispersal ability and habitat availability in the fragmented landscape. In the present study, we discuss how a key ecological process (i.e., movements of local species) is strongly related to adjacent landscape changes and fragmented forest patches. Furthermore, the local microclimate can be greatly altered due to open water evaporation and influence the ecosystems directly.

Traditionally, buffer analysis with landscape pattern analysis had been performed to evaluate the land use dynamics associated with dam construction, which are characterized by different distances to a river channel or dam site (Zhao et al., 2012). In a previous study around the Manwan reservoir, landscape effects appeared to be greatest primarily within the 2000-m to 3000-m buffer zone, and the greatest change in patch density occurred within 1,000 m of the dam site during 1974–2004 (Zhao et al., 2012). In the present study, the combined application of the connectivity model with GIS was effective for the spatial and temporal assessment of landscape connectivity dynamics before and after dam construction. We selected 10 km (distance from Manwan Dam) as the buffer zone to analyze the upstream and downstream functional connectivity dynamics. Our results suggest that dECA(PC) may be an appropriate indicator for identifying critical priority habitat patches as connectivity providers in the areas upstream and downstream of Manwan Dam.

Correlations Between Forest Fragmentation and Ecological Processes Related to the Landscape Connectivity and Habitat Availability

As the influence of dam construction extends well beyond the reservoir area, forest fragmentation and stress are discovered in upstream and downstream ecosystems from dams. In the Amazon basin, studies found the lack of a strategic dam construction plan could drive deforestation and lead to severe break in connectivity (Finer and Jenkins, 2012). It is proved that the continuity and abiotic conditions of habitat are disrupted by forests fragmentation, and leads to great changes in populations of animals and plants (Laurance et al., 2018), as well as disruptions of species interactions (Galetti and Dirzo, 2013). Thus, assessing functional connectivity in the fragmented forest landscape is effective for integrating fragmented forest patches and the dispersal activities of local species (Bunn et al., 2000). The impacts of habitat loss may be aggravated to varying degrees by the fragmentation of the habitat network (Saura et al., 2011). Considering the fragmentation process of forest patches, we used the landscape-based, functional connectivity indicator dECA(PC) to identify that landscape characteristic that determines the amount of available habitat, regardless of whether that habitat is available via interpatch connectivity. The dECA(PC) indicator was able to identify six different importance degrees of habitat patches as connectivity providers and conservation protectors, indicating the large forest patches yield the highest importance degrees for maintaining landscape connectivity.

Our study documented the terrestrial ecological processes that were affected by habitat fragmentation associated with dam construction. The isolated or connected patches in the fragmented landscape, particularly the small ones, were influenced by the potential dispersal abilities. As shown in our study, fragmentation of forest patches was greater in 2004 than in 1988 and 1974. The connection scenarios under different dispersal distance scenarios identified the isolated or connected patches for target species as they were strongly dependent on these potential dispersal thresholds. When the connection scenario was applied, the dECA(PC) index ranked each patch as a connectivity provider in relation to its habitat availability. And we identified that the greatest changes in the importance of habitat links among small patches occurred at a dispersal distance of 400 m by evaluating the results from all scenarios. Many connected patches with higher importance of habitat areas and links were assumed to be more important than isolated patches for the maintenance and improvement of landscape connectivity.

Responses to the Landscape Pattern Changes With Respect to Different Biological Traits and Dispersal Capabilities of Local Species

For many endemic species in forest-dwelling patches, responses to landscape pattern changes related to connectivity were not always the same. When we applied functional connectivity analyses to the entire forest landscape near the river channel, the most important problem to overcome was the large number of forest-dwelling species with varied movement abilities and other traits. The key issue of dispersal distance threshold selection remains, as these distances may vary with landscape pattern dynamics related to landscape connectivity (Saura et al., 2011). Although some researchers concentrate their efforts on the traits of endangered and endemic species in different regions around the world (Lander et al., 2010), insufficient data were available in the present study regarding the dispersal abilities and other traits of local species in the study region. Thus, there is some uncertainty inherent in the process of modeling connection scenarios and measuring landscape connectivity (Decout et al., 2012). Although this lack of information can reduce the efficacy of the functional connectivity models used to identify habitat patches as connectivity providers (Saura et al., 2011), our results show that some indicators, such as ECA(PC), rely less on the actual dispersal activities of local species, which are highly sensitive to changes in habitat area. Therefore, the potential dispersal distances of various endemic species were often assumed in the functional connectivity models.

The scale of dispersal capacities considered in this study may affect forest connectivity. In this case study, the organisms involved may include reptiles, amphibians, birds, plants (seeds), and their pollinators, and other endemic or endangered species. The dispersal distance thresholds are likely related to the movement abilities of these endemic species. Previous studies have suggested that only a small number of endemic and endangered species populations should be considered target species in functional connectivity analysis (Saura and Rubio, 2010). As many studies have reported species' dispersal distances of within a few hundred meters, we chose dispersal thresholds of 200, 400, 600, and 800 m (equal intervals) for our connectivity scenarios (Liu et al., 2014). Target species such as *Macaca nemestrina*, *Prebytis phayrei*, *Eothenomys custos* or the seeds of target plant species may be more sensitive to changes in forest spatial patterns. They may benefit to a greater extent from available stepping stones, and their biological traits and dispersal capabilities will be specific to the Manwan reservoir ecosystem. Future studies should address the landscape connectivity dynamics of cascade dams (such as Xiaowan and Dachaoshan Dams) in Lancang River, as the different species and related ecological flows may be affected by the advanced forest spatial framework dynamics of the Manwan reservoir ecosystem.

CONCLUSION

This study analyzed changes in a modified ECA index in response to landscape dynamics to characterize the effects of dam construction on landscape connectivity. The overall connectivity measured by the ECA successively decreased from 1974 to 2004. With the change in landscape pattern, the connectivity upstream of Manwan Dam was much greater than downstream in 1974; however, in 1988 and 2004, the total ECA values upstream were lower than those downstream, indicating a large impact of dam construction on landscape connectivity. The spatio-temporal variation of forest networks on landscape connectivity in the Manwan basin indicated that dam construction had some negative ecological effects on landscape connectivity and forest conservation. The degree of connectivity was stable for most of the large habitat patches under the four dispersal distances (200, 400, 600, and 800 m). Only 8, 12, and 18% of patches in 1974, 1988, and 2006, respectively, exhibited obvious changes in connectivity. The greatest individual changes were found at the 400 m species dispersal distance in key forest patches located near the boundary of the study area. For the purposes of forest conservation, these crucial patches require more attention. As dispersal distance increased, dECA tended to increase slightly in all three years (1974, 1988, and 2004). Moreover, the rank correlations between forest patch area and the three dPC fractions indicated that, as forest availability metrics, dPC and its three fractions can effectively quantify the percentage importance of the connectivity on forest patches. These correlations also revealed that connectivity varied with dispersal distance. The BC(PC) index suggested that some large area or high quality habitat patches near Manwan Dam were significant in maintaining the forest connectivity of the networks in the Manwan basin. This research provides a case study of the analysis of landscape connectivity based on network analysis. In addition, for biodiversity and forest conservation efforts, future studies will require more information about the movement abilities of local species and incorporate this information into the calculation of the ECA index.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Complex Small-Holder Agriculture in Rainforest Buffer Zone, Sri Lanka, Supports Endemic Birds

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The Sinharaja rainforest in southwestern Sri Lanka is a protected forest in a largely agriculture-dominated landscape. In keeping with global UNESCO global biosphere reserves planning, the Sinharaja is surrounded by a buffer zone of regenerating forest and villages with small tea plots and multi-strata tree gardens (homegardens). Globally, however, conservation planning lacks standards on buffer zone management. We ask what relationships exist between village land use and bird assemblages, which are effective ecosystem indicators. Birds have been little studied across land use and vegetation structure in actively managed, large, protected forest buffer zones. To that end, we ran spatially- and temporally-replicated bird point counts across tree gardens, forest fragments, and tea plots within a Sinharaja village. Tree gardens held a greater abundance of birds across habitat association, conservation concern, diet, and endemic species than forest fragments or tea plots. Forest fragments and tree gardens hosted statistically similar numbers of birds in some subsets, but their species assemblages differed. In tea plots, greater shade tree species richness correlated with greater bird abundance and species richness. Our results support the argument for programs to support complex small-scale tree-based agroforestry embedded in buffer zone regenerating forest.

Keywords: agroforestry, tree garden, forest fragment, homegarden, rainforest, Sinharaja, tea, buffer zone

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INTRODUCTION

Geological isolation and varied climate and topography produced the unique species assemblages of Sri Lanka, as in other parts of south Asia (Ripley and Beehler, 1990; Bossuyt, 2004; Kaluthota and Kotagama, 2005; Kotagama et al., 2006; Sodhi et al., 2009; Wikramanayake and Buthpitiya, 2017). In combination with the western Ghats of India, the island comprises a biodiversity hotspot with high endemism across taxa (Gunawardene et al., 2007). Twenty-seven of Sri Lanka's observed birds are confirmed endemic and an additional six are proposed endemic (Warakagoda et al., 2013; Iucn., 2016). However, formerly largely forested, Sri Lanka has lost half its forest cover since 1930 (Naresa., 1991; Reddy et al., 2018). The loss in keeping with that of much of South Asia, which lost almost 30% of forest cover in the same period (Reddy et al., 2018). Reflecting Sri Lanka's large-scale forest cover and habitat loss, seventeen of the island's endemic birds are vulnerable, near threatened, or endangered (Warakagoda et al., 2013; Iucn., 2016; Abeyarama and Seneviratne, 2017). The Sinharaja rainforest, a National Park, UNESCO Man and the Biosphere Reserve, UNESCO World

Heritage Site, and a Bird Life International Important Bird Area (IBA) in the southwest wet zone of Sri Lanka, is one of the only remaining stretches of relatively undisturbed, connected, lowland rainforest on the island (Gunatilleke et al., 2005). It contains significant avian phylogenetic diversity (Abeyarama and Seneviratne, 2017). In a nation of great climate and topographic heterogeneity, the Sinharaja lowland rainforest is particularly important to preserving Sri Lanka's biodiversity, including avifauna (Gunatilleke and Gunatilleke, 1983; Gunatilleke et al., 2017).

Consistent with UNESCO's global biosphere reserves organization, a buffer zone surrounds the Sinharaja rainforest (Unesco., 1996). Forest reserve buffer zones can help maintain local ecology (Robinson et al., 2013). However, there is a lack of global consensus on buffer zone management (Margles et al., 2010; Allan et al., 2017).

The Sinharaja's buffer consists of regenerating forest and forest villages, which comprise homes, small tea plots, and multi-strata tree gardens (homegardens) (Wijesooriya and Gunatilleke, 2003; Dewi et al., 2013). Tree gardens reflect a system of indigenous tree culture common throughout South and Southeast Asia that is ancient but still evolving (Kumar and Nair, 2006; Martin et al., 2018). They provide medicine, food, construction material, fuel, fodder, and income to residents across the tropics from rural to urban settings. Tree gardens contribute to food security and local economies (Jaman et al., 2016; Sangakkara and Frossard, 2016; Paembonan et al., 2018; Rousta et al., 2018; Park et al., 2019). They are managed for resilience to climate and economic changes (Weerahewa et al., 2012). Tree gardens help maintain local and regional biodiversity through the tropics (Watson and Eyzaguirre, 2002; Kumar and Nair, 2006; Galluzzi et al., 2010; Kumar and Nair, 2011; Schroth et al., 2013), with specific research from Sri Lanka (Mohri et al., 2013), Indonesia (Michon et al., 1986; Mohri et al., 2013), Vietnam (Trinh et al., 2003; Mohri et al., 2013), Thailand (Timsuksai and Rambo, 2016), Malaysia (Moore et al., 2016), India (Das and Das, 2015), and Brazil (Peroni et al., 2016). In Sri Lanka, tree gardens make up almost half of total forest area and fourteen percent of the country's total land area (Mattsson et al., 2013; Reddy et al., 2018). Research from 2010 estimated that they comprised one fifth of the country's aboveground carbon stocks (Mattsson et al., 2013). They are actively supported by government policies (Fao., 2009; Pushpakumara et al., 2012; Chokkalingam and Vanniarachchy, 2013; Galhena et al., 2013; Mattsson et al., 2017). Understanding how and to what ends they contribute to conservation goals is necessary.

We studied bird use of a Sinharaja buffer zone village and its tree gardens. Birds provide ecological, economic, and scientific value, all of which make them important research subjects. The ecosystem services they provide include pollination, seed dispersal, and insect control (Sekercioglu, 2006). Bird-tourism is a significant and growing part of global eco-tourism, and draws foreign visitors specifically to the Sinharaja (Sekercioglu, 2002; Goodale et al., 2014; Arachchi, 2020). Birds are also effective ecosystem indicators across landscapes (Macarthur, 1964; O'Connell et al., 2000; Sekercioglu et al., 2004). Previous studies of bird populations in intensively managed tropical landscapes compared other agroforestry systems to intact forest (Thiollay, 1995; Perfecto et al., 1996; Calvo and Blake, 1998; Mas and Dietsch, 2004; Waltert et al., 2004; Beukema et al., 2007; Harvey and Villalobos, 2007; Van Bael et al., 2007; Tscharntke et al., 2008; Clough et al., 2009; Sekercioglu, 2012). Others examined tree gardens, agroforestry systems, and regenerating forest, but few did so in small-scale land use areas within the buffer zone of a large, undisturbed, conservation area (Sidhu et al., 2010; Kottawa-Arachchi and Gamage, 2015; Engelen et al., 2016; Prabowo et al., 2016; Perera et al., 2017). Yet tree gardens in buffer zones contain plants that provide food and shelter for birds (Martin et al., 2018). There is a need to quantify how the structure and size of buffer zone land use translates to bird presence around the Sinharaja (Waltert et al., 2011; Goodale et al., 2014).

To that end, we quantified the bird assemblages observed in small-scale tree gardens, forest fragments, and tea plots within the buffer zone village. We asked: (1) How does bird assemblage vary with land use? (2) Are there relationships between vegetation characteristics and bird assemblages? (3) What land use type hosts the greatest number of multi-species flocks?

Research suggests that the greater a habitat's complexity, the greater the complexity of its species assemblage (Macarthur, 1964; Roth, 1976). We expected to see that tree gardens would host larger and more complex species assemblages than tea plots. We expected more complex vegetation would host more complex bird assemblages. Since multi-species flocks are a documented forest phenomenon, we expected to see more flocks in forest fragments (Goodale et al., 2014).

MATERIALS AND METHODS

Study Site

Pitakele village is a community of thirty-plus households bordering the core of the Sinharaja Forest Reserve (6°26′N 80°21′E, 300–700 m in altitude), at the end of a jungle road in the northwest of the reserve's buffer zone (**Figure 1**). It receives an average annual rainfall of 3 m with a dry season from January to March (Munidasa et al., 2002). The region's average daily temperatures vary between 22 and 28°C (Ashton et al., 2001; Gunatilleke et al., 2005).

Like other rainforest-embedded villages in Sri Lanka, the homes of Pitakele lie along and upslope of a river, surrounded by tree gardens and often downslope of cultivated tea. Tea plots comprise 39% village land area, tree gardens comprise 27%, and forest fragments comprise 17% (Martin et al., 2018; **Figure 1**). Tea plots in Pitakele include shade trees, typically *Gliricidia sepium*, but also kitul (*Caryota urens*), other palms, and rainforest or cultivated tree garden species. Tea (*Camellia sinensis*) land borders second-growth rainforest, which was logged in the 1970s, or rubber (*Hevea brasiliensis*) or Caribbean pine (*Pinus carribea*) plantings (Kotagama and Goodale, 2004). The primary source of income for many Pitakele villagers is from picking tea. The village tree gardens average 0.12 ha in size with a mean species richness of 64 trees, shrubs, herbs, and climbers (Martin et al., 2018). At least 219 different species are grown across Pitakele's homegardens (Martin et al., 2018). The overstories of these tree

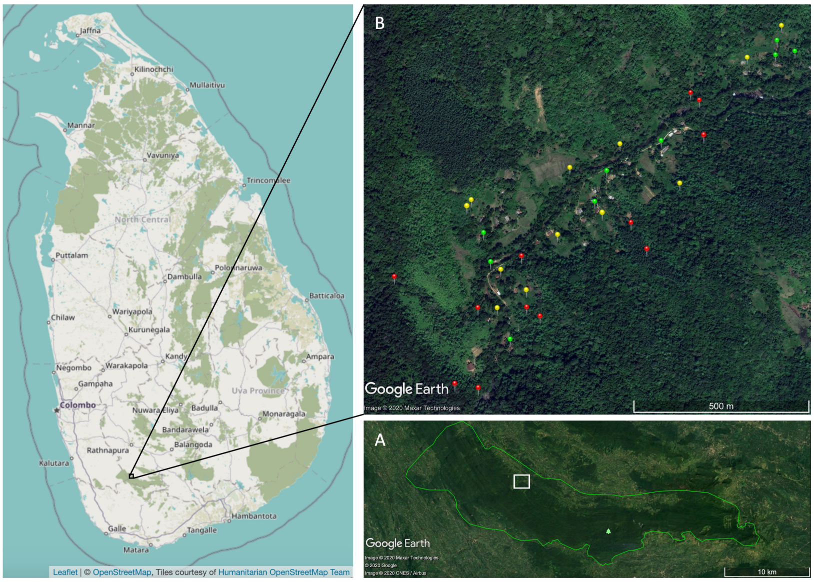

FIGURE 1 | (A) Pitakele is located in southwest Sri Lanka. Satellite imagery via Google Earth clearly shows the dark band of the protected Sinharaja rainforest. **(B)** Bird point counts follow the Pitakele river valley. Green pins are tree gardens, yellow pins are tea, and red pins are forest fragment. Pitakele is embedded in the Sinharaja. Adapted from Google Earth and Open Street Map.

gardens are dominated by betel palm (*Areca catechu*), coconut (*Cocos nucifera*), and kitul palm (*Caryota urens*); lower strata by mango (*Mangifera indica*) and jack (*Artocarpus heterophyllus*) (Martin et al., 2018). Secondary forest fragments lie on rocky ground close to the river or steep slopes less favorable for growing crops. They average 0.12 ha in size (Martin et al., 2018). Some forest fragments connect to the Sinharaja's core reserve. Our study area is approximately 100 ha. Pitakele village is representative of settlements that about the whole Sinharaja (**Figure 1**).

Sampling Design

We conducted thirty-three 20 m-radius bird point counts, with nine point counts in tree gardens, 12 in tea plots, and 12 in forest fragments. We recorded all birds seen and heard within a plot, including birds in flight, for 30 min (since it is a relatively small point count plot and flock observations can last for 10–60 min after first observation) (Farley et al., 2008). Other point counts within Sri Lanka have been conducted using the variable circular plot method (Wijesundara and Wijesundara, 2014). Previous studies within the Sinharaja buffer zone have been run along transects (Kotagama and Goodale, 2004). We used point counts to account for small-scale differences in land use. Bird point counts are non-invasive.

We ran each point count five times between January and March 2018. No plot was closer to the edge of the land use area than 20 m, the radius of the plot. We visited each site between 7:00 and 10:30 a.m. For every bird, we noted if they were part of a multi-species flock, i.e., moving with birds of other species in a close association. We conducted the point counts over the dry season, when winter migrants are present and many resident species breed (Jayarathna et al., 2013). We did not sample on mornings when it rained and randomized dates and times of the site visits.

Vegetation Surveys

We counted all trees within 10 m of the point count plot center and measured their diameter at breast height. We measured the total tree species richness of the plots, counting trees per species. We measured tree basal area from the center of the plot by using an angle gauge (metric basal area factor 2.5) in a variable radius plot, a standard forestry method (Packard and Radtke, 2007).

Analysis

For all variables, we calculated Moran's I tests. Where Moran's I test ruled out spatial autocorrelation, we ran further analyses. We tested all variables for normal distribution using the Shapiro-Wilks test ($p > 0.05$).

To answer how bird assemblage varied with land use, we analyzed point count data by total bird abundance, richness, and diversity; habitat association, conservation significance, and diet; and endemic species. Assemblage subsets by habitat association and diet reflect functional relationships between birds and habitat. Conservation significance shows if and how the landscape contributes to conservation goals. We looked at individual endemic species because Sri Lanka and the Sinharaja are important for endemic species. These subsets are commonly tested and can be used for cross-study comparison (Tscharntke et al., 2008; Maas et al., 2009; De Lima et al., 2012; Sekercioglu, 2012; Goodale et al., 2014). We tested species assemblage via multivariate analyses of variance (MANOVA).

We adopted habitat classifications (forest, open landscape, or both) from Goodale et al. (2014), which based its identifications on Ali and Ripley (1987) and Grimmett et al. (1999). Where bird-habitat associations were not identified by Goodale et al. (2014), we used Warakagoda et al. (2013) to classify them. We classified birds as of conservation concern if they were listed as "Near Threatened," "Vulnerable," or "Endangered" by the 2016 IUCN Red List. All of the birds identified as of conservation concern are declining in number (Iucn., 2016). We grouped birds by diet (frugivorous, nectarivorous, insectivorous, granivorous, or carnivorous) following Goodale et al. (2014), who used Rasmussen and Anderton (2012). We tested each subset's mean abundance per plot. We tested mean endemic species richness per plot. We tested the mean abundance of individual endemic species observed at least three times. On normally distributed variables we ran analysis of variance (ANOVA) by land use type. If significant, we then ran a Tukey *post hoc* test. On non-normally distributed variables, we ran a Kruskal-Wallis test with a Bonferroni correction. We tested species assemblage variation per land use type by running three pair-wise MANOVAs of total bird species abundance and endemic bird species abundance. We square-root transformed the data for both MANOVAs to minimize the influence of the most common species. We used Bray-Curtis distance, 999 permutations, and a Bonferroni correction with alpha = 0.05. We ran a non-metric multidimensional scaling (NMDS) analysis (**Figure 3**) to visualize differences.

To answer question 2, whether bird assemblages varied with vegetation characteristics, we ran generalized linear regressions on total bird abundance, bird species richness, and abundance of conservation concern species by basal area measured by variable radius plot, and basal area, stem density, and tree species richness within 10 m of plot center. We used Gaussian distributions. To test for land use-specific correlations, we subdivided the data by land use. We ran GLMs by land use separately because other studies have observed that relationships between birds and vegetation characteristics can vary with type of habitat (Duguid et al., 2016). We ran ANOVA with Tukey *post hoc* analysis or Kruskal-Wallis with Bonferroni correction to check how basal area, tree species richness, and stem density varied with land use.

To answer question 3, what land use type hosted the greatest number of multi-species bird flocks, we analyzed flock presence, or the mean number of flocks observed in a plot, and flock size, the mean number of birds in a plot that were part of a flock. We ran the Kruskal-Wallis test with a Bonferroni correction on both variables, which were non-normally distributed.

RESULTS

We observed 1,269 individual birds of 76 species across the 33 plots. We observed 59 species in tree gardens, 48 species in forest fragments, and 44 species in tea plots. We observed 17 endemic species.

Assemblage Variation

Bird abundance and Shannon-Weiner diversity were higher in tree gardens than in forest fragments or tea plots (**Figure 2**) [$F_{(2,30)} = 20.79$, $p < 0.001$] (Kruskal-Wallis chi-square = 16.39, $df = 2$, $p < 0.001$); and bird species richness was higher in forest fragments than in tea plots [$F_{(2,30)} = 22.16$, $p < 0.001$].

Birds associated with both open lands and forest, endemic birds, frugivorous birds, and nectarivorous birds (only the purple-rumped sunbird, *Leptocoma zeylonica*) were observed in higher abundances in tree gardens than in either forest fragments or tea plots (**Table 1**). Forest-associated birds and insectivorous birds were more abundant in both tree gardens and forest fragments than in tea plots (**Table 1**). Species of conservation concern were more abundant in tree gardens than in tea plots, and their numbers in forest fragments statistically overlapped both (**Table 1**). Similarly, endemic bird species richness was greater in tree gardens than in tea plots and their numbers in forest fragments statistically overlapped both (**Table 1**). Open land-associated birds were more abundant in tree gardens than in forest fragments, and their abundance in tea plots statistically overlapped both (**Table 1**). Carnivorous birds did not vary across land use type.

MANOVA analysis showed that bird composition differed between land use [$F_{(2,30)} = 5.22$, $p < 0.001$, $r^2 = 0.26$].

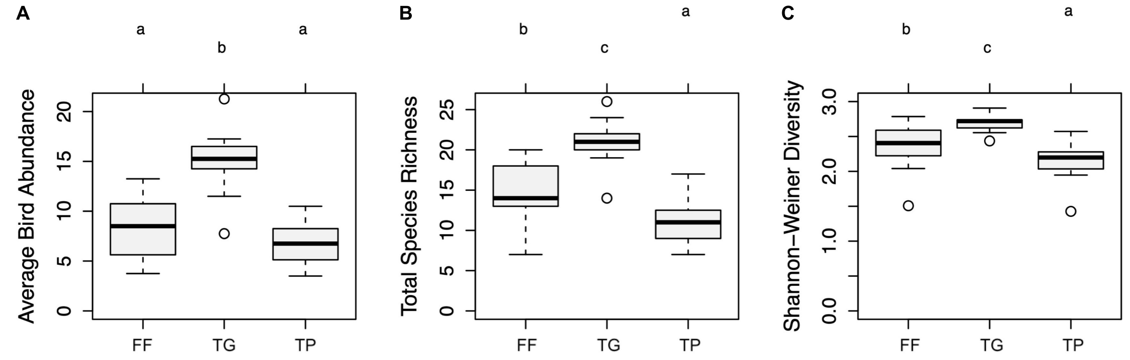

FIGURE 2 | (A) Bird abundance, species richness per point count, and diversity by land use: FF = forest fragment, TG = tree garden, TP = tea. Letters indicate differences in Tukey *post hoc* tests ($p < 0.05$) and Kruskal-Wallis tests with Bonferroni correction a > b > c. **(B)** Bird abundance by habitat association and land use. **(C)** Endemic bird abundance and species richness and abundance of birds of conservation concern by land use.

TABLE 1 | Mean abundance per point count visit of bird assemblage subsets.

Group	Number species	Forest fragment	Tree garden	Tea plot	Chi-square or *F*-test
Frugivorous	**23**	**3.06 (1.93)^{a}**	**8.47 (2.54)^{b}**	**3.73 (1.48)^{a}**	**$F_{(2,30)}$ = 19.86*****
Nectarivorous	**1**	**0.69 (0.46)^{a}**	**1.72 (0.51)^{b}**	**0.88 (0.56)^{a}**	**$F_{(2,30)}$ = 10.44*****
Granivorous	4	0.00 (0.00)	0.61 (0.55)	0.10 (0.24)	
Carnivorous	6	0.04 (0.14)	0.11 (0.17)	0.04 (0.09)	1.99
Insectivorous	**42**	**4.73 (1.21)^{b}**	**3.97 (1.47)^{b}**	**2.00 (0.80)^{a}**	**$F_{(2,30)}$ = 15.88*****
Forest-associated	**24**	**16.17 (4.47)^{b}**	**17.44 (5.89)^{b}**	**8.67 (5.27)^{a}**	**$F_{(2,30)}$ = 8.53*****
Open land-associated	**18**	**2.17 (1.99)^{a}**	**11.33 (6.16)^{b}**	**4.83 (3.72)^{ab}**	**11.04****
Both	**34**	**15.75 (8.64)^{a}**	**30.78 (7.89)^{b}**	**13.5 (5.22)^{a}**	**$F_{(2,30)}$ = 14.62*****
Endemic	**17**	**1.67 (1.07)^{a}**	**3.00 (0.89)^{b}**	**1.44 (0.97)^{a}**	**8.67***
Conservation concern	**8**	**0.88 (0.67)^{ab}**	**1.31 (0.74)^{b}**	**0.52 (0.65)^{a}**	**6.07***
Endemic species richness		**3.58 (1.89)^{ab}**	**5.33 (1.76)^{b}**	**2.67 (1.31)^{a}**	**$F_{(2,30)}$ = 6.05****

Groups by diet are ordered by frequency of observation per land use. Subsets observed most often in tree gardens are listed first, then subsets observed most often in forest fragments. We highlight in gray each subset's greatest abundance per land use. Standard deviation follows abundance in parenthesis. Subsets are bolded where their variation is significant by ANOVA with Tukey post hoc test or Kruskal-Wallis test with Bonferroni correction.

Letters indicate differences in Tukey post hoc tests ($p < 0.05$) and Kruskal-Wallis tests with Bonferroni correction a > b > c.

**$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.*

Multivariate means for bird assemblages differed between forest and tree garden, [$F_{(1,19)} = 3.08$, $p = 0.001$, $r^2 = 0.17$], between tree garden and tea [$F_{(1,19)} = 3.17$, $p < 0.001$, $r^2 = 0.14$], and between forest fragment and tea plots [$F_{(1,22)} = 6.97$, $p < 0.001$, $r^2 = 0.24$] (see **Figure 3**). MANOVA analysis showed that endemic bird composition differed between land use [$F_{(2,30)} = 5.22$, $p < 0.001$, $r^2 = 0.26$]. Multivariate means for endemic bird assemblages differed between forest and tree garden [$F_{(1,19)} = 3.78$, $p = 0.003$, $r^2 = 0.17$], between tree garden and tea [$F_{(1,19)} = 2.51$, $p = 0.02$, $r^2 = 0.12$], and between remnant forest fragment and tea [$F_{(1,22)} = 2.97$, $p = 0.005$, $r^2 = 0.12$].

Of the endemic bird species that varied significantly across land use type according to ANOVA and the Tukey *post hoc* test, four species were observed most often in tree gardens and one in forest fragments (**Supplementary Table 1**).

Variation With Vegetation

Tree basal area, tree species richness, and stem density was statistically greater in forest fragments and tree gardens than in tea plots (**Table 2**).

GLMs showed significant but relatively weak correlations between bird abundance and tree species richness [$F_{(1,31)} = 5.07$, $b = 7.17$, $r^2 = 0.14$, $p = 0.03$]; and bird species richness and tree species richness [$F_{(1,31)} = 7.33$, $b = 11.72$, $r^2 = 0.19$, $p = 0.01$]. When regressions were run in subsets of land use type, bird abundance and species richness were strongly related to tree species richness in tea [$F_{(1,10)} = 16.7$, $b = 4.35$, $r^2 = 0.63$, $p = 0.002$; $F_{(1,10)} = 5.90$, $b = 8.66$, $r^2 = 0.37$, $p = 0.04$].

Flocks

Flock presence did not vary significantly with land use (**Table 2**). Flock size was higher in forest fragments than in tea plots (**Table 2**).

DISCUSSION

Across habitat association, conservation concern, and diet group, more birds and a greater variety of them used tree gardens than forest fragments or tea plots in the buffer zone village. Tree gardens hosted the most endemic species and species of conservation concern. Species assemblages differed between forest fragments, tree gardens, and tea plots. More frugivores, species associated with both forests and open lands, and endemic species were observed in tree gardens than in forest fragments or tea plots. Within tea plots, greater bird abundance and species richness correlated with greater tree species richness.

The literature shows that tree gardens can host similar amounts of birds to protected forests but lose species from their assemblages, and that bird use of agroforestry more generally is driven by proximity to protected forest. Tree gardens can host the same amount of or more birds than protected forest (Kottawa-Arachchi and Gamage, 2015; Prabowo et al., 2016). Some species observed in forest landscapes are lost in agriculture or tea (Engelen et al., 2016; Perera et al., 2017). Other studies have compared differences in bird assemblages between other agroforestry systems and forests, reporting results that vary with place and system (Thiollay, 1995; Beukema et al., 2007). For example, while one study from Sumatra, Indonesia, reported less species richness in complex agroforests than in primary forest (Thiollay, 1995), another Sumatra study in different agroforests showed little difference in bird diversity (Beukema et al., 2007). While Scales and Marsden (2008) of biodiversity change across habitats reported that small-scale agroforestry usually holds less biodiversity than retained forest, it depended on the system. In reviews, Waltert et al. (2004) and Clough et al. (2009) observed that abundance and species richness declines with monodominance and distance from intact rainforest. In single studies Anand et al. (2008) and Goodale et al. (2014) found that distance to intact rainforest had a larger effect on bird abundance and species richness than specific land use. Engelen et al. (2016) did not observe a difference in homegarden bird assemblages at

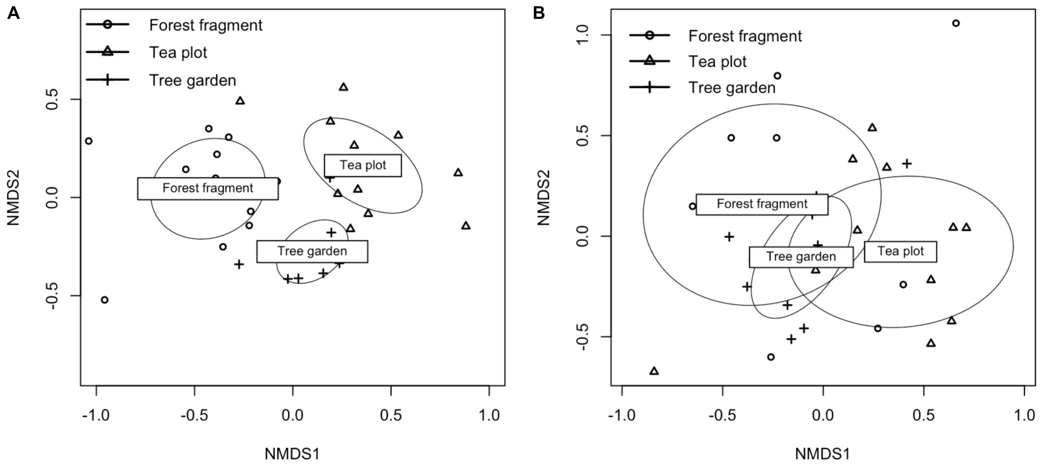

FIGURE 3 | (A) Non-metric-multidimensional scaling of all bird species abundance by land use in two dimensions using Bray-Curtis distance, convergent solution reached after 20 runs. Ellipses capture standard deviation of point for each land use type. **(B)** Non-metric-multidimensional scaling of endemic bird species abundance by land use in two dimensions using Bray-Curtis distance.

TABLE 2 | Variation of multi-species flocks and vegetation across land use types.

Variable	Forest	Tree garden	Tea	Chi-square or F-test
Flock presence	0.29 (0.22)	0.14 (0.12)	0.10 (0.19)	
Flock size	**9.93 (3.95)^{b}**	**6.4 (3.14)^{ab}**	**4.6 (3.38)^{a}**	**$F_{(2,21)} = 3.954$***
Basal area	**95.83 (44.99)^{b}**	**55.56 (24.09)^{b}**	**13.33 (12.47)^{a}**	**21.648*****
Tree species richness	**8 (2.27)^{b}**	**6.22 (2.04)^{b}**	**1.42 (0.95)^{a}**	**$F_{(2,30)} = 37.35$*****
Stem density	**17.92 (4.68)^{b}**	**16.11 (7.19)^{b}**	**4.42 (6.14)^{a}**	**$F_{(2,30)} = 15.93$*****

Values are shaded gray in the land use where they are highest. Standard deviation follows in parenthesis. Variables are bolded where their variation is significant by ANOVA with Tukey post hoc test or Kruskal-Wallis test with Bonferroni correction.

Letters indicate differences in Tukey post hoc tests ($p < 0.05$) and Kruskal-Wallis tests with Bonferroni correction a > b > c.

**$p < 0.05$; ***$p < 0.001$.*

different distances from protected forest. Based on this literature, Pitakele needs to be seen specifically as a buffer zone village with all plots proximate to intact forest.

Bird Abundance by Habitat Association and Diet

While tree gardens host different bird communities than forest fragments, birds of varied habitat association, including forest-associated species, use tree gardens in the buffer zone. Research from the Sinharaja and India's western Ghats found that the bird community in buffer zones outside of conserved forests retained more than 70% of forest interior species (Goodale et al., 2014). The high number of forest-associated birds in tree gardens could be due to the variety of food and shelter provided by a multi-strata tree garden (Tews et al., 2004; Perera et al., 2017). Open land-associated birds may also use these resources. Most of the tree gardens border open areas but not forest fragments. However, second-growth rainforest around the Sinharaja's core is becoming dense, entering the late stem exclusion phase of forest development which, locals observed, propels forest birds to its edges (Oliver and Larson, 1996). This may increase the use of tree gardens by forest species. Future research can further identify specific vegetation to support birds.

Flock size in Pitakele was observed to be highest in forest fragments. Goodale et al. (2014), in comparing bird flocks and communities between primary forest, pine plantations, and open agriculture, observed that flock densities in buffer areas in general were similar to those of intact primary forests, but flocks were smaller. Our results show that flocks are present in buffer zone tree gardens with fewer birds than in forest fragments. While buffer zone tree gardens host multi-species flocks, tree gardens do not replace forest fragments in bird flock use.

Tscharntke et al. (2008) and Sekercioglu (2012) report that species richness of large frugivorous and insectivorous birds decline in agroforests as compared to original primary rain forest; whereas nectarivores, small-to-medium frugivores, omnivores, and sometimes granivores and small frugivorous birds do better in agroforestry landscapes. Our results differ in that we observed statistically similar numbers of insectivores in tree gardens as forest fragments. This may be due to the closeness of Pitakele's tree gardens to intact rainforest.

Tea Shade Tree Diversity

Our results show that diversity in shade tree systems benefits bird abundance and species richness in this protected area buffer zone. More complex agroforestry systems result in more complex bird communities (Perfecto et al., 1996; Calvo and Blake, 1998; Mas and Dietsch, 2004; Waltert et al., 2004; Harvey and Villalobos, 2007; Van Bael et al., 2007; Anand et al., 2008; Clough et al., 2009). The direct relationships between tree species richness and bird diversity and abundance within tea plots demonstrates that this principle holds true on small land use areas in the conservation buffer zone.

Endemic Birds

Endemism is globally high on islands, where biodiversity is at high risk (Scharlemann et al., 2004; Ricketts et al., 2005; Kier et al., 2009). Agriculture has disproportionately expanded in Endemic Bird Areas (Scharlemann et al., 2004). Studies show that endemic birds decrease with the intensity of land use in human-modified tropical landscapes (Maas et al., 2009; Waltert et al., 2011; De Lima et al., 2012; Davies et al., 2015). Tropical forest conversion to farmland can result in the replacement of endemics by widespread species (Maas et al., 2009; Waltert et al., 2011; Dallimer et al., 2012; De Lima et al., 2012; Sekercioglu, 2012).

We observed endemics in greater abundance within tree gardens than in the other land uses and in greater species richness in tree gardens than in tea plots. The Sri Lanka gray hornbill (*Ocyceros gingalensis*), and the Sri Lanka junglefowl (*Gallus lafayetii*) were observed significantly more in tree gardens than in tea plots or forest fragments. The white-throated flowerpecker (near threatened, *Dicaeum vincens*) was observed significantly more in tree gardens than in tea plots, with statistically intermediate values in forest fragments. The Sri Lanka hanging parrot (*Loriculus beryllinus)* was observed significantly more in tree gardens and tea plots than forest fragments. We observed five other endemics most often in tree gardens without statistical significance (**Supplementary Table 1**). The endemic, vulnerable red-faced malkoha (*Phaenicophaeus pyrrhocephalus*) was observed only in forest fragments. We note that while Perera et al. (2017), who also examined birds in a SW Sri Lankan forest buffer zone, did not observe forest endemics in buffer zone tree gardens, their study included tea plots as tree garden, had only five of these plots, and ran their point counts outside a smaller protected area. A Sri Lanka-wide survey of birds observed half the number of endemic species in tree gardens across the country as this study (Bambaradeniya, 2003). Since most of this study's observed endemics are forest-associated birds, this data is buffer-zone specific. Waltert et al. (2011) observed correlations between endemic species richness in agroforestry with tree abundance and tree species richness. We suggest that habitat diversity may contribute to Pitakele tree gardens hosting endemic bird species. Our results and the literature suggest that endemic birds are present in the buffer zone tree gardens due to proximity to the large protected area and tree garden habitat complexity. We do not suggest that individual land uses support entire species or subsets. The complete buffer zone matrix and extensive edge habitat available in the village buffer define these habitats.

Management Implications

Tropical reserve systems are often encroached. Successful conservation depends on buffer land cover that is also profitable for residents—but conservation planning lacks global standards on buffer zone management (Budhathoki, 2004; Margles et al., 2010; Waltert et al., 2011; Dewi et al., 2013; Robinson et al., 2013; Goodale et al., 2014; Lui and Coomes, 2016; Allan et al., 2017). Programs like the EU's Small Grants Program for Operations to Promote Tropical Forests Program have focused on developing resilient and self-supporting communities within tropical conservation buffer zones (RECOFTC., 2008; Rands et al., 2010). Agroforestry can integrate forests in a multifunctional landscape for conservation, including specifically in the Sinharaja (Michon et al., 1986; Bhagwat et al., 2008; Jose, 2009; Dewi et al., 2013; Kothalawala et al., 2013). Complex cover benefits birds. This study shows that programs for tree garden agroforestry in buffer zones like that of the Sinharaja can support habitat for vulnerable and endemic birds, including forest-associated ones. However, tree gardens do not replace forest fragments or protected core forest. We suggest pursuing further research on the ecological significance of tree gardens broadly in tropical protected area buffer zones.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

MA conceived the study. MA, BS, and JH planned methodology. MA and JH planned analyses. JH collected the data, and analyzed and wrote the manuscript with input from MA and BS. 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/fevo.2021.608434/full#supplementary-material

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Improving Habitat Quality at the Local and Landscape Scales Increases Wild Bee Assemblages and Associated Pollination Services in Apple Orchards in China

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Bees provide key pollination services for a wide range of crops. Accumulating evidence shows the effect of semi-natural habitats at the landscape level and local management practices on bee diversity in fields. However, most of the evidence is derived from studies in North America and Europe. Whether this paradigm is applicable in China, which is characterized by smallholder-dominated agricultural landscapes, has rarely been studied. In this study, we aimed to investigate how bee diversity affected apple production, and how landscape and local variables affected bee diversity and species composition on the Northern China Plain. The results showed that bees significantly increased apple fruit set compared to bagged controls. Wild bee diversity was positively related to apple seed numbers. Higher seed numbers reduced the proportion of deformed apples and thus increased fruit quality. Wild bee abundance was positively correlated with flowering ground cover, and both the abundance and species richness of wild bees were positively affected by the percentage of semi-natural habitats. We conclude that apple quality can benefit from ecological intensification comprising the augmentation of wild bees by semi-natural habitats and flowering ground cover. Future pollination management should therefore reduce the intensification level of management at both the local and landscape scales.

Keywords: deformation, flowering ground cover, landscape composition, pollinators, seed number

INTRODUCTION

Pollinators provide essential pollination services to 75% of major global crops (Klein et al., 2007) and 87.5% of wild plants (Ollerton et al., 2011). Pollinators not only increase crop yield (Hoehn et al., 2008; Garibaldi et al., 2011; Woodcock et al., 2019) but also improve food quality and nutrient content (Eilers et al., 2011; Chaplin-Kramer et al., 2014; Smith et al., 2015). Among pollinators, bees (Hymenoptera: Apoidea) are important pollen vectors of flowers due to their universality, species diversity, and specific pollen-carrying body structures (Michener, 2007).

Unfortunately, dramatic declines are reported in both honeybee colonies and wild bee diversity, which seriously threaten the provision of pollination services (Biesmeijer et al., 2006; Potts et al., 2010). The reasons for the decline in wild bees are mainly attributed to local agricultural intensification and landscape simplification (Potts et al., 2010; Tscharntke et al., 2012). Wild bees need continuous floral and nest resources during their life history to grow and reproduce, but agricultural habitats cannot meet their full resource demands due to the short crop flowering period and frequent human disturbance (Mandelik et al., 2012). Wild bees have to forage for resources in other surrounding habitats. As a result, the composition and configuration of different habitat types may drive the dispersal and distribution of bees in the whole landscape, which further affects wild bee diversity and associated pollination services to crops (Williams and Kremen, 2007; Tscharntke et al., 2012).

Semi-natural habitats are often the population source for wild bees to disperse into surrounding fields due to the diverse available resources, and it is therefore encouraged that such habitats should be protected to improve bee diversity and associated crop pollination services (Öckinger and Smith, 2007; Klein et al., 2012). In contrast, the contribution of agricultural habitats to bee resources is uncertain. Previous studies have shown that a large percentage of agricultural habitats in landscapes may decrease pollinator resources and associated pollination services due to pollinator dilution (Holzschuh et al., 2016; Proesmans et al., 2019). However, other studies suggested that flowering crops may provide important floral resources for wild bees, and mass flowering crops therefore enhance wild bee densities at the landscape scale (Westphal et al., 2003; Holzschuh et al., 2012). Furthermore, the evidence for landscape structure affecting wild bee diversity is mainly derived from Europe and North America, which are characterized by large field sizes (Steward et al., 2014). Our understanding of the relationship between landscape variables and bee diversity in smallholder agricultural landscapes has remained very limited (Zou et al., 2017; Wu et al., 2021), but it is urgent to consider this scenario because approximately 2.5 billion people depend on smallholder agriculture for survival worldwide (IFAD and UNEP, 2013).

In addition to landscape structure, local management practices may also affect bee diversity, such as pesticide application (Park et al., 2015; Sgolastra et al., 2020) and flowering ground cover (Campbell et al., 2017; Wu et al., 2019). A growing number of studies have shown that local management practices can interact with landscape variables, and they may counteract the negative effects of each other (Rundlöf et al., 2008; Park et al., 2015; Wu et al., 2019). Landscape complexity can also constrain the effectiveness of local management practices (Batary et al., 2011; Concepcion et al., 2012). However, the consistency of local and landscape scales and their interactions across global agricultural landscapes still need further verification due to the limited number of studies (Kennedy et al., 2013). In particular, evidence from Asian smallholder farming landscapes is needed (Steward et al., 2014), as most results are drawn from studies in Europe and North America (Archer et al., 2014).

China is the most important producer of crops profiting from pollination, accounting for 30–50% of global pollination benefits (Lautenbach et al., 2012), and is generally characterized by small field sizes (Cui et al., 2018). China has also faced agricultural intensification and landscape simplification in recent decades, inducing the loss of wild bee diversity and pollination services (Meng et al., 2012). Few studies have been conducted to investigate pollinator diversity and pollination services in China and how local and landscape variables affect the diversity and species composition of pollinators (Garibaldi et al., 2013; Zou et al., 2017; Wu et al., 2019).

To narrow the knowledge gap, we focus on the pollination services of apple (*Malus domestica*), a self-incompatible fruit crop. Apple is cultivated worldwide, half of which is produced in China (United States Department of Agriculture [USDA], 2019). However, it has been reported that apple is experiencing global pollination deficits due to insufficient pollinators (Garratt et al., 2014; Pardo and Borges, 2020; Wu et al., 2021). Previous research (Pardo and Borges, 2020) and our preliminary investigations have shown that bees are the main pollinators of apple. In this study, we attempted to answer the following questions: (1) What is the dependence of Fuji apple production on pollination services provided by bees? (2) How does bee diversity affect apple quality and quantity in natural pollination? (3) How do wild bee diversity and species composition respond to local and landscape variables? We hypothesized that (1) bees provide important pollination services for apples, (2) apple quality and quantity are positively affected by bee diversity, and (3) improving habitat quality at local and landscape scales increases wild bee assemblages and associated pollination services in apple orchards.

MATERIALS AND METHODS

Study Sites

The study was conducted in Changping District (40°2′–40°23′ N, 115°50′–116°29′ E), one of the major apple-producing areas in China, in the northwest suburbs of Beijing (**Figure 1**). The altitude ranges from 30 to 1,400 m. The local climate is continental, with an average annual temperature of ∼12°C and an average annual rainfall of ∼550 mm. The mountainous area dominated by shrublands and orchards accounts for 59% of the total area of the district. The plain area, lying southeast of the district, is dominated by orchards, urban areas, and woodlands.

"Fuji" is the main cultivated apple variety in this study area. Twelve apple "Fuji" orchards were selected, surrounded by different landscape contexts that varied with structural complexity within a 1-km radius. The orchards were at least 2 km apart from each other to reduce possible autocorrelation between landscape structure and bee samples.

Pollination Treatments

In each orchard, three rows of apple trees were selected, with intervals of at least one row and at least 5 m away from the edge. Within each row, five trees with intervals of one tree were selected. On each tree, two branches and, on each branch, two inflorescences were randomly chosen to count the number of flower buds before bloom. One inflorescence on each branch

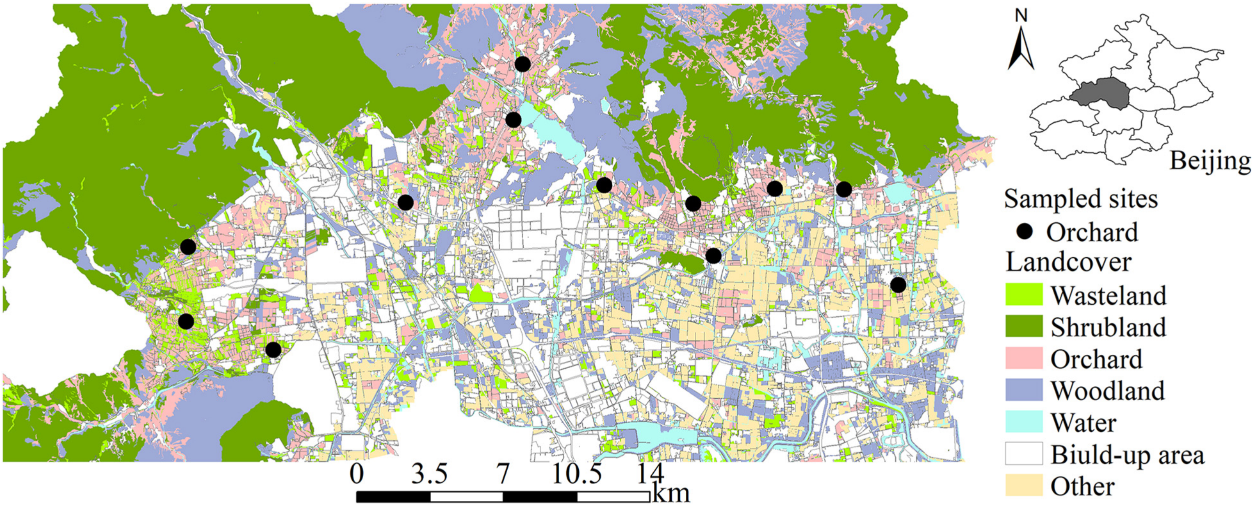

FIGURE 1 | The distribution of sampling sites.

was covered with nylon mesh (1 mm width) bags as a pollinator exclusion treatment, and the other inflorescence was freely exposed to pollinators as a natural pollination treatment. In total, 30 inflorescences were covered, and the other 30 inflorescences were uncovered at each site. After the flowers faded, bags were removed, and all inflorescences were marked with colored tabs for later harvest.

Bee Sampling

Apple is self-incompatible, and previous research and our preliminary field investigation have shown that bees are its main pollinator (Pardo and Borges, 2020). Pollinating bees were sampled continuously during the whole apple flowering period using pan traps (April1 4–28, 2015). At each site, within each selected row, three colored pan traps (blue, yellow, and white following Westphal et al., 2008, with 21 cm diameter and 10 cm depth) were placed at a height of 1.5 m above the ground and 10 m apart from one another. Pan traps were filled with approximately 300 mL of detergent water solution (two drops of detergent per 5 L of water) and then emptied and refilled every 2 days. All bee specimens were collected and preserved in 75% alcohol and then pinned for subsequent identification to the species level. Bee data from nine traps per orchard were pooled for the entire sampling period, and bee abundance refers to total bee individuals collected by pan traps per orchard.

Local Management Survey

To protect bees, no pesticides or fungicides were applied by farmers during the apple flowering period, and flowering ground cover was the main local factor affecting bee diversity within orchards. We placed five 1 m × 1 m quadrats at the four corners and the center of the bee sampling area during the apple bloom. Species richness and coverage of ground flowering plants in five quadrats were recorded and averaged to achieve mean values at each site.

Landscape Parameters

The land cover types in selected landscapes were classified into shrubland, woodland, wasteland, orchard, urban area, water area, and other. Shrublands are mainly distributed in mountains and are characterized by large areas of natural shrub species, such as *Vitex negundo* var. *cannabifolia* and *Cotinus coggygria*. The main habitat types in the plain area are woodland, orchards, wasteland, and urban areas. The dominant tree species of woodland are *Pinus tabuliformis*, *Ginkgo biloba*, *Populus* × *tomentosa*, *Platycladus orientalis*, and *Robinia pseudoacacia*. Wasteland was defined as areas where plants naturally generated with limited human disturbances. We defined the combination of shrubland, woodland, and wasteland as a semi-natural habitat. Land use maps within a radius of 1 km surrounding the study sites were digitized according to the extensive field inspections (resolution of 2 m) based on Online Bing Maps of the landscapes.[1] We chose this spatial scale because the foraging distance of most wild bees was less than 1 km (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010). The landscape metrics and area percent of each habitat within a 1-km radius of the study sites were calculated at the class level using FRAGSTATS 4.2 (McGarigal et al., 2002). The area percentage of the semi-natural habitats was further calculated by summing the area percentage of the corresponding habitats.

Pollination Services

Fruit set, seed number, and deformation were measured to reflect the degree of pollination services. Framers usually thin the fruit clusters if there are multiple apples on one inflorescence. One week after flowers faded and before hand thinning in early May, we recorded the number of set apples on the marked inflorescences, although we were missing the data in two orchards where hand thinning was conducted by farmers before our visit. Approximately 6 1/2 months after the flowers faded, apples

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[1] http://www.arcgis.com/home/webmap/viewer.html

were ripe. In the middle of October, we picked all ripe apples from the marked inflorescences prior to commercial harvest and then labeled them by the treatment, tree, row, and orchard. Because of the low self-fertilized fruit set, only nine apples grew ripe on the pollinator-excluded inflorescences. The seed number of each fruit was counted. Therefore, we have fruit set data from 10 orchards and other apple quality parameters from 12 orchards. The deformation of each apple was determined visually by the same investigator. After placing each apple horizontally, if the shape of the apple was severely skewed to one side, it was deformed; if the apple shape was normal, it was not deformed.

Statistical Analysis

First, to investigate the effects of pollination treatment on fruit set, the generalized linear mixed effects model (glmer, in lme4 package, Bates et al., 2015) was computed with binomial error distribution. The fixed effect was pollination treatment, and the random effect was inflorescences nested within trees within rows within orchards.

Second, we analyzed the effects of bee diversity on pollination service parameters in the open pollination treatment at the site level. Fruit set, seed number, and deformation were added into the full linear models as the response variables, respectively. Honeybee abundance and one of wild bee variables [wild bee abundance, wild bee species richness, or wild bee diversity (Shannon–Weaver index, the diversity function, R package "vegan," Oksanen et al., 2019)] were added as explanatory variables (**Table 1**), considering the significant positive relationship between abundance and species richness of wild bees (Pearson's $r = 0.90$, $p < 0.001$). The correlation among bee variables was tested according to correlation test (the cor.test function, R package "stats," R Core Team, 2018).

Third, we used generalized linear models to assess the effects of the local management practice and landscape composition parameters on bees. In the case of overdispersion, generalized linear models with a negative binomial distribution (glm.nb, R package "MASS," Ripley et al., 2018) were used. Flowering ground cover, percent of semi-natural habitats, percent of orchards, and the two-way interaction between the local management practice and landscape composition variables were included in full models as explanatory variables, and honeybee abundance as well as abundance, species richness, and diversity of wild bees were included as the response variables, respectively.

In the second and the third analyses, we used the dredge function in MuMIn package (Barton, 2018) to select the best-fitting models for each response variable based on AICc (Akaike's information criterion). If ΔAICc < 2, the model containing more explanatory variables was chosen, and we used the rsq function (R package "rsq," Zhang, 2020) to calculate adjusted R^2 for generalized linear models. Spatial autocorrelation of the final model residuals was tested for each response variable using the "ncf" package (Bjornstad, 2019), and no significant spatial autocorrelation was detected in any case. The models were further validated based on visual inspection of the plotted residuals versus the predicted values (Zuur et al., 2009). All of the above analyses were performed using R (version 3.5.1, R Core Team, 2018).

Finally, redundancy analyses (RDA) was conducted to assess the effects of local and landscape variables on the species composition of wild bees in Canoco 5 (Šmilauer and Lepš, 2014). The percentage of semi-natural habitats and flowering ground cover were the environmental variables. Prior to analyses, species data were Hellinger-transformed to allow the use of the ordination method, due to the presence of many zero values (Legendre and Gallagher, 2001).

RESULTS

Bee Diversity and Composition

In total, 1,616 bee individuals were collected. Wild bees accounted for 53.1% (858) of all individuals and represented 43

TABLE 1 | Results from linear models (lm) indicating the effects of bees on apple fruit set (a), seed numbers (b), and deformation (c), and the effect of seed numbers on deformation (c).

Response variables	Explanatory variables in full models	AICc of optimal models	Explanatory variables in optimal models	Estimate	Std. Error	*t* value	Pr (>$\vert t\vert$)
(a) Fruit set	Ahoney + Dwild	−0.8	Intercept	0.74	0.74	12.66	< 0.001
	Ahoney + Awild	−0.8	Intercept	0.74	0.74	12.66	< 0.001
	Ahoney + Rwild	−0.8	Intercept	0.74	0.74	12.66	< 0.001
(b) Seed numbers	Ahoney + Dwild	39.7	Intercept	2.32	2.13	1.09	0.302
			Dwild	2.38	1.04	2.30	0.045
	Ahoney + Awild	41.1	Intercept	7.18	0.32	22.17	< 0.001
	Ahoney + Rwild	41.1	Intercept	7.18	0.32	22.17	< 0.001
(c) Deformation	Seed numbers	103.3	Intercept	88.24	26.28	3.36	0.007
			Seed	−8.84	3.62	−2.44	0.035
	Ahoney + Dwild	105.2	Intercept	24.83	4.68	5.30	< 0.001
	Ahoney + Awild	105.2	Intercept	24.83	4.68	5.30	< 0.001
	Ahoney + Rwild	105.2	Intercept	24.83	4.68	5.30	< 0.001

Ahoney, honeybee abundance; Awild, wild bee abundance; Rwild, species richness of wild bees; Dwild, wild bee diversity.

species (**Supplementary Table A1**). The most abundant wild bee species were *Andrena minutula* and *Andrena hebes*, accounting for 17.8 and 6.2% of the total bees, respectively. In addition, 758 honeybees (*Apis mellifera*) were collected.

Relationships Between Bee Diversity and Pollination Services

There were 3,082 flowers and 216 ripe apples measured, and only nine ripe apples were collected in the pollinator-excluded control. The fruit set in the open pollination treatment was significantly greater than that in the bagged control ($z = 9.017$, $p < 0.0001$, **Figure 2**). The fruit set in the open pollination treatment was not related to honeybee abundance or abundance, species richness, or diversity of wild bees (**Table 1**). The number of seeds in naturally pollinated apples increased with wild bee diversity ($t = 2.30$, $R^2 = 0.28$, $p = 0.045$, **Figure 3A**) and was negatively correlated with the apple deformation ($t = -2.44$, $R^2 = 0.31$, $p = 0.035$, **Figure 3B**).

Effects of Local Management and Landscape Composition on Bees

Wild bee abundance increased with flowering ground cover within orchards ($z = 2.63$, $R^2 = 0.35$, $p = 0.009$, **Figure 4A**). Both the abundance ($z = 3.22$, $R^2 = 0.35$, $p = 0.001$, **Figure 4B**) and species richness ($z = 2.23$, $R^2 = 0.33$, $p = 0.026$, **Figure 4C**) of wild bees were positively correlated with the percentage of semi-natural habitats. Wild bee diversity did not significantly respond to local or landscape predictors (**Table 2**).

The RDA results showed that the percentage of semi-natural habitats explained the greatest percentage of all variance (Explains = 25%, pseudo-$F = 3.3$, $p = 0.004$), and significantly affected wild bee species composition. The effect of flowering ground cover was marginal and explained 11.9% of the variation (pseudo-$F = 1.7$, $p = 0.076$). Most species were positively affected by the percentage of semi-natural habitats, except for *Andrena solidago* (AndSol) and *Lasioglossum* sp2 (LasSp2). The effect of flowering ground cover on *Lasioglossum vulsum* (LasVul) was negative, but it was positive on other wild bee species (**Figure 5**).

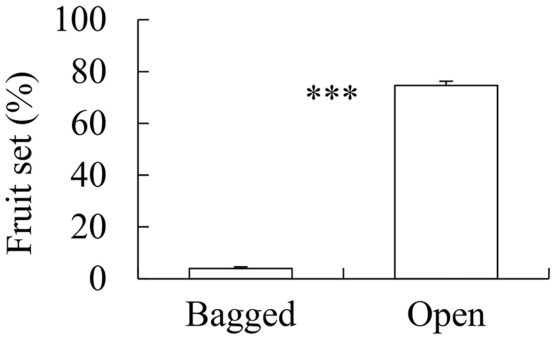

FIGURE 2 | The difference in apple fruit set between bagged and open treatments. ***$p < 0.001$.

DISCUSSION

In this study, we found that bees significantly improved apple fruit set and provided critical pollination services for apple production. Seed number increased with wild bee diversity. A higher seed number reduced the proportion of deformed apples and thus increased fruit quality. Flowering ground cover positively affected wild bee abundance. Both the abundance and species richness of wild bees benefited from semi-natural habitats. Implementing measures of ecological intensification at both local and landscape scales therefore improves wild bee diversity and associated pollination services in Chinese agricultural landscapes.

Apple is a self-incompatible fruit crop and thus needs pollinators to transport pollen among different varieties (Ramírez and Davenport, 2013; Pardo and Borges, 2020). Our results showed that pollinators significantly increased apple fruit set compared with the exclusion control. Previous studies have shown that honeybees and wild bees are the most important pollinator groups of apples (Pardo and Borges, 2020). Our results suggested that wild bee diversity significantly increased apple seed numbers, which further decreased the proportion of deformed apples, but without a relationship between honeybees and apple pollination predictors. Similar to the findings in American and Hungarian apple orchards (Mallinger and Gratton, 2015; Földesi et al., 2016), apple pollination was more strongly related to wild bee diversity than honeybees. Because of their greater complementarity with ecological traits and resource use (Hoehn et al., 2008; Fruend et al., 2013), wild bee assemblages could promote the spatial and temporal stability of pollination services (Garibaldi et al., 2011) and buffer environmental disturbances (Williams et al., 2010) as well as climate change (Bartomeus et al., 2013). In contrast, honeybees sometimes rob nectar from an apple flower without pollinating it (Delaplane and Mayer, 2000) and may be low-efficacy pollinators for apples (Ramírez and Davenport, 2013). However, in intensive agricultural landscapes, the number of honeybees may far exceed that of wild bees due to the lack of semi-natural habitats (Rollin et al., 2013). In this case, farmers have to rely on honeybees, and honeybees may provide important pollination services for crops (Breeze et al., 2011), although their pollination efficiency may be low (Garibaldi et al., 2013; Pérez-Méndez et al., 2020), and their population is at risk of decline (Biesmeijer et al., 2006; Potts et al., 2010). Therefore, wild bees may provide a more reliable contribution to pollination services in changing environments than honeybees, which cannot be replaced but only supplemented by honeybees (Garibaldi et al., 2013).

However, there was no significant relationship between bees and fruit set, possibly due to the limitations of pan trap sampling. Although pan traps are effective, make it easier to sample several sites simultaneously, and lack collector bias (Westphal et al., 2008), they represent a passive sampling method, are not restricted to apple flower visitors, and have difficulty catching certain taxa (e.g., large bumblebees) (Popic et al., 2013). On the other hand, instead of wild bee species richness or diversity index, functional diversity of pollinators (Gagic et al., 2015) or trait matching of pollinators and crops (Garibaldi et al., 2015) might provide better prediction of the relationship between pollinators

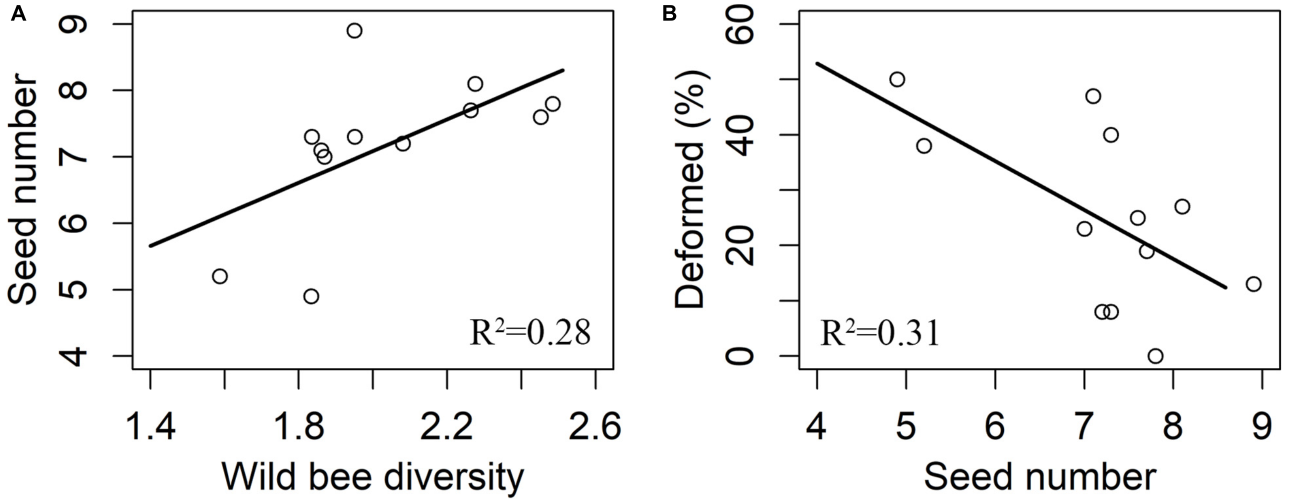

FIGURE 3 | Responses of seed number to bees **(A)** and the effect of seed number on deformation **(B)**. R^2 means adjusted *R*-squared of the final model.

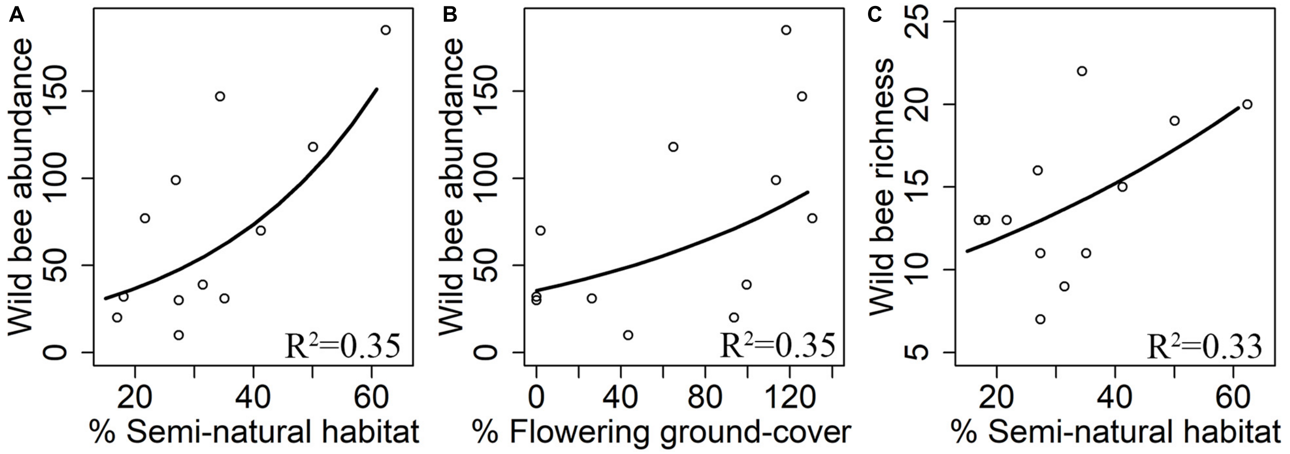

FIGURE 4 | Effects of flowering ground cover and landscape composition on abundance **(A,B)** and species richness **(C)** of wild bees. R^2 means adjusted *R*-squared of the final model.

TABLE 2 | Results from general linear models (or those with a negative binomial distribution) indicating the effects of landscape variables, flowering ground cover, and their interaction on the abundance (a), species richness (b), and diversity (c) of wild bees, as well as honeybee abundance (d). FGC = flowering ground cover, SNH = percentage of seminatural habitats.

Response variables (model)	AICc of optimal models	Explanatory variables in optimal models	Estimate	Std. Error	*z* value	*p* value
(a) Wild bee abundance (glm.nb)	126.2	Intercept	2.44	0.41	5.97	< 0.001
		FGC	0.0074	0.0028	2.63	0.009
		SNH	0.035	0.011	3.22	0.001
	127.6	Intercept	2.96	0.48	6.12	< 0.001
		SNH	0.036	0.014	2.67	0.008
(b) Wild bee species richness (glm)	70	Intercept	2.22	0.212	10.48	< 0.001
		SNH	0.013	0.0056	2.23	0.026
	71.7	Intercept	2.1	0.23	9.27	< 0.001
		FGC	0.0023	0.0016	1.4	0.16
		SNH	0.011	0.0056	1.99	0.047
(c) Wild bee diversity (glm)	7.5	Intercept	2.04	0.08	25.52	< 0.001
(d) Honeybee abundance (glm.nb)	129.0	Intercept	4.15	0.29	14.52	< 0.001

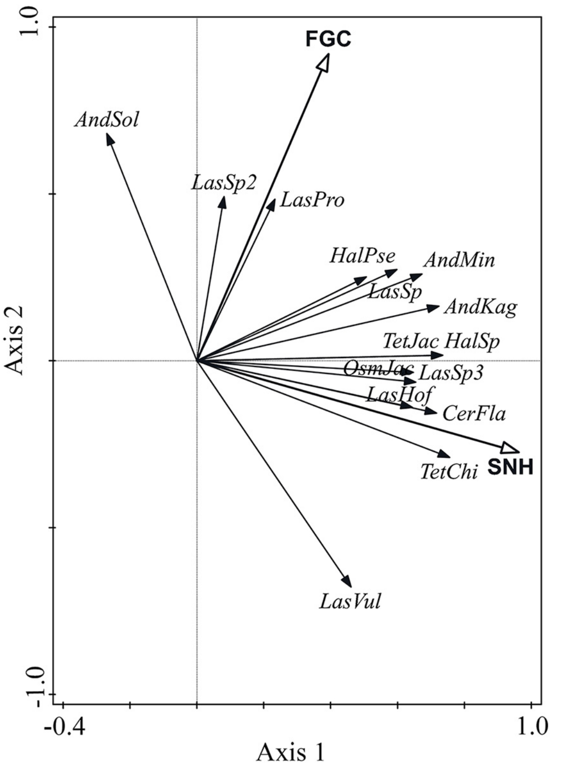

FIGURE 5 | RDA biplot showing the effects of flowering ground cover (FGC) and percent of semi-natural habitats (SNH) on wild bee species composition. The first 15 species with the highest fit in the ordination plot are displayed. AndSol = *Andrena solidago*, LasSp2 = *Lasioglossum* sp2, LasPro = *Lasioglossum proximatum*, HalPse = *Halictus pseudovestitus*, AndMin = *Andrena minutula*, LasSp1 = *Lasioglossum* sp1, AndKag = *Andrena kaguya*, TetJac = *Tetralonia jacoti*, HalSp = *Halictus* sp, OsmJac = *Osmia jacoti*, LasSp3 = *Lasioglossum* sp3, LasHof = *Lasioglossum hoffmanni*, CerFla = *Ceratina flavipes*, TetChi = *Tetralonia chinensis*, LasVul = *Lasioglossum vulsum.*

and pollination services; these approaches require more efforts and biological knowledge about the functional traits of all species, which are currently unavailable in our research region.

Wild bees benefited from flowering ground cover in our study, possibly due to additional pollen and nectar provided by the floral vegetation for wild bees during apple blooming. The apple flowering period is short and pulsed, but the demand of wild bees for foraging resources is long term to meet their needs for growth and reproduction. Similar positive effects of flowering ground cover on wild bees were also detected in apple orchards in United Kingdom (Campbell et al., 2017), China (Wu et al., 2019), and United States (Kammerer et al., 2016), and other fruit crops [such as mango in South Africa (Carvalheiro et al., 2012), sweet cherry in Germany (Holzschuh et al., 2012), and blueberry in the United States (Blaauw and Isaacs, 2014)], using sown flower strips or wild flowering vegetation within orchards. However, ground cover often promotes the abundance of wild bees, not species richness or diversity (Campbell et al., 2017; Wu et al., 2019). In orchards, flowering ground cover diversity is relatively low due to frequent disturbance and is even limited by agricultural practices, such as plowing, mowing, and application of pesticides and herbicides, resulting in an average of only 3.1 species per site in our study. Low diversity of floral vegetation may decrease their attraction to diverse wild bees, which may result in wild bee diversity or species richness not responding to flowering ground cover. Therefore, keeping or growing diverse flowering plant species within orchards may be more conducive to attracting richer wild bee species into orchards to provide pollination services for crops (Burkle et al., 2020).

Furthermore, the available floral resources provided by flowering ground cover may buffer the effect of the percentage of orchards on bees, resulting in no significant relationship between the percentage of orchards and bees in this study. Our results showed that semi-natural habitats promoted both the abundance and species richness of wild bees, and they therefore may contribute more to protecting wild bee resources than flowering ground cover in orchards. Different plant species possess various flowering phenologies, and rich flowering plant resources in semi-natural habitats, which not only meet the needs of wild bees for different nutrition statuses but also increase the possibility of acquiring resources during different periods of their life history (Ogilvie and Forrest, 2017). Moreover, the low level of human disturbance provides high-quality nesting sites for wild bees. Therefore, the restoration of diverse and high-quality semi-natural habitats is vital to improve wild bee diversity and associated pollination services in agricultural landscapes (Öckinger and Smith, 2007; Klein et al., 2012).

Previous studies have shown that local management may interact with landscape variables (Kennedy et al., 2013). For example, natural habitat modulated the effect of pesticide use in American apple orchards (Park et al., 2015), and flowering ground cover buffered the negative effects of plantation forests with intensive management and distance from natural shrubland in Chinese apple orchards (Wu et al., 2019). In our study, we did not find an effect of interactions between local and landscape scales on bees, but contrasting responses of different wild bee species to these environmental variables were detected based on the RDA analysis. For example, *A. solidago* benefited from flowering ground cover and negatively responded to the percentage of semi-natural habitats. Contrary to *A. solidago*, *L. vulsum* showed opposite responses to these two spatial scale factors. Bee species responded differently to local and landscape variables, possibly due to their specific resource requirements (Aguirre-Gutiérrez et al., 2016), but available resources were relatively scarce at the local and landscape scales in intensive agricultural landscapes. For example, although the average flowering ground cover is approximately 68%, the species richness of flowering vegetation is only 3.1 in our study. Low richness of flowering ground cover may increase the possibility that some wild bees dislike this pollen and nectar due to their unique requirements for foraging resources (Potts et al., 2003; Cusser and Goodell, 2013). Furthermore, various resource requirements among bee species result in local and landscape factors that may change bee functional diversity by mediating their species composition, such as foraging behavior, dietary specialization, and pollination efficiency, and further affect associated pollination services (Tscharntke et al., 2008; Forrest et al., 2015; Martins et al., 2015). We should therefore restore various high-quality semi-natural habitats at the landscape scale and improve the flowering vegetation diversity within orchards, to maximize the benefit to pollinators with diverse functional traits, other beneficial insects, and associated multifunctional ecosystem services (Tscharntke et al., 2008; Westphal et al., 2015; Albrecht et al., 2020).

CONCLUSION

Our findings demonstrate that bees provide important pollination services for apples in Chinese smallholder farming agricultural landscapes. Wild bees improve apple quality by increasing seed number. Wild bees could benefit from flowering vegetation resources in orchards and the surrounding complex landscapes. Future pollination management should therefore avoid intensification management at both the local and landscape scales and implement ecological intensification measures to improve wild pollinator diversity and maximize pollination services in agricultural landscapes.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

YL acquired the funding and conceived the experiment. PD and PW collected the data. HX and PD identified the bees. XL and PD identified plants. PW and PD analyzed data and wrote the original draft of the manuscript under the advice of YL, MW, SF, and AO. All authors reviewed and revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.621469/full#supplementary-material

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Mammal Persistence Along Riparian Forests in Western India Within a Hydropower Reservoir 55 Years Post Construction

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While the negative impacts of dam construction on downstream river stretches and riparian forests are well studied, the status of wildlife presence and persistence in upstream reservoir deltas is virtually unknown. We investigated the drivers of terrestrial mammal occupancy and persistence along riparian forests of Koyna reservoir in western India 55 years after its construction. We adopted a catchment-wide field design grounded in the river continuum concept and sampled different stream orders within the reservoir. Camera traps, nested in an occupancy modeling framework, were deployed across 72 riparian sites and replicated for four seasons across all stream types. We recorded a total of nineteen species of terrestrial mammals during the study period. Multi-season occupancy models revealed three key patterns of mammal persistence: (a) ungulates were more frequently photo-captured in riparian forests; gaur and wild pig had the highest proportions of the total sampled area (0.84 ± 0.12 SE; 0.77 ± 0.07 SE, respectively); (b) small-sized ungulates were more vulnerable to local extinction than large-bodied ungulates; extinction probability was highest for barking deer (0.59 ± 0.07) and lowest for sambar (0.15 ± 0.07); and (c) distance from stream played major roles in determining mammal detection. Riparian forests are fundamentally important to ecosystem functioning and biodiversity conservation, and using the data from this study, managers can plan to sustain high mammal persistence along riparian forests at Koyna reservoir or similar Indian reserves. Further, our robust sampling approach, grounded in the terrestrial-riverine continuum concept, can be applied globally to understand species assemblages, aiding in multi-landscape and wildlife management planning.

Keywords: dammed river, occupancy modeling, colonization, extinction, reservoir biodiversity, river continuum

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INTRODUCTION

The river continuum concept was the first unified hypothesis proposing that rivers and associated watersheds should be viewed as a continuum to understand the complete structure and functioning of a river (Vannote et al., 1980). Like river systems, riparian forests form their own continuum running along rivers and streams, from headwaters to perennial rivers, and hence riparian vegetation is also likely to conform to the river continuum concept. Riparian forests as ecotones protect riverbanks from erosion resulting in bank stability (Pinay et al., 2018), drive organic matter and nutrients into streams (Vannote et al., 1980), moderate temperature extremes in river environments (Dugdale et al., 2018), and are predicted to function as hotspots for climate change adaptation (Seavy et al., 2009; Capon et al., 2013). Hence, riparian forests are key constituents of terrestrial-aquatic continua and reflect the functional status of an entire catchment. Large animal ecology in riparian forests has been long studied and was probably first highlighted in mainstream conservation science by the pioneering studies of Naiman (1988); Pastor et al. (1988), and Naiman and Rogers (1997). These studies summarized how large ungulates influence riparian system dynamics primarily by their foraging behavior. There have been few recent studies highlighting the importance of riparian forests for forest mammals, but the riverine-continuum concept is slowly gaining traction across various ecosystems, especially with important works of Santos et al. (2011) and Zimbres et al. (2018). In India, there have been frequent general discussions about dam effects on biodiversity, but detailed empirical studies on the dynamics and distribution of forest mammals within riparian forests remain virtually non-existent. In regards to riparian forests, studies have mainly focused on riparian obligate species like otters (Umapathy and Durairaj, 1995; Hussain and Choudhury, 1997; Anoop and Hussain, 2006a,b; Perinchery et al., 2011; Prakash et al., 2012; Raha and Hussain, 2016), or certain large mammals in floodplains/wetland-dependent species, such as Asiatic buffalo and rhinocerous (Chatterjee and Bhattacharyya, 2021). Chatterjee and Bhattacharyya (2021) found that even though wetland-dependent mammals have been studied, there remains a large knowledge gap in regards to these species ecology and conservation.

A novel avenue for riparian ecology research opened up very recently with studies of Datry et al. (2014, 2016, 2017a,b), which stressed the ecology of dry and intermittent rivers, as perennial river systems have received the majority of research attention historically. Following the research on fluvial dynamics of perennial and temporary rivers, Sánchez-Montoya et al. (2016) studied dry streams as corridors for large mammals using an innovative animal footprint method. These studies have all contributed to the development of the terrestrial riverine continuum concept, but they have also all been conducted largely in free-flowing rivers and associated riparian forests. Within altered habitats, especially in upstream hydropower reservoirs, research on forest mammals in riparian forests is still lacking. These altered habitats are interesting especially because the riparian forests experience high levels of flooding and drought owing to uneven rainfall patterns. Unlike natural watersheds, the water level in reservoirs is operated by dam authorities which alters the normal hydrological cycle of the river (Alho, 2011). Species occupancy patterns in an environment of such dynamic water level fluctuations is key to provide insights into how species persist within these reservoirs. With this background in the river continuum framework, we aimed to identify the drivers of mammal assembly and persistence in a human-altered watershed, a dammed river which now forms the Koyna Wildlife Sanctuary in the northern Western Ghats.

MATERIALS AND METHODS

Study Area: The Koyna Hydroelectric Project is the largest completed hydropower station in India with a total capacity of 1960 MW. It is comprised of four dams, the largest of which, the Koyna Dam, was completed in 1963, forming the Shivsagar Reservoir (Bokil, 1999). The reservoir is now protected as Koyna Wildlife Sanctuary (hereafter referred to as "Koyna"). Koyna forms an important corridor between Mahabaleshwar-Panchgani Ecologically Sensitive Zone in the north and Chandoli National Park in the south; Koyna and the Chandoli National Park together form the Sahyadri Tiger Reserve. With seven land cover types (Jelil et al., 2020; **Figure 1**), Koyna covers 423.55 km^2 and the vegetation in the sanctuary is classified as southern tropical evergreen forest and southern moist deciduous forest (Champion and Seth, 1968). Red clay is the main soil type. The mean annual rainfall in Koyna is $\sim$ 5,000 mm, which falls predominantly from June–September (Joglekar et al., 2015). Koyna was declared a wildlife sanctuary in 1985, and private forests owned by villagers before resettlement now persist as grasslands, scrub and moist deciduous forests (Joglekar et al., 2015). Joglekar et al. (2015) reported that the relative inaccessibility and undulating terrain supports some of the few remaining undisturbed tall evergreen forests in the northern Western Ghats, and hosts large mammals such as the common leopard (*Panther pardus*), dhole (*Cuon alpinus*), sloth bear (*Melursus ursinus*), Indian gaur (*Bos gaurus*), and sambar (*Rusa unicolor*). The last confirmed record of tiger (*Panthera tigris*) from Chandoli National Park was in 2018 (Jelil et al., 2020), but the species has not been recorded in Koyna since 2007.

Field Study Design: We used stream types as sampling strata with the river stretch divided into three sections (**Table 1**). In each section, we assessed riparian forests associated with a perennial order, two intermittent orders, four ephemeral orders and eight headwater orders (**Figures 1**, **2**). We sampled four locations in both the perennial and intermittent order and eight locations in both ephemeral and headwaters orders. In total, we sampled 24 locations in each of the three sections resulting in 72 total sampled locations. The riparian buffer was set at 1 km in either direction of the stream edge in the perennial habitat, at 500 m in the intermittent, 200 m in ephemeral and 100 m in headwater streams. The study was carried out from April 2018 to March 2020 encompassing four seasons (two summer and winter seasons, i.e., summer 2018, winter 2018, summer 2019, and winter 2019). Summer season data collection was conducted from April to July and winter data collection from November to February. This amounted to *c.* 480 days of survey effort in the 2 year period.

Camera Trapping Surveys: The camera traps were deployed up to 1 km from the waterway for the perennial stream-type, up to 500 m for the intermittent stream-type, up to 200 m for the

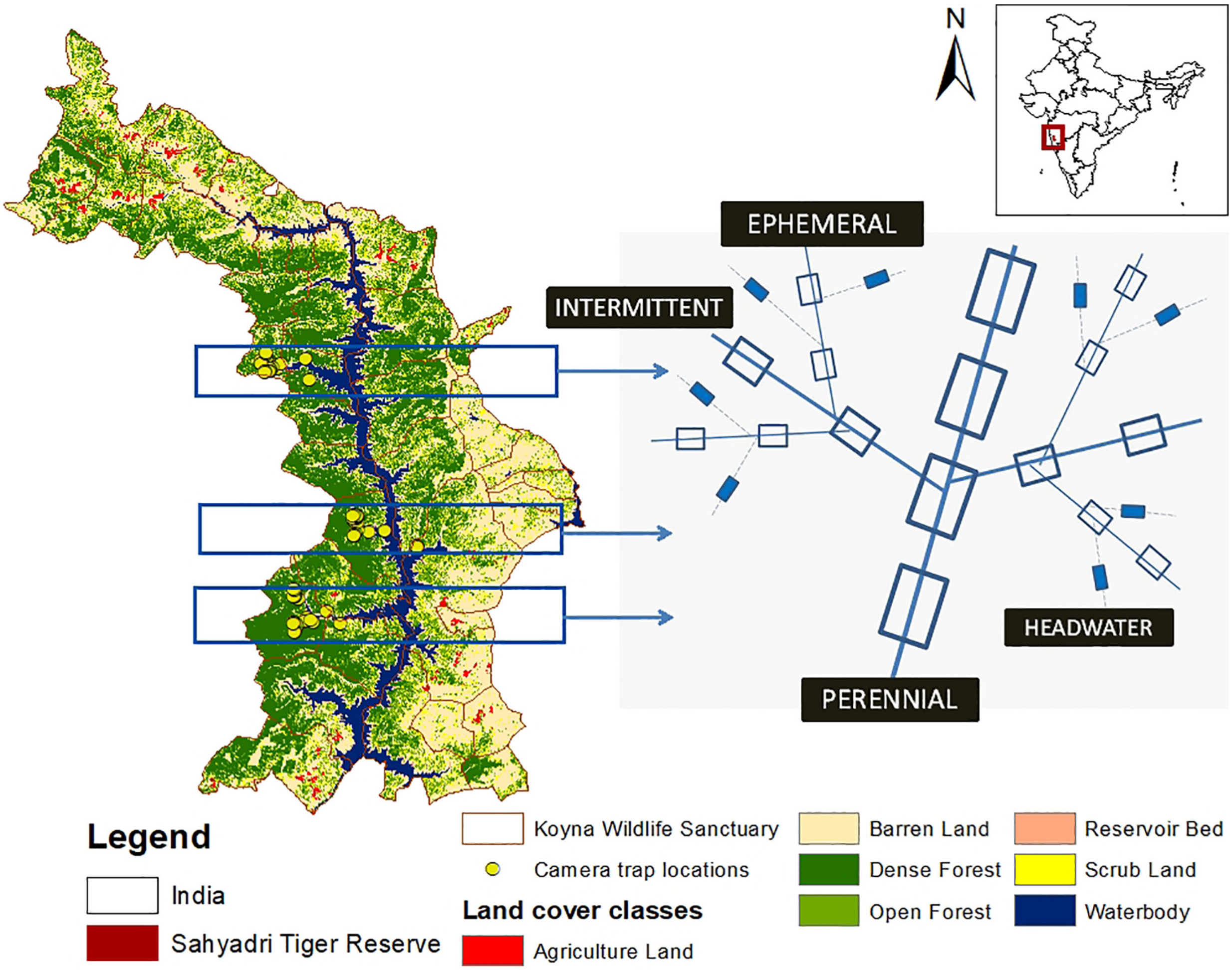

FIGURE 1 | Map of study area detailing the field survey design and the camera trap locations. In each of three sections of the river we sampled four kinds of stream types: perennial, intermittent, ephemeral and headwater streams.

TABLE 1 | Description of riparian habitat complexes/habitat types selected for the study and the rationale/basis for selecting the habitat types.

Stream type	Description	Mean altitude ± SE (m)	Buffer width fixed (m)	Mean distance of cameras from stream edge ± SE (m)
Perennial	Water flows in these stretches all year round	645.67 (±1.27)	1,000	251.08 (±16.68)
Intermittent	Water flows for more than half of the year (6–8)	649.58 (±1.08)	500	123.08 (±8.05)
Ephemeral	Water flows for less than half of the year (3–5)	653.25 (±2.12)	200	66.67 (±2.92)
Headwater	Water drains out immediately (> 1 month)	666.29 (±3.31)	100	15.62 (±1.57)

Two criteria were considered, (a) water flow in the stream types (b) mean elevation of habitats. The riparian buffer selected for perennial streams was 1,000 m, intermittent streams was 500 m, ephemeral streams was 200 m and headwater streams was 100 m.

ephemeral stream type, and up to 100 m for headwater stream type. Mean values for the distance of the camera-trap site to the waterway shown in **Table 1**. At each of the 72 sites, a single Cuddeback white flash (C1 model) camera trap was deployed by affixing it at a height of *c.* 60–70 cm to suitable trees. These were set to take consecutive images (set 5 s apart) when triggered. Cameras were checked regularly in field after deployment to limit the missing survey replicates. The mean of the trapping days in summer 2018 was 24.4 (±0.62 SE) days, winter 2018 was 39.89 (±1.75 SE), summer 2019 was 40.97 (±0.89 SE) days and winter 2019 was 35.05 (±1.73 SE) days. The trapping effort in summer 2018 was lower because initially we had fewer number of

FIGURE 2 | Different habitat types selected for the study.

camera traps available for this study, and hence, we had to cover the 72 sites in two rounds. However, during the next sessions, more camera traps were at our disposal and all 72 cameras could be deployed at once. In any case, the different number of camera traps days is likely to increase confidence intervals and thereby means that any differences in effects due to variable effort are conservative.

Riparian Habitat Assessment: To test habitat factors influencing species occupancy, circular vegetation plots were established in all the 72 riparian buffers for collection of fine-scale habitat data. Keeping the camera trap location as the center, the number of trees and fallen logs were assessed within 10 m radius plots covering 314 m^2. Percent canopy cover, elevation, the adjacent stream type and the distance to stream edge were recorded from the center of the plot. We set the radius of the plot to be short to conserve time in the field.

Data Analyses: Images retrieved from the camera traps were identified to species level excluding random captures of birds, and data were sorted into species-specific folders for all sites by season. Images were considered to be independent when they were at least 30 min apart (Linkie and Ridout, 2011; Rovero and Zimmerman, 2016; Allen et al., 2018, 2020).

Occupancy Modeling Framework: We constructed species-specific multi-season occupancy models (MacKenzie et al., 2002, 2006) using PRESENCE 12.6 (Hines, 2006). We modeled occupancy of species that had at least 20 independent captures across all four seasons. We arranged our camera trap data into 7 day occasions (weekly replicates) to record detection and non-detection to create detection history matrices for each site. A detection was coded as (1), non-detection was coded as (0) and a missing survey was coded as (.), which in our case would mean that a camera stopped working during the deployed time. We finally compiled our detection history matrices with four replicates for summer 2018, seven for winter 2018, summer 2019 and winter 2019. Hence, we had 25 replicates across all four seasons, i.e., we had 25 × 7 days = 175 occasions for each of the 72 sites covering all four seasons.

For all multi-season models, the model parameterization was fixed to initial occupancy, local colonization, extinction and detection. The parameters used in multi-season models were:

ψ: occupancy probability (probability that the area is occupied by the species)

p_i: detection probability (probability of detection species in survey i, given the species is present)

γ_i: colonization probability (probability of unoccupied site being colonized between seasons i and i + 1)

ε_i: extinction probability (probability of occupied site going extinct between seasons i and i + 1)

Predictor Variables: The riparian habitat covariates were selected *a priori* because of their likely importance in driving wildlife occupancy along streams (**Table 2**). To minimize model overfitting, which often risks the inclusion of spurious variables (Burnham and Anderson, 2002), we tested for pair-wise correlations between covariates using Pearson's correlation analyses. This was done using *cor* function and plotted using *corrplot* function in the corrplot 0.84 (Wei and Simko, 2017) package in R 4.0.0 (R Core Team, 2020). Correlation threshold was fixed at $r \geq 0.7$ (Dornmann et al., 2013; **Supplementary Code 1** and **Supplementary Figure 1**) and when correlation between two variables was higher than 0.7, we removed one of the two covariates. Since cameras were set at specific distances from stream edge at each of the stream types, we sensed a possible correlation of habitat type with distance to stream. However, since habitat type was a categorical variable it was not possible to test for correlation using the above method, since that only works with continuous variables. Regression models allow to test for this by using square root of the R^2 value as a surrogate that can be treated similarly to correlation. This works for a regression model considering a continuous variable (in our case distance from stream edge) as dependent variable and a categorical variable (stream type) as independent variable. Again, the correlation threshold was fixed at 0.7 (**Supplementary Code 2**).

Simultaneously, we ran a principal component analysis (PCA) to test for multicollinearity in addition to the pair-wise correlation analysis. We ran the PCA using the *prcomp* function in the factoextra 1.0.7 package (Kassambara and Mundt, 2020) in R (**Supplementary Code 3**, **Supplementary Figure 2**, and **Supplementary Table 1**).

Model Selection: For model selection, χ^2 goodness-of-fit test (MacKenzie and Bailey, 2004) using 999 parametric bootstraps was run to estimate overdispersion parameter $\hat{c}$ (Burnham and Anderson, 2002). This was done keeping in mind the caveat described by Burnham and Anderson (2002) that estimating $\hat{c}$ for every model would make the correct use of model selection criteria tricky, hence they recommend that the global model should be used as the basis for estimating a single variance inflation factor $\hat{c}$. We evaluated model fit with program PRESENCE by using the "assess model fit" function, while creating the design matrix of the global model. Finally, to account for overdispersion (where $\hat{c} > 1$) indicating a lack of fit, the model selection was done using quasi AIC (QAIC), and model parameters were adjusted by multiplying the standard errors by

TABLE 2 | Description of covariates with *a priori* hypotheses along riparian forests.

Covariate	**Expected influence**		
	Species	**Parameter with expected effect**	**Supporting citation**
Elevation	Gaur, sambar, barking deer	ψ (+), γ (+), ε (−)	Schaller, 1967; Johnsingh et al., 2004
	Porcupine, wild pig	ψ (+), γ (+), ε (−)	Timmins et al., 2015, 2016
Number of trees	Gaur, sambar, barking deer, porcupine	ψ (+), γ (+), ε (−)	Schaller, 1967
	Wild pig	ψ (−), γ (−), ε (+)	
Canopy cover	Gaur, sambar, barking deer, porcupine, wild pig	ψ (+), γ (+), ε (−)	Duckworth and Hedges, 1998; Duckworth et al., 1999; Greiser Johns, 2000; Timmins and Ou, 2001
Distance from stream	Gaur, sambar, barking deer, porcupine, wild pig	p (−)	Timmins et al., 2015
Season	Gaur, sambar, barking deer, porcupine, wild pig	p (+/−)	

a factor of $\sqrt{\hat{c}}$ (Burnham and Anderson, 2002). The QAIC was computed using the following formula:

$$\text{QAIC} = -2\log \text{Like}/\hat{c} + 2k$$

where,

log Like = log likelihood of the model

$\hat{c}$ = dispersion parameter from the global model

k = number of parameters in the model

The estimates of occupancy (ψ), seasonal colonization (γ), local extinction (ε), and detection probability (p) were obtained through the null models of each species. Graphs were created using ggplot2 (Wickham, 2016) and ggpubr 0.4.0 (Kassambara, 2020) R packages.

RESULTS

Our camera trap efforts accounted for 10, 021 trap nights across all four seasons—1757 trap nights in summer 2018, 2872 in winter 2018, 2868 in summer 2019 and 2524 in winter 2019. We photo-captured 19 species of terrestrial mammals (**Table 3** and **Figure 3**). Our camera capture threshold criterion of at least 20 independent captures was fulfilled by 10 species in summer 2018, 10 in winter 2018, six in summer 2019 and 10 in winter 2019. Only five species fulfilled this criterion across all four seasons and hence multi-season models were run for these five species—gaur (*Bos gaurus*), wild pig (*Sus scrofa*), sambar (*Rusa unicolor*), barking deer (*Muntiacus muntjak*), and porcupine (*Hyxtrix indica*).

Final Set of Predictor Variables: The pairwise correlation test showed that distance from stream edge and type of stream/habitat had high correlation (0.94) (**Supplementary Code 2**) and hence stream type was removed from the final variable set. Further, distance from stream, number of fallen logs, and percent understory cover were removed from the occupancy, colonization and extinction models because the test for multi-collinearity (PCA) demonstrated these covariates to have low contribution in the overall dataset. However, we retained distance from stream as a covariate to model species detection probabilities. The final list of covariates after both correlation and multi-collinearity analyses were used as occupancy, seasonal colonization, local extinction and detection probability covariates in the occupancy models (**Table 4**).

Model Selection: We detected evidence of overdispersion for two species viz., gaur ($\hat{c}$ = 2.83) and sambar ($\hat{c}$ = 2.05) (**Table 4**). No model overdispersion was detected for barking deer ($\hat{c}$ = 0.03), wild pig ($\hat{c}$ = 0.88) and porcupine ($\hat{c}$ = 0.85) (**Supplementary Table 2**). Top ranking models for each species (ΔQAIC $\leq$ 2) were considered which accounted for 83 and 95% of the QAIC model weight for sambar and gaur, respectively. For barking deer, porcupine and wild pig, top ranking models (ΔAIC $\leq$ 2) accounted for 67, 81, and 93% of AIC model weights, respectively.

Occupancy modeling results (occupancy, colonization, extinction and detection probability parameter estimates with standard error SE are reported within parentheses):

Porcupine (0.43 ± 0.01) had the highest detection probability followed by wild pig (0.37 ± 0.02), sambar (0.31 ± 0.01), barking deer (0.29 ± 0.02), and gaur (0.27 ± 0.03). Indian gaur (0.84 ± 0.12) had the highest proportion of occupied sites followed by wild pig (0.77 ± 0.07), porcupine (0.65 ± 0.07), sambar (0.49 ± 0.10), and barking deer (0.49 ± 0.08). Sambar (0.63 ± 0.10) had the highest probability to colonize unoccupied sites between seasons, followed by wild pig (0.62 ± 0.08), gaur (0.57 ± 0.15), porcupine (0.47 ± 0.06), and barking deer (0.24 ± 0.05). Barking deer (0.59 ± 0.07) had the highest probability to go extinct from a previously occupied site between seasons, followed by porcupine (0.43 ± 0.05), gaur (0.39 ± 0.11), wild pig (0.32 ± 0.04), and sambar (0.15 ± 0.07) (**Figure 4**).

Predictors of species occupancy, detection, local colonization and extinction between seasons (β estimates with standard error SE are reported within parentheses):

Barking Deer: Barking deer occupancy was positively affected by elevation (0.09 ± 0.01) and number of trees (0.05 ± 0.02), and negatively by canopy cover (−0.06 ± 0.01). Its colonization probability was positively affected by canopy cover (0.03 ± 0.01), and negatively by elevation (−0.04 ± 0.01) and number of trees (−0.01 ± 0.02). Its extinction probability was negatively affected by elevation (−0.05 ± 0.01), canopy cover (−0.01 ± 0.01), and number of trees (−0.05 ± 0.02). Its detection was higher at sites near to streams (−0.01 ± 0.01) (**Figures 5**, **6** and **Supplementary Tables 3–6**).

TABLE 3 | List of all species photo-captured during the study period from riparian forests of Koyna Wildlife Sanctuary.

Species	Summer 2018	Winter 2018	Summer 2019	Winter 2019
Porcupine	156 (8.87)	191 (6.65)	158 (5.51)	149 (5.90)
Gaur	83 (4.72)	71 (2.47)	83 (2.89)	147 (5.82)
Wild pig	101 (5.74)	86 (3.00)	253 (8.82)	137 (5.42)
Sambar	67 (3.81)	89 (3.10)	148 (5.16)	193 (7.64)
Barking deer	64 (3.64)	59 (2.05)	52 (1.81)	36 (1.42)
Mouse deer	34 (1.93)	35 (1.21)	10 (0.34)	17 (0.67)
Sloth bear	30 (1.71)	24 (0.83)	54 (1.88)	15 (0.59)
Leopard	21 (1.19)	53 (1.84)	17 (0.59)	41 (1.62)
Common palm civet	33 (1.87)	98 (3.41)	15 (0.52)	110 (4.35)
Small Indian civet	23 (1.31)	18 (0.62)	13 (0.45)	94 (3.72)
Ruddy mongoose	17 (0.97)	32 (1.11)	12 (0.41)	66 (2.61)
Dhole	2 (0.11)	10 (0.35)	6 (0.21)	50 (1.98)
Indian pangolin	3 (0.17)	5 (0.17)	1 (0.034)	3 (0.11)
Gray mongoose	4 (0.23)	2 (0.07)	–	–
Indian hare	16 (0.91)	8 (0.28)	9 (0.31)	19 (0.75)
Indian gerbil	2 (0.11)	–	–	–
Stripe-necked mongoose	–	16 (0.56)	4 (0.14)	6 (0.23)
Rusty spotted cat	–	1 (0.03)	–	1 (0.039)
Brown palm civet	–	–	–	2 (0.079)

We report the number of captures and overall capture rates (expressed per 100 trap nights in parentheses) across all four seasons.

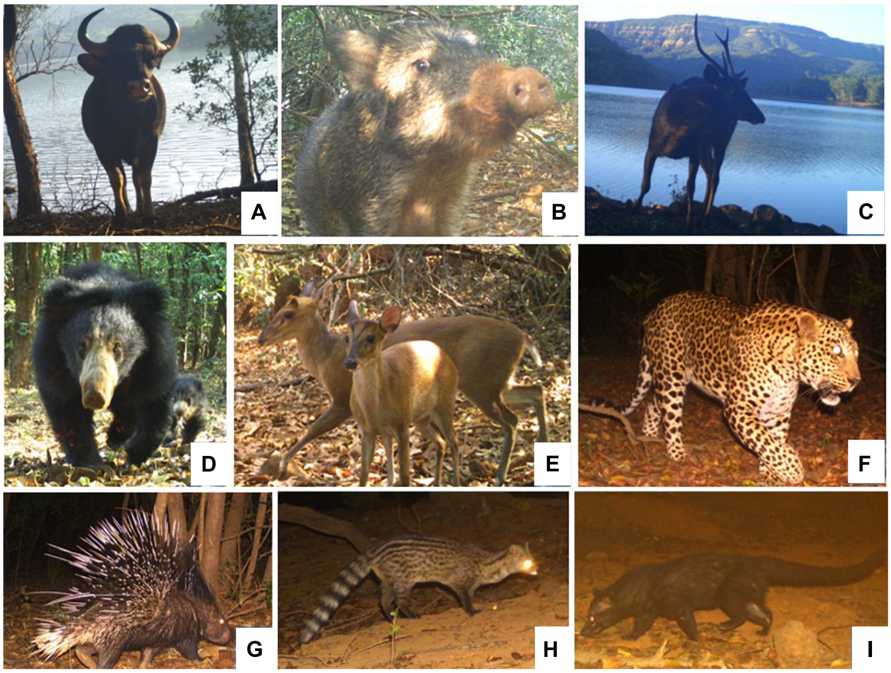

FIGURE 3 | Select camera trap images of highly 'phot-captured' mammals during the study. **(A)** 'gaur' *Bos gaurus*; **(B)** wild pig *Sus scrofa*; **(C)** sambar *Rusa unicolor*; **(D)** sloth bear *Melursus ursinus*; **(E)** barking deer *Muntiacus 'muntjac'*; **(F)** leopard *Panthera pardus*; **(G)** porcupine *Hystrix indica*; **(H)** small Indian civet *'Vivericula' indica*; **(I)** common palm civet *Paradoxurus 'hermaphrodites'*.

Porcupine: Porcupine occupancy was positively affected by canopy cover (0.01 ± 0.01), number of trees (0.03 ± 0.01), and negatively by elevation (−0.01 ± 0.01). Its colonization probability was positively affected by canopy cover (0.02 ± 0.01), number of trees (0.01 ± 0.01) and negatively by elevation (−0.03 ± 0.01). Its detection was higher closer to streams (−0.001 ± 0.001) and it was also affected by season. None of the covariates considered could explain porcupine extinction probability (**Figures 5**, **6** and **Supplementary Tables 3–6**).

TABLE 4 | Final list of habitat covariates used in the occupancy models.

Parameter	Site-specific covariate	Type of variable	Mean values (range)
ψ, γ, ε	Elevation (m)	Continuous	655.72 (633–695)
	Canopy cover (%)	Continuous	61.15 (0–90)
	Number of trees	Continuous	19.68 (0–50)
p	Distance from stream edge (m)	Continuous	Perennial: 251.08 (90–358) Intermittent: 123.08 (90–168) Ephemeral: 66.67 (40–100) Headwater: 15.62 (5–25)
	Season	Categorical	–

Gaur: Gaur detection (-0.02 ± 0.01) were higher at sites near streams. Its detection was also affected by season. Its occupancy, colonization and extinction probabilities were not explained by any of the covariates considered in the occupancy models (**Figure 6** and **Supplementary Tables 3–6**).

Sambar: Sambar occupancy, colonization and extinction probability were not influenced by any of covariates. However, sites near to streams (-0.001 ± 0.001) and season affected its detection probability (**Figure 6** and **Supplementary Tables 3–6**).

Wild Pig: Wild pig extinction probability was positively affected by elevation (0.02 ± 0.01), and negatively by canopy cover (-0.02 ± 0.01), number of trees (-0.06 ± 0.08). Its detection was higher near streams (-0.01 ± 0.01), and was also affected by season. No factors could explain its occupancy and colonization (**Figures 5**, **6**; **Supplementary Tables 3–6**).

DISCUSSION

Three key patterns emerge from our study. Firstly, ungulates were the most frequently photo-captured mammals in camera traps, with higher occupancy probability in riparian forests. Apart from ungulates, small mammals were also captured, however, large carnivores which included leopard *Panthera pardus*, dhole *Cuon alpinus* and sloth bear *Melursus ursinus* had low captures rates (**Table 3**). Pioneering studies by Naiman (1988); Pastor et al. (1988), and Naiman and Rogers (1997) found substantial evidence of large ungulates shaping structure of riparian forests in temperate ecosystems by selective browsing, dispersing seeds, and thereby affecting riparian plant community and ultimately modifying channel morphology (Naiman and Rogers, 1997). A similar kind of ungulate dominance in terms of high occupancy and persistence was found in riparian forests in Koyna.

Secondly, we observed an ungulate body size effect on colonization and extinction probabilities, in that the smallest ungulate, barking deer (20–30 kg), had highest extinction probability (0.59 ± 0.07) and lowest colonization probability (0.24 ± 0.05), while the much larger sambar (100–350 kg) had highest colonization probability (0.63 ± 0.10) and lowest extinction probability (0.15 ± 0.07) (**Figure 4** and **Supplementary Table 7**). This indicates that smaller ungulates are more vulnerable to vacate previously occupied sites (local extinction) than larger ungulates, perhaps due to resource competition. In a larger landscape context, however, the opposite of this pattern has been recorded, i.e., large herbivores are more vulnerable to extinction through large-scale anthropogenic factors (Ripple et al., 2015). However, at local scales, more empirical studies are needed to understand this pattern further. Body size has been successfully used to explain ungulate niche differentiation with regards to food requirements and predator sensitivity (Veldhuis et al., 2019). Previous studies in parts of Asia show that smaller ungulate species persist more widely than larger species (Karanth, 2016; Phumanee et al., 2020). Whereas muntjac and wild pig occurred at more sites than sambar and gaur in Thailand (Phumanee et al., 2020), gaur and pig were the least and most wide-ranging species in Karnataka Western Ghats landscape (Karanth, 2016). Contrastingly, Lamichhane et al. (2020) found that barking deer had lowest site occupancy in comparison to other species in Shuklaphanta National Park, Nepal. Hence, there exists much variation in ungulate occupancy patterns in regards to body size, perhaps influenced by local habitat, environmental factors and anthropogenic pressure. We found that large ungulates occur at a higher number of sites, and that gaur and pig both had higher rates of occupancy, in contrast to Karanth (2016) study.

Thirdly, distance from stream edge was a dominant predictor of mammal detection probabilities (**Figure 6** and **Supplementary Table 3**). As distance from stream increased, we observed a drop in the probabilities suggesting that ungulates in riparian forests congregate near streams. It is now well established that rivers, riparian forests and adjacent upland forests are part of a single large contiguous system composed of different smaller units of landscape. Hence viewing riparian forests as part of river continuum framework is essential. Among other riparian habitat factors, elevation was an important feature that influenced species persistence across seasons conforming with the previous occupancy study by Karanth (2016). Canopy cover and number of trees also affected species occupancy, colonization and extinction in our study, as we had hypothesized (**Table 2**).

Testing the role of riparian forests, especially in regards to stream proximity, is important to understand how climate change will affect ungulate communities (Speakman and Król, 2010; Fuller et al., 2014; Shreshtha et al., 2014; Veldhuis et al., 2019), because increasing land temperatures, changing rainfall regimes and habitat fragmentation increase the risk of regional extinctions (Ripple et al., 2015). The integration of food and water requirements, predation risk and thermoregulation constraints yields a multi-dimensional framework that generates testable predictions to understand ungulate assemblages (Veldhuis et al., 2019). Our work adds to this framework by documenting persistence of forest mammals in riparian forests. Our testing focused on habitat cover and proximity to water and this offers insights into mammal persistence in an altered habitat regime.

Mammal Persistence in Koyna Reservoir: Nilsson and Dynesius (1994) report two major impacts of dams to be the permanent inundation of vast areas of land and disruption of the seasonal flood regime along the river. Other local disturbances due to dam construction may be highly variable globally; however, Alho (2011) generally describes what land mammals

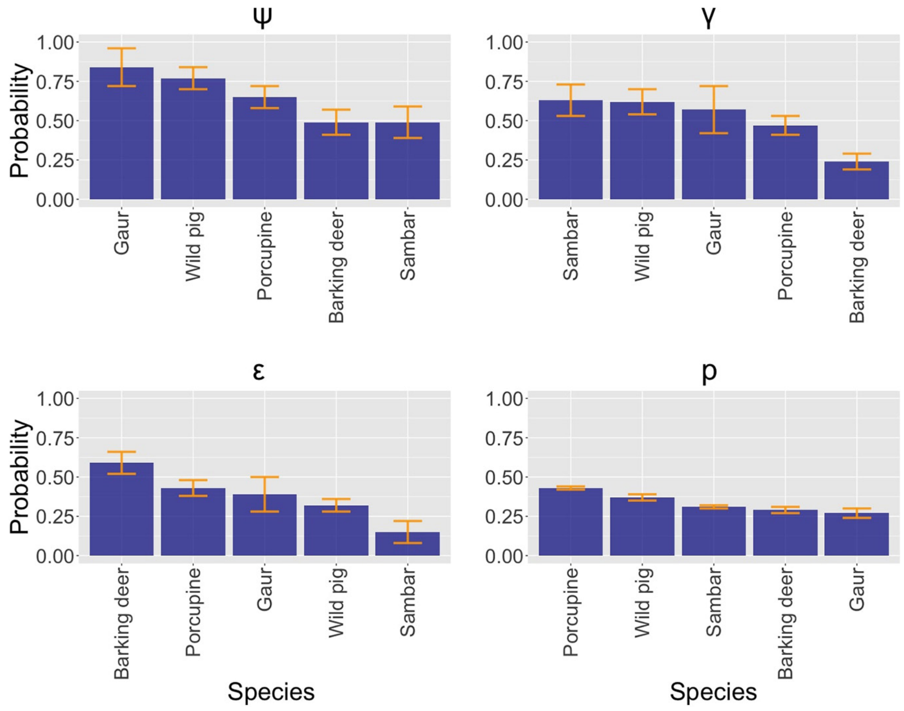

FIGURE 4 | Probability estimates of occupancy, colonization, extinction and detection of all the five species.

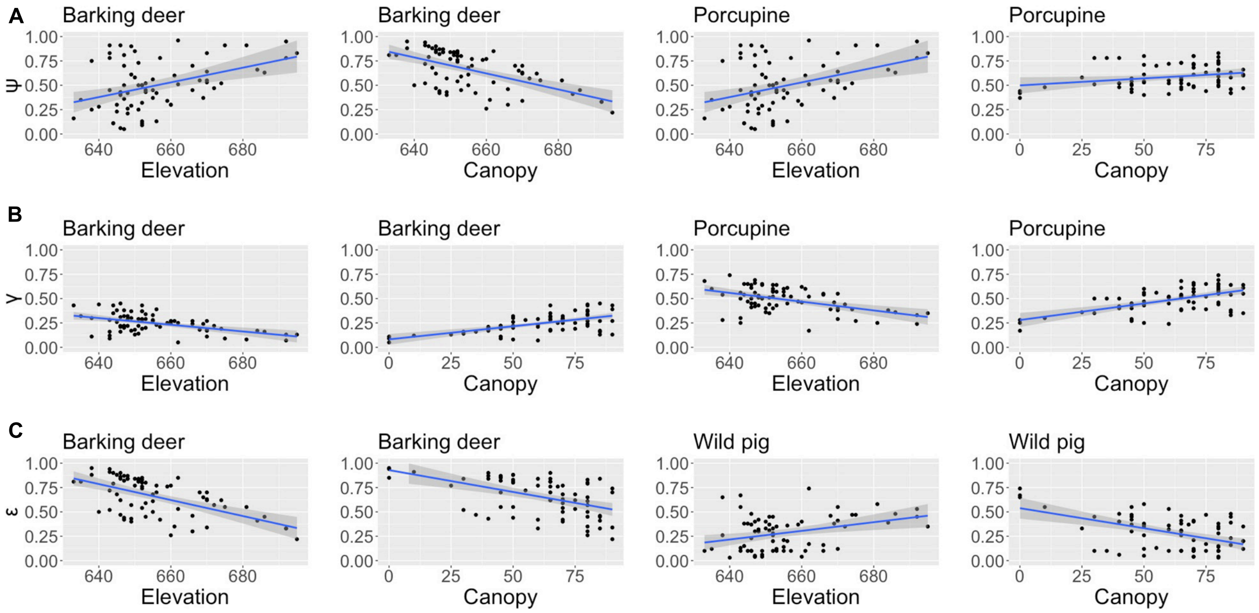

FIGURE 5 | Factors affecting species **(A)** occupancy, **(B)** colonization, and **(C)** extinction probabilities of common mammal species. The number of trees also showed statistically significant relationships to these probabilities, similar to those of canopy openness shown here (**Supplementary Tables 4–6**).

face when a river dam is constructed. The prolonged noise produced by machinery, light, presence of workers and other activities during the period of construction disturb wild animals, which will then try to escape to adjacent habitats. Large dams take a long time to complete—Koyna Dam construction began in 1954 and was completed in 1963. The formation of the reservoir displaces resident animals to nearby areas where higher densities of individuals of the same species are already resident. This phenomenon is termed as the reservoir's extended effect (Sá, 1995; Alho, 2011). This renders free ranging individuals

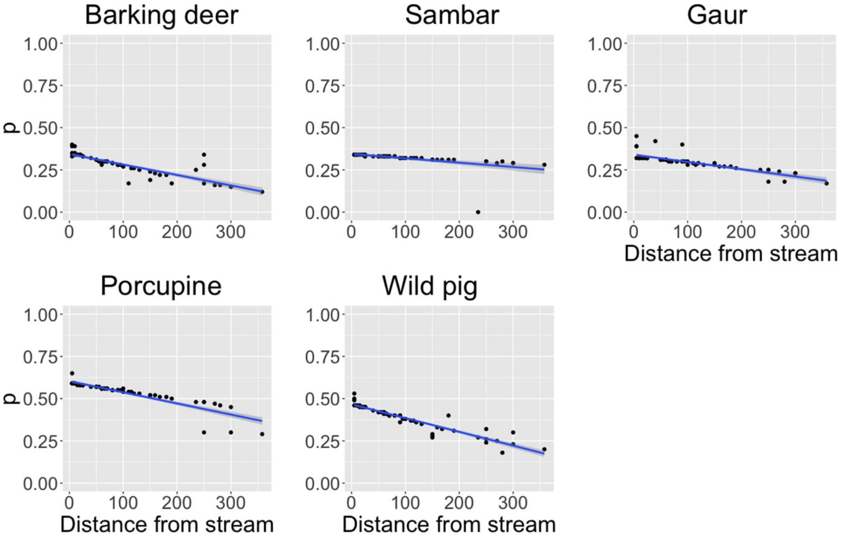

FIGURE 6 | Effect of distance from stream on species detection probabilities.

without fixed home ranges more vulnerable and they eventually submit to resident individuals in disputes/competition over natural resources. The result is that animals displaced by the effects of reservoir will die or move to more vulnerable areas. However, once a reservoir is complete and a substantial amount of time has passed, mammals adapt to their surroundings. In our case, 55 years have passed since the Koyna Dam was completed. The landscape has since experienced numerous changes in terms of land and river structure as well the socio-political context. Many villages in the valley have been relocated, firstly when the dam was being constructed and secondly when the area was notified as a wildlife sanctuary in 1985. Tigers also experienced local extinction from Koyna landscape with the last confirmed tiger record from Koyna in 2007. With this study, we know the present status of wildlife in the reservoir, acknowledging that severe changes in mammal community may have taken place which went predominantly undocumented. However, this may be treated as a baseline study on mammal ecology in reference to the Koyna Hydropower Dam five decades after its construction.

Management Implications: Our findings have high relevance for management of riparian forests and accordingly how species can be managed within a reservoir. Habitat variables that contribute to species-specific occupancy and long-term well-being were identified which can be prioritized in management plans. By conserving these factors, wildlife authorities can increase long term species persistence and strategically attempt to limit seasonal and local species extinctions. In addition to highlighting species-habitat relationship patterns of mammals utilizing riparian forests, the information generated in this study provides a strong empirical basis for developing catchment-wide and multi-species strategies for conservation management. Management strategies that have focused only on one key aspect and have simplified riverscapes have inevitably failed. Multi-landscape planning that encompasses streams, rivers and adjacent riparian forests which go beyond conventional planning of a single landscape unit, have had overarching benefits (Naiman and Rogers, 1997; Hermosa et al., 2012; Adams et al., 2014). We implemented a novel field design to study riparian forest use across an entire catchment. This approach employs a robust sampling design by incorporating riparian forests adjacent to all stream types of a catchment which presents a better understanding of mammalian occupancy along different stream types. Following this design, researchers can study species assemblages and help management agencies to efficiently draft plans that manage multiple species rather than focusing on only one charismatic 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.

ETHICS STATEMENT

The animal study was reviewed and approved by the Wildlife Institute of India. There was no handling of animals. All surveys were non-invasive in nature (camera traps). All necessary codes of conduct were followed and surveys were permitted by national (Wildlife Institute of India/National Tiger Conservation Authority) and state (Maharashtra Forest Department) authorities.

AUTHOR CONTRIBUTIONS

RK, CB, and SJ: study design. SJ, AG, and NG: data collection. SJ: data analysis and writing. RK, MH: supervision, assistance with data analysis and writing. 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/fevo.2021.643285/full#supplementary-material

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Ecological Correlates of 20-Year Population Trends of Wintering Waterbirds in Deep Bay, South China

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Along the East Asian-Australasian flyway (EAAF), waterbirds are threatened by a wide range of human activities. Studies have shown that wintering populations of many species have declined in Australia and Japan; however, long term data along China's coast are limited. In this study, we analyzed data collected from monthly bird surveys to quantify population trends of wintering waterbirds from 1998 to 2017 in the Deep Bay area, South China. Of the 42 species studied, 12 declined, while nine increased significantly. Phylogenetic comparative analysis revealed that population trends were negatively correlated to reliance on the Yellow Sea and body size. Further, waterbird species breeding in Southern Siberia declined more than those breeding in East Asia. These findings, coupled with a relatively high number of increasing species, support the continual preservation of wetlands in the Deep Bay area. This study provides another case study showing that data collected from wintering sites provide insights on the threats along migratory pathway and inform conservation actions. As such, we encourage population surveys in the EAAF to continue, particularly along the coast of China.

Keywords: bird, coastal wetlands, conservation, East Asian-Australasian flyway, Ramsar site, shorebirds

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INTRODUCTION

Studying population trends of threatened species to identify drivers of population change is crucial for conservation. This is challenging for mobile species, such as migratory waterbirds (Webster et al., 2002; Piersma et al., 2016). Many waterbird species travel across hemispheres annually, and their populations can be impacted by a wide range of environmental and anthropogenic factors in breeding grounds, stopover sites, and wintering grounds (Amano et al., 2010; Catry et al., 2013; Clemens et al., 2016; Howard et al., 2020). The driving factors can vary greatly in scale, ranging from global climate change to local habitat transformation (Amano et al., 2010; Pavón-Jordán et al., 2015). As such, quantification of population trends at different locations (breeding, stopover, and wintering) can provide useful information to assess migratory waterbird conservation status and evaluate the threats along their migratory pathways (Murray et al., 2017; Wang et al., 2018).

Waterbirds of the East Asian-Australasian flyway (EAAF) have been attracted conservation attention. Habitat transformation along the coast of China, especially in the Yellow Sea area, has caused prominent declines of several species; this is supported by the studies revealing declines of species that rely on Yellow Sea as essential stopover sites at wintering sites in Japan, Australia, and New Zealand (Amano et al., 2010; Murray et al., 2015, 2017; Studds et al., 2017). Besides habitat transformation, waterbirds of the EAAF also experience a wide range of other threats (Wang et al., 2018), including hunting (Gallo-Cajiao et al., 2020), alien invasive species (Gan et al., 2009), pollution (Zhao et al., 2016), and climate change (Iwamura et al., 2013; Wikramanayake et al., 2020).

Previous studies have quantified population trends of migratory waterbirds in China, but the population trends of nearly half (48%) of species were unknown because of the lack of long-term, systematic survey data (Wang et al., 2018; Wetlands International, 2021). Systematic surveys along the coast of China only began in 2005 (Bai et al., 2015). However, systematic waterbird surveys were done in the Deep Bay area, South China since 1998. This represents a valuable dataset to quantify population trends of waterbirds in the EAAF because of two major reasons. First, the area represents one of the most important wintering sites for waterbirds, since the area holds over 20% of EAAF populations for 13 waterbird species (Bai et al., 2015). Second, to our knowledge, the dataset is from the longest ($\geq$20 years) systematic survey of wintering waterbird populations along the coast of China.

The quantification of waterbird population trends in the Deep Bay makes it possible for us to evaluate the impacts of different threats along the EAAF. This has been done through comparative trait-based analysis to assess the influence of species traits on population trends of EAAF waterbirds in Japan (Amano et al., 2010), Australia, and New Zealand (Murray et al., 2017). In the present study, we applied a similar approach on the wintering population in the Deep Bay area, providing the first case study along the coast of China. We take a three-step approach. First, we quantified the population trends of 42 wintering waterbird species in the Deep Bay area. Second, we used remote sensing to quantify the extent of habitat transformation, providing baseline information to evaluate the influence of local habitat changes on population trends. Lastly, we performed a comparative trait-based analysis to identify species traits associated with local and regional threats that correlate with population trends among species. From this work, we provide insight on the threats at different geographical scales and provide recommendations on the conservation of threatened waterbirds along the EAAF.

MATERIALS AND METHODS

Bird Survey

The Hong Kong Bird Watching Society started to conduct surveys on wintering waterbirds in the Deep Bay area in 1979, providing data to the international counts organized by the International Waterfowl Research Bureau and Asian Wetland Bureau (Melville, 1980; Carey, 1994). Since 1998, the Hong Kong Government began to fund the monitoring of waterbirds—systematic, monthly surveys have been carried out in the Deep Bay area, which encompasses two regions: (1) the northwest New Territories, Hong Kong Special Administrative Region China, and (2) Futian Mangrove National Nature Reserve, Shenzhen, Guangdong Province, China. The study area contains a mixture of different wetland types, including commercial aquaculture ponds, mangroves, and intertidal mudflats (more details in Pang et al., 2020). Synchronized surveys were conducted along 16 fixed, non-overlapping transects distributed across the study areas by trained surveyors. Among these 16 transects, 15 are located in Hong Kong while one are in Shenzhen, China. The surveyor recorded the abundance of all waterbird species, using binoculars and/or telescopes. To maintain survey consistency, all surveyors had over 3 years of birdwatching experience and received training provided by the Hong Kong Bird Watching Society. The training consisted of two parts, including lectures and practical sessions. The lectures provided candidate surveyors information on the project background, survey methods, and safety issues. For the practical sessions, all candidate surveyors were required to join at least three surveys led by a trained surveyors. For the time of survey, all surveys were done during high tide, when the intertidal mudflat was largely submerged, and waterbirds visited high-tide roosting areas.

Habitat Changes

To quantify the extent of habitat transformation in the Deep Bay area from late 1990s to late 2010s, we used Système Pour l’Observation de la Terre (SPOT) images and open data. SPOT 4 and SPOT 5 images taken, respectively in 2000 and 2008 during dry season (October to February) of Hong Kong were selected to eliminate cloud contamination. SPOT images were employed due to their high resolution (6–10 m), allowing for visualization of greater detail in the land cover and more precise land use classification. All remote sensing images were processed through geometric correction, false color composition, image mosaic, and supervised classification using the ArcGIS 10.5. Over 1,000 training samples were obtained from different sources to improve the image classification accuracy. For 2018, the habitat/land use data were obtained from WWF open data[1] and supplemented by Google Earth high spatial resolution images. Land use was classified into 15 habitats according to the methodology stated in the Terrestrial Habitat Mapping proposed by the Sustainable Development Unit, Hong Kong Government[2]. The 15 habitat types was further categorized into five habitats, including aquaculture ponds, human settlement, intertidal mudflat, mangrove, and other vegetation.

Population Trends

We included data collected from 3 months (December, January, and February), when migratory waterbirds complete their southward migration and have not started northward migration (Clemens et al., 2016). In total, 60 surveys were included in the analyses (3 months × 20 years). To avoid spurious results caused by rare and infrequent species, we selected species with at least 10 individuals recorded in 10 surveys. To quantify wintering bird population trends, we used generalized additive mixed models (GAMM) to determine non-linear population trends. We quantified the trends for three focal periods, including

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[1] https://globil-panda.opendata.arcgis.com/datasets/mai-po-wetland-habitats

[2] https://www.epd.gov.hk/epd/english/environmentinhk/eia_planning/sea/terresthab.html

the entire study period (1998–2017) and two 10-year periods (1998–2007 and 2008–2017) because we aimed to understand the population trends over the entire study period and if the trends changed during the study period. We included the number of birds as a dependent factor and year (e.g., December 1998, January 1999, and February 1999 regarded as the winter of 1998) as an independent factor. To account for variation between sites, we included transect as a random factor. We used the package poptrend in software R to fit a log-linear model with quasipoisson or negative binomial distribution using restricted maximum likelihood (Knape, 2016; R Core Team, 2019). We chose the data distribution based on examination of model residuals and explained deviance (Bell et al., 2020). We used the function change of R package poptrend to estimate percentage of population change; we considered that there was a significant trend when the standard errors did not overlap with zero, positive values indicated increasing trends whereas negative values indicated decreasing trends.

Factors Influencing Population Trends

To explore the relationships between population trends and selected species traits, we obtained linear changes in population by estimating linear population trends using generalized linear mixed models (GLMM) with logit link function and zero-inflated Poisson or negative binomial error. Estimates (percentage of population changes) of GAMM were not used because the estimates are sensitive to initial counts which resulted in exceptionally large increases in some species (black-winged stilt, great knot, Pacific golden plover; **Table 1**). Zero-inflated models were used because over 67% of count were zeros. We included the total number of birds recorded as a dependent factor, year as an independent factor, and transect as a random factor. Then we examined the correlation between linear population changes of species (slope coefficient of year) and species traits using phylogenetic generalized least squares (PGLS), which accounts for phylogenetic relationships between species (Felsenstein, 1985). We obtained the phylogeny of the study species from the BirdTree database[3]. We developed a consensus phylogeny from 1,000 plausible phylogenetic trees using Hackett phylogenetic backbones (9,993 OTUs) (Jetz et al., 2012). We constructed the consensus phylogeny and did the PGLS using the function consensus.edges and pgls in R package phytools respectively (Revell, 2012). The eight species traits included in our models were breeding range, wintering range, breeding habitat, wintering habitat, body size, reliance on Yellow Sea as key habitats, reliance on aquaculture ponds, and intertidal mudflats. We collected information on distribution range and habitat use from Billerman et al. (2020). We followed the categorization in Amano et al. (2010) for breeding range (East Asia, South Siberia, and High Arctic), wintering range (East Asia, Southeast Asia, and the Oceania), breeding habitat and wintering habitat (generalist, freshwater, and coastal specialists). Body size was recorded as the maximum body size for each species using data in Billerman et al. (2020). Species relying on the use of Yellow Sea as their staging sites were reported to show population decline recently (Melville et al., 2016); to explore the effect of the Yellow Sea-reliance on the population trend in the Deep Bay area, species were categorized into those depending on the Yellow Sea and those that do not. Reliance on the Yellow Sea is defined as having more than 30% of the EAAF population staging during migration or breeding in the Yellow Sea, with data collected from Barter (2002); Amano et al. (2010), Wetlands International (2021), and Choi et al. (2020). In the Deep Bay area, waterbirds relying on either aquaculture ponds or intertidal mudflats may be influenced by a change in coverage of aquaculture ponds and intertidal mudflats. We quantified the reliance on aquaculture ponds and intertidal mudflats into four levels by calculating the proportion of individuals recorded from these two habitats (heavy $\geq$ 50%; moderate = 10–50%; light = 1–9% and; no = 0%), following the approach of Fujioka et al. (2010) who evaluated the importance of rice fields to shorebirds. We assessed multicollinearity in independent factors by calculating generalized variance inflation factors (GVIF); we excluded wintering ground that has GVIF > 2 (Fox and Monette, 1992). We built models for the three focal periods separately. To identify the most influential factors from the full models, we used the function dredge in the package MuMIn in software R to build models by fitting all possible combinations of independent factors (Barton, 2011). We determined the best models according to Akaike's Information Criterion values corrected for small sample size (AICc); candidate models with < 2 units of difference in AICc value with the top model were considered as the set of best fitting models (Burnham and Anderson, 2002). We calculated final estimates and standard errors for species traits by averaging the parameters from the best fitting models. We applied Wald's Z test to test the significance of the correlations between annual population changes and species traits (Bolker et al., 2009). We did the analysis separately for three focal periods: 1998–2017, 1998–2007, and 2008–2017. GLMM was built using the R package glmmTMB (Brooks et al., 2017).

RESULTS

We recorded 130 wintering waterbird species from 1998 to 2017, and we included 42 species in the analysis. Of the 42 species, the population of nine species (black-faced spoonbill, black-winged stilt, Chinese pond heron, common greenshank, Eurasian curlew, great knot, little grebe, Pacific golden plover, pied avocet) increased, and 12 species (black-headed gull, common moorhen, common sandpiper, common shelduck, Dalmatian pelican, Eurasian coot, Eurasian teal, Eurasian wigeon, green sandpiper, gray heron, lesser black-backed gull, northern pintail) declined from 1998 to 2017 (**Table 1** and **Figures 1**, **2**). Among the nine increasing species, three species (black-faced spoonbill, little grebe, and Pacific golden plover) increased consistently in both 10-year periods (1998–2007 and 2008–2017). Among the 12 declining species, eight species (black-headed gull, common shelduck, Dalmatian pelican, Eurasian teal, Eurasian wigeon, green sandpiper, lesser black-backed gull, and northern pintail) decreased consistently in both 10-year periods. Five species exhibited reverse trends in the two 10-year periods; common greenshank, intermediate egret, pied avocet, and wood sandpiper

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[3] http://birdtree.org/

TABLE 1 | Estimated percentage of population changes for 42 wintering waterbirds species in the Deep Bay area from 1998 to 2017 calculated by generalized additive mixed models using the package poptrend in software R.

Family	Species	Common name	Maximum count	1998–2017	1998–2007	2008–2017	WPE trend
Anatidae	*Tadorna tadorna*	Common shelduck	1,320	−99 (−99, −99)	−99 (−99, −99)	−99 (−99, −99)	Unk
Anatidae	*Anas crecca*	Eurasian teal	5,017	−90 (−94, −80)	−66 (−75, −53)	−66 (−75, −53)	Dec
Anatidae	*Anas Penelope*	Eurasian wigeon	4,206	−89 (−94, −79)	−70 (−81, −49)	−58 (−74, −29)	Dec
Anatidae	*Anas querquedula*	Garganey	126	41 (−68, 550)	−44 (−85, 104)	144 (−32, 821)	Dec
Anatidae	*Anas acuta*	Northern pintail	5,230	−90 (−95, −77)	−65 (−77, −46)	−68 (−79, −49)	Dec
Anatidae	*Anas clypeata*	Northern shoveler	12,520	−31 (−72, 53)	−69 (−85, −31)	129 (12, 331)	Unk
Anatidae	*Aythya fuligula*	Tufted duck	8,000	470 (−22, 3,325)	302 (−20, 1,732)	20 (−72, 357)	Unk
Ardeidae	*Nycticorax nycticorax*	Black-crowned night heron	658	160 (−45, 1,504)	−34 (−84, 212)	302 (5, 1,437)	Sta
Ardeidae	*Ardeola bacchus*	Chinese pond heron	126	86 (29, 173)	−14 (−39, 16)	134 (75, 212)	Sta
Ardeidae	*Bubulcus ibis*	Eastern cattle egret	77	22 (−52, 198)	−23 (−67, 70)	88 (−16, 335)	Sta
Ardeidae	*Casmerodius albus*	Great egret	825	43 (−8, 123)	56 (4, 130)	0 (−29, 42)	Dec
Ardeidae	*Ardea cinerea*	Gray heron	816	−38 (−51, −20)	−10 (−24, 8)	−29 (−42, −13)	Unk
Ardeidae	*Larus fuscus*	Intermediate egret	700	−30 (−68, 48)	89 (0, 269)	−62 (−80, −27)	Unk
Ardeidae	*Egretta garzetta*	Little egret	1,555	−21 (−52, 23)	33 (−9, 94)	−32 (−53, −1)	Sta
Charadriidae	*Pluvialis squatarola*	Gray plover	833	127 (−15, 521)	−1 (−56, 125)	142 (7, 542)	Dec
Charadriidae	*Mesophoyx intermedia*	Kentish plover	26	−93 (−99, 109)	−87 (−99, 131)	−70 (−98, 449)	Unk
Charadriidae	*Charadrius dubius*	Little ringed plover	200	−45 (−77, 23)	14 (−43, 129)	−47 (−75, 9)	Unk
Charadriidae	*Pluvialis fulva*	Pacific golden plover	782	1,813 (146, 17,246)	304 (55, 1,045)	304 (55, 1,035)	Unk
Rallidae	*Fulica atra*	Eurasian coot	762	−98 (−99, −87)	−39 (−77, 59)	−94 (−99, −63)	Dec
Laridae	*Larus ridibundus*	Black-headed gull	14,300	−69 (−85, −25)	−42 (−59, −12)	−42 (−60, −14)	Unk
Laridae	*Charadrius alexandrinus*	Lesser black-backed gull	4,303	−87 (−98, −9)	−63 (−85, −4)	−63 (−86, −6)	Unk
Laridae	*Larus saundersi*	Saunders's gull	114	−51 (−87, 84)	−41 (−74, 32)	−13 (−66, 116)	Dec
Pelecanidae	*Pelecanus crispus*	Dalmatian pelican	22	−99 (−99, −99)	−99 (−99, −94)	−99 (−99, −80)	Dec
Phalacrocoracidae	*Phalacrocorax carbo*	Great cormorant	8,139	119 (−8, 446)	54 (−29, 230)	37 (−33, 214)	Unk
Podicipedidae	*Podiceps cristatus*	Great crested grebe	413	−72 (−96, 124)	−14 (−84, 413)	−65 (−93, 107)	Unk
Podicipedidae	*Tachybaptus ruficollis*	Little grebe	82	146 (73, 257)	57 (16, 126)	42 (9, 89)	Unk
Rallidae	*Gallinula chloropus*	Common moorhen	118	−58 (−77, −28)	59 (−2, 158)	−72 (−84, −54)	Unk
Recurvirostridae	*Himantopus himantopus*	Black-winged stilt	669	65,425 (793, 4,706,921)	87,404 (1,051, 7,248,016)	−18 (−83, 289)	Unk
Recurvirostridae	*Recurvirostra avosetta*	Pied avocet	15,920	300 (84, 907)	716 (294, 1,691)	−57 (−78, −22)	Unk
Scolopacidae	*Tringa nebularia*	Common greenshank	1,480	138 (3, 407)	352 (99, 819)	−49 (−68, −20)	Unk
Scolopacidae	*Tringa tetanus*	Common redshank	918	279 (−35, 2,637)	88 (−18, 382)	88 (−18, 378)	Unk
Scolopacidae	*Actitis hypoleucos*	Common sandpiper	44	−29 (−51, 0)	−17 (−39, 12)	−15 (−40, 13)	Unk
Scolopacidae	*Gallinago gallinago*	Common snipe	40	−12 (−58, 63)	−6 (−33, 27)	−6 (−34, 26)	Unk
Scolopacidae	*Calidris alpine*	Dunlin	5,720	−91 (−99, 149)	−96 (−99, −28)	94 (−87, 5,003)	Unk
Scolopacidae	*Numenius arquata*	Eurasian curlew	1,592	153 (37, 406)	103 (16, 261)	19 (−28, 92)	Unk
Scolopacidae	*Calidris tenuirostris*	Great knot	115	5,497 (403, 42,102)	229 (−43, 2,307)	1,648 (172, 9,502)	Dec
Scolopacidae	*Tringa ochropus*	Green sandpiper	18	−55 (−69, −39)	−32 (−42, −21)	−32 (−43, −21)	Unk
Scolopacidae	*Tringa stagnatilis*	Marsh sandpiper	2,428	9 (−96, 2,657)	5 (−82, 385)	2 (−81, 385)	Unk
Scolopacidae	*Tringa erythropus*	Spotted redshank	2,500	−95 (−99, 59)	−32 (−96, 1,136)	−85 (−99, 205)	Unk
Scolopacidae	*Calidris temminckii*	Temminck's stint	46	33 (−66, 406)	123 (−23, 589)	−42 (−81, 71)	Unk
Scolopacidae	*Tringa glareola*	Wood sandpiper	262	−6 (−50, 75)	117 (17, 296)	−57 (−74, −28)	Unk
Threskiornithidae	*Platalea minor*	Black-faced spoonbills	423	811 (415, 1,471)	184 (115, 266)	184 (117, 270)	Inc

Text color indicate significant increasing (blue) and declining (orange) trends. WPE (waterbird population estimates) trends indicates the assessment of population trends along the East Asian-Australasian flyway on the waterbird population estimates online database; Sta, stable; Inc, increase; Dec, decrease; Unk, unknown (Wetlands International, 2021).

increased from 1998 to 2007 and then decreased from 2008 to 2017, whereas northern shoveler decreased from 1998 to 2007 and increased from 2008 to 2017.

In the Deep Bay area, satellite maps revealed a consistent decline in coverage of intertidal mudflat (56–43%), and a consistent increase in coverage of mangrove (8–15%) and other vegetation (3–14%) from 2000 to 2018 (**Figure 3**). The coverage of aquaculture pond decreased from 2000 to 2008 (30–20%) and then increased from 2008 to 2018 (20–28%), whereas the coverage of human settlements

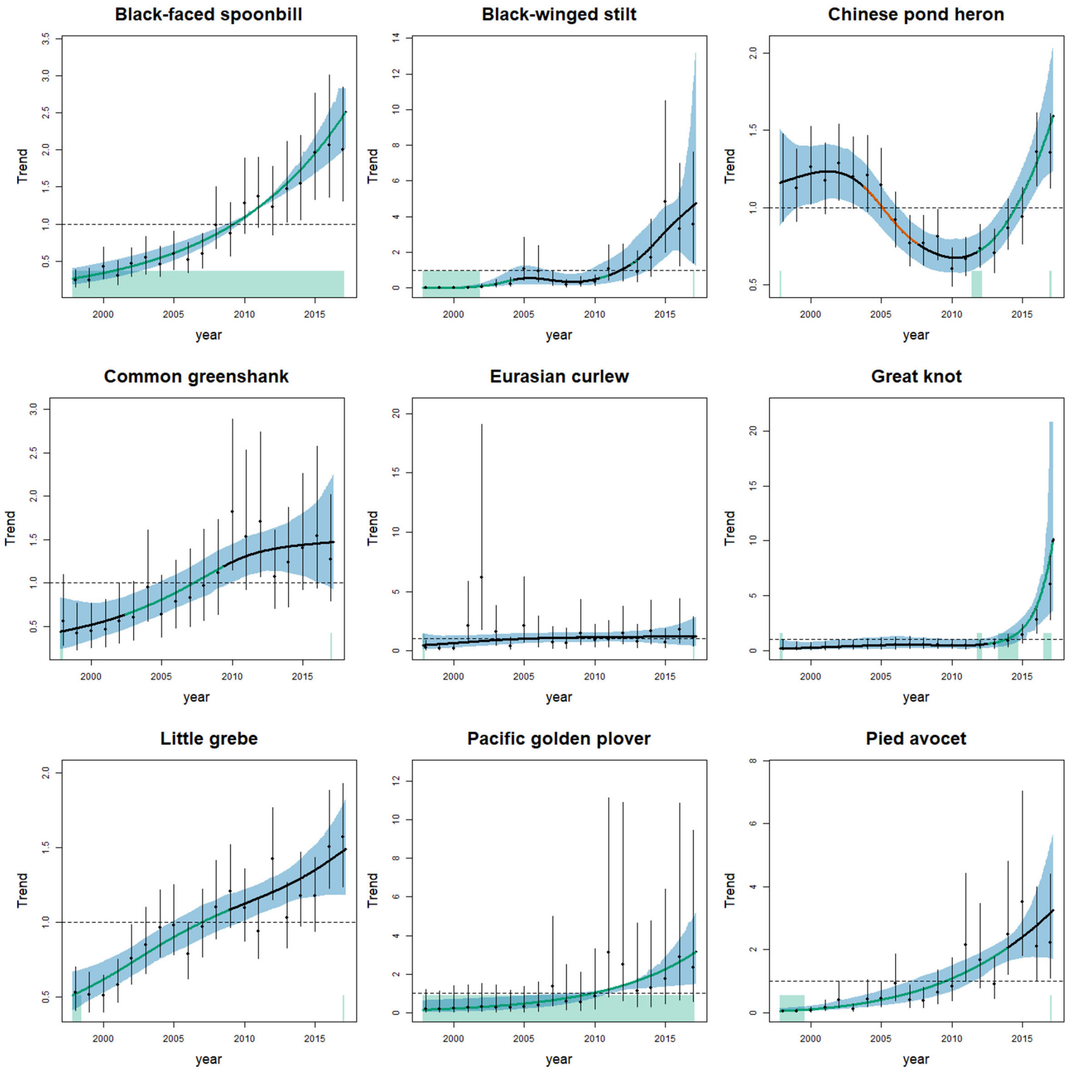

FIGURE 1 | Relative changes in the abundance of nine wintering waterbird species that showed a significantly increasing trend from 1998 to 2017 in the Deep Bay area. Solid lines indicate estimated long-term trends. The trend lines are colored for the period with significantly increasing (green) or decreasing (orange) trends. Vertical lines and blue shaded areas indicate the 95% confidence intervals. The green rectangle at the bottom of panels indicate periods with significantly positive curvature. The y-axis shows the partial residuals of year in the generalized additive mixed models.

increased from 2000 to 2008 (3–5%) and decreased from 2008 to 2018 (5–1%).

Body size, breeding habitat, breeding range, wintering habitat, reliance on the Yellow Sea, and dependence on aquaculture ponds were included in the most parsimonious models of PGLS (**Supplementary Table 2**). Species breeding in Southern Siberia declined more than those breeding in East Asia from 1998 to 2007 (Estimate = −0.204 ± 0.072; P = 0.008; **Figure 4**) and from 2008 to 2017 (Estimate = −0.166 ± 0.049; P = 0.001), whereas the species breeding High Arctic had similar trends with those breeding in the other two ranges in three focal periods (**Table 2** and **Figure 4**). From 1998 to 2007, species that relied on the Yellow Sea declined more (Estimate = −0.193 ± 0.073; P = 0.013). From 2008 to 2017, body size had a negative impact on population changes (Estimate = −0.003 ± 0.001; P < 0.001).

DISCUSSION

In this study, we quantified the 20-year population trends of wintering waterbirds in the Deep Bay area. The overall population trends of most study species (26 out of 42) are unknown (Wetlands International, 2021; **Table 1**)—this study supplements information to quantifying their population trends along the rapidly changing EAAF. Further, we identified species traits of waterbirds that correlated with their population trends, which shed light on the threats they experience across their breeding, migratory, and wintering grounds.

Declining Species and Threats

We identified 12 species that displayed apparent declines. Three of these species (Eurasian coot, northern pintail, and

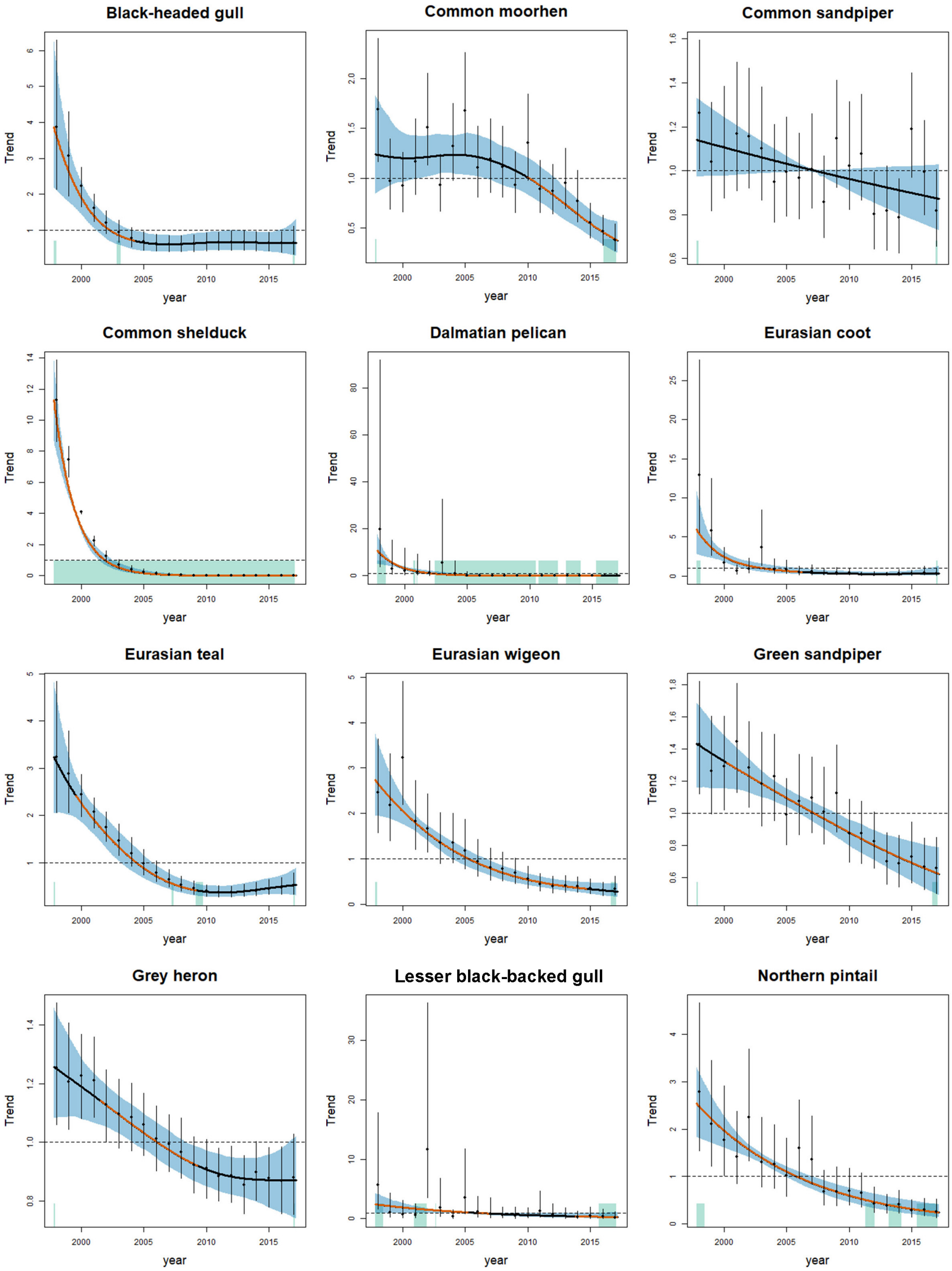

FIGURE 2 | Relative changes in the abundance of 12 wintering waterbird species that showed a significantly decreasing trend from 1998 to 2017 in the inner Deep Bay area. Solid lines indicate estimated long-term trends. The trend lines are colored for the period with significantly increasing (green) or decreasing (orange) trends. Vertical lines and blue shaded areas indicate the 95% confidence intervals. The green rectangle at the bottom of panels indicate periods with significantly positive curvature. The y-axis shows the partial residuals of year in the generalized additive mixed models.

Dalmatian pelican) were assessed to be declining in a regional assessment (Wetlands International, 2021), suggesting that they have dwindling populations along the EAAF and deserve immediate conservation attention. For the other nine declining species, it is uncertain if the decline we detected was confined to the Deep Bay area because of different trends observed in other wintering sites or limited population data elsewhere. It is of conservation concern that four (out of six) duck species declined significantly, including the common shelduck, common teal, Eurasian wigeon, and northern pintail. The common teal displayed opposite population trends in two wintering sites, decreasing in Japan and increasing in Poyang Lake, China,

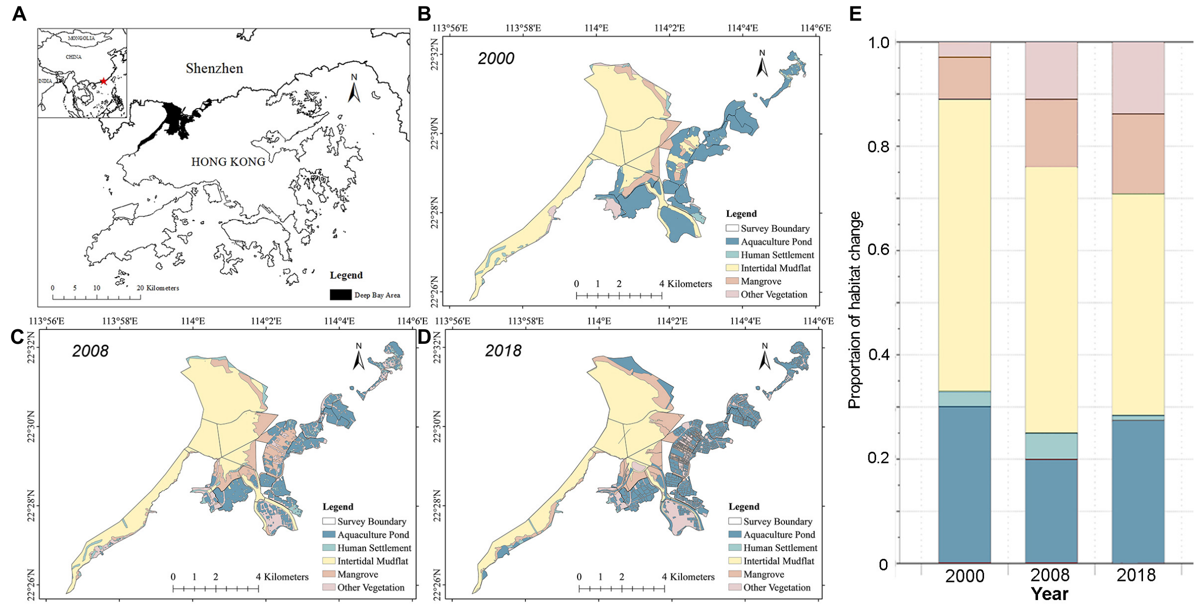

FIGURE 3 | Habitat maps of the study area in the Deep Bay area **(A)**, South China in **(B)** 2000, **(C)** 2008, and **(D)** 2018; and **(E)** proportion of habitat coverage in the study area in 2000, 2008, and 2018.

whereas the Eurasian wigeon decreased in Poyang Lake but remained stable in Japan (Kasahara and Koyama, 2010; Wang et al., 2017). The common shelduck declined dramatically, with no record after 2013. In contrast, recent survey data detected an increasing trend of the common shelduck along the coast of China between 2012 and 2019 (Choi et al., 2020). The Deep Bay area is one of the southernmost wintering grounds for the common shelduck. Other studies have shown that if population decline occurs, fewer birds move as far south for wintering, such that the decline can be first detected in the southernmost wintering ground (Cresswell and Bauer, 2014; Clemens et al., 2016).

Limited information is available for the other declining species (black-headed gull, lesser black-backed gull, common moorhen, common sandpiper, green sandpiper, and gray heron). In addition to the lack of long-term data from other wintering sites, the vast breeding range of these species also renders flyway-wide population estimation challenging, if not impossible. Continued monitoring at wintering sites, especially along the coast of China, will elucidate whether these species declining in the Deep Bay area are experiencing a species-wide population decline or changing wintering distribution.

Increasing Species and Habitat Transformation

In this study, we identified nine species (out of 42) that increased significantly. Such proportion of increasing species (21%) was higher than that in Australia (0%) (Clemens et al., 2016), but similar to that in Japan (29%) (Kasahara and Koyama, 2010). Among these increasing species, the black-faced spoonbill is the only species with sufficient data elsewhere supporting a population increase at a regional scale due to international conservation efforts for almost three decades (Sung et al., 2017; Wetlands International, 2021). For other species, there has been no information suggesting a growing population along the EAAF. In the Deep Bay area, there were considerably decline in coverage of intertidal mudflat (56–43%) whereas the changes were small for aquaculture pond (30–28%) and mangrove (8–15%) (**Figure 3**). However, the change of wetland area in the Deep Bay was small compared to that some stopover and wintering sites of waterbirds along the coast of China [e.g., the Yellow Sea area (>50% from 1950 to 2010) (Murray et al., 2015) and Yancheng Nature Reserve in Jiangsu Province (>72% from 1976 to 2007) (Zuo et al., 2012)] (**Figure 3**). Therefore, it is possible that the habitat degradation in other wintering sites led to redistribution of wintering populations, resulting in increasing trends for some species in Hong Kong.

Ecological Correlates of Population Trends

The low variation in wetland coverage may have contributed to our results that population trends of wintering populations were correlated with species traits associated with breeding grounds and stopover sites, rather than wintering sites. For the effect of breeding grounds, we found that species breeding in Southern Siberia declined more than those breeding in East Asia, while both had similar trends with the species breeding in High Arctic (**Figure 4**). Many species have vast breeding ranges; the difference may be related to large-scale environmental changes, such as climate change. A global study found that waterbird populations decreased more with decreasing latitude under climate change

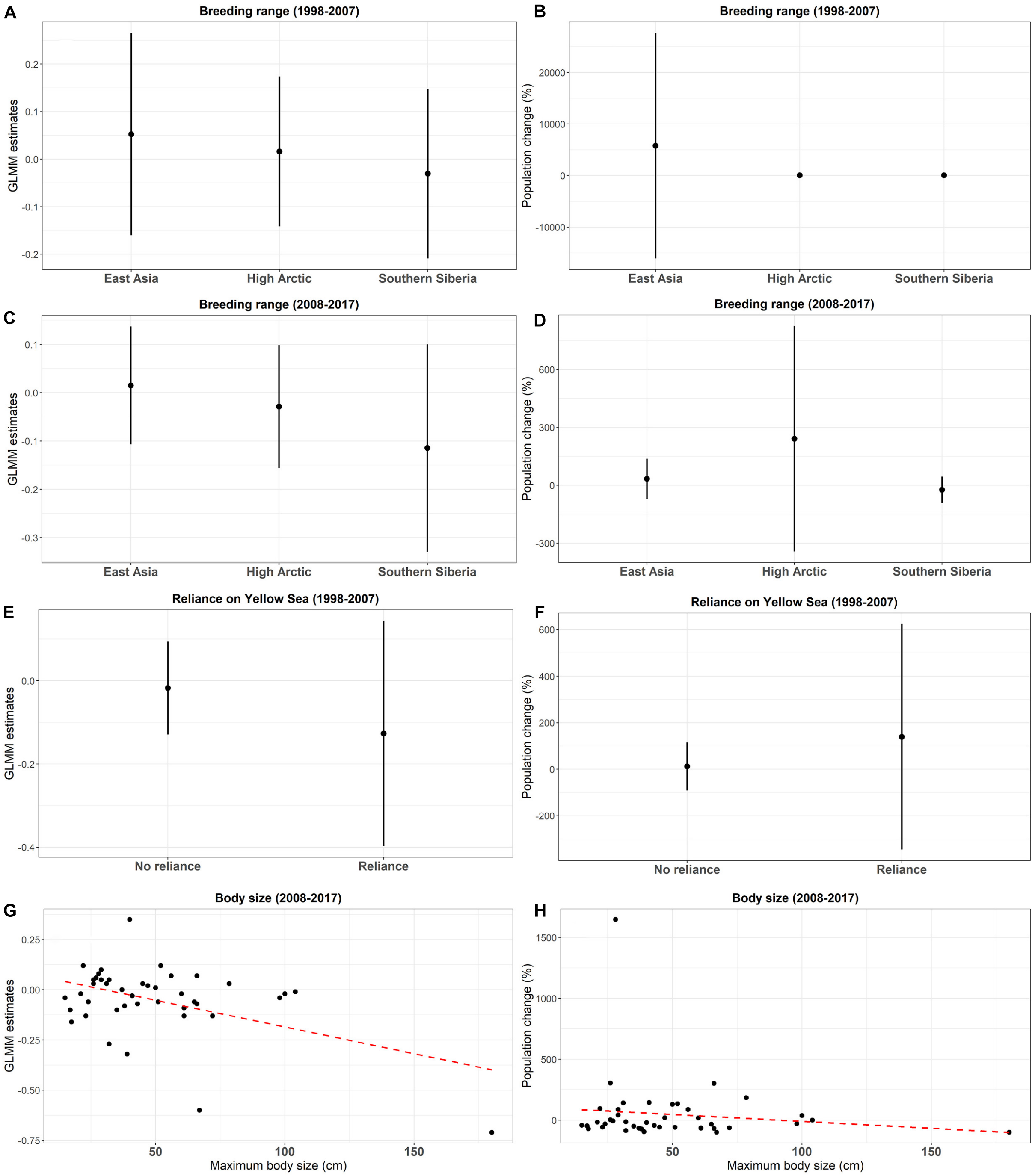

FIGURE 4 | Estimates of generalized linear mixed models (GLMM) (left column) and percentage of populations changes (estimated by generalized additive mixed models) (right column) for the significant species traits in the phylogenetic generalized least squares (PGLS) models for population trends of waterbirds in the inner Deep Bay area: panels **(A,B)** breeding range from 1998 to 2007, panels **(C,D)** breeding range from 2008 to 2017, panels **(E,F)** reliance on Yellow Sea from 1998 to 2007, and panels **(G,H)** body size from 2008 to 2017. For panels **(A–F)**, dots represent means and lines indicate standard deviations. For panels **(G,H)**, the red lines indicate linear regression lines for the relationship between GLMM estimates and percentages of population changes and body sizes.

(Amano et al., 2020), which is opposite of our findings. Alternatively, migratory distance correlates with breeding ground and may explain the influence of breeding ground. In a study of land birds in Finland, long-distance migrants declined more than short-distance migrants under a warming climate (Virkkala et al., 2018). It is also possible that Southern Siberia experienced region-wide habitat degradation, although such data are currently unavailable to evaluate this possibility.

TABLE 2 | Estimates of factors influencing population changes of 42 wintering water species in the Deep Bay area from 1998 to 2017 in the best phylogenetic generalized least squares models.

Factors	Estimate	SE	Z	P
1998–2017 (Pagel's λ = 0.152)				
Body size	−0.001	0.001	1.592	0.112
Breeding range (High Arctic)	−0.015	0.046	0.318	0.750
Breeding range (Southern Siberia)	−0.072	0.038	1.892	0.059
Yellow Sea	−0.040	0.035	1.134	0.257
Breeding habitat (freshwater)	−0.020	0.063	0.324	0.746
Breeding habitat (generalist)	−0.093	0.064	1.459	0.145
Aquaculture	0.010	0.016	0.665	0.506
1998–2007 (Pagel's λ = 0.582)				
Breeding range (High Arctic)	−0.168	0.086	−1.950	0.060
Breeding range (Southern Siberia)	**−0.204**	**0.072**	**−2.849**	**0.008**
Breeding habitat (freshwater)	0.196	0.131	1.494	0.145
Breeding habitat (generalist)	−0.085	0.107	−0.795	0.433
Wintering habitat (freshwater)	−0.208	0.133	−1.562	0.128
Wintering habitat (generalist)	−0.061	0.086	−0.714	0.481
Yellow Sea	**−0.193**	**0.073**	**−2.638**	**0.013**
Body size	0.000	0.001	0.365	0.718
Aquaculture	0.010	0.040	0.245	0.808
Mudflat	0.036	0.065	0.546	0.589
2008–2017 (Pagel's λ = 0)				
Breeding range (High Arctic)	−0.112	0.065	1.740	0.082
Breeding range (Southern Siberia)	**−0.166**	**0.049**	**3.361**	**0.001**
Body size	**−0.003**	**0.001**	**4.526**	**<0.001**
Wintering habitat (freshwater)	−0.068	0.084	0.809	0.418
Wintering habitat (generalist)	0.082	0.061	1.328	0.184
Yellow Sea	−0.099	0.057	1.745	0.081
Breeding habitat (freshwater)	−0.125	0.108	1.157	0.247
Breeding habitat (generalist)	−0.176	0.091	1.932	0.053

Bold rows indicates significant factors. Pagel's lambda (λ) indicates the strength of phylogenetic signals in the models.

We found that species that rely on the Yellow Sea declined more than other species, which agrees to previous studies along the EAAF (Amano et al., 2010; Clemens et al., 2016). Despite the tremendous ecological value of the tidal flats in the Yellow Sea area, tidal mudflats have declined by over 50% in the last 50 years, mainly due to coastal reclamation (Murray et al., 2015). Urgent conservation actions are essential to reverse the negative impacts of such rapid habitat loss and degradation. Extended from our study, there are more passage migrant species (both spring and autumn) relying on the Yellow Sea (e.g., curlew sandpiper, red knot, red-necked stint) than wintering species in the Deep Bay area, therefore it is worthwhile to investigate if reliance on the Yellow Sea also influences population trends of spring and autumn migrants.

In this study, larger species declined more than small species from 2008 to 2017, which might be related to hunting (Purvis et al., 2000). Both large and small waterbird species are hunted (Barter et al., 1997), however, larger species are favored by contemporary hunters (Gallo-Cajiao et al., 2020). Supporting this, the Dalmatian Pelican and ducks, the larger species in this study, has experienced a drastic decline across the EAAF, with hunting as the major threat (Batbayar et al., 2007; Ming et al., 2012). It should be noted that body size did not influence population trends from 1998 to 2007. As hunting intensity of waterbirds was probably similar or lower in recent years, we believe that there may be other contributing factors. Larger species are more vulnerable to population decline because of their lower fecundity (Purvis et al., 2000). Other threats (e.g., habitat degradation or climate change) in breeding, stopover or other wintering sites may lead to a more drastic population decline in larger species. Nonetheless, our results signal further studies to determine the effect of various threats, especially hunting, on waterbirds of different body sizes (Fox and Monette, 1992).

CONCLUSION

We quantified the wintering populations of 42 species, providing important baseline information to evaluate their flyway-wide conservation status. Conservation attention should be paid to the declining species, including ducks and larger species that are susceptible to hunting. Compared to other studies, a relatively high proportion of species exhibited increasing trends, providing evidence to support the continued protection against development of wetlands in the Deep Bay area. Population trends of wintering waterbirds were affected by factors associated with breeding and stopover grounds, particularly the negative impacts of habitat transformation in the Yellow Sea area. Our results enhance our understanding of the population status and threats to waterbird species, which allow us to formulate and prioritize conservation actions for waterbird species along the rapidly changing EAAF.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study does not involve any procedures that need ethical review and approval.

AUTHOR CONTRIBUTIONS

Y-HS, CP, TL, and YY: experimental design. CP, TL, PW, and YY: data collection. Y-HS, CP, TL, PW, and YY: data analysis. Y-HS, CP, PW, and YY: manuscript preparation. All authors contributed to manuscript revision, read 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/fevo.2021.658084/full#supplementary-material

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Modeling Potential Dispersal Routes for Giant Pandas in Their Key Distribution Area of the Qinling Mountains, China

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The national surveys on giant panda (*Ailuropoda melanoleuca*) population and habitat quality have shown a high-density population of this species in the Qinling Mountains, China. We investigated five adjacent nature reserves (NR), i.e., the key distribution area of giant pandas in the Qinling Mountains, to model and identify the potential dispersal routes for giant pandas. We hypothesized that giant pandas will spread to neighboring areas when the population of the species keeps increasing. Habitat suitability was firstly evaluated based on environmental and disturbance factors. We then identified source and sink patches for giant pandas' dispersal. Further, Minimum Cumulative Resistance (MCR) model was applied to calculate cost of movement. Finally, the Current Theory was adopted to model linkages between source and sink patches to explore potential dispersal routes of giant pandas. Our results showed that (1) the three large source patches and eight potential sink patches were identified; (2) the 14 potential corridors were predicted for giant pandas dispersing from source patches to the neighboring areas; (3) through the predicted corridors, the giant pandas in the source patches could disperse to the west, the south and the east sink patches. Our research revealed possible directional patterns for giant pandas' dispersal in their key distribution area of the Qinling Mountains, and can provide the strong recommendations in policy and conservation strategies for improving giant panda habitat management in those identified sink patches and also potential dispersal corridors.

Keywords: giant panda, the Qinling Mountains, dispersal route, modeling, minimum cumulative resistance, Current Theory

INTRODUCTION

The "corridor" theory illustrates passage ways for wildlife movement including dispersal routes, which are essential in ecology and conservation, especially in areas with road disturbance and human activities (Liu et al., 1999). Protection of endangered as well as vulnerable wildlife populations and their habitat requires numerous efforts, for instance, constructing the necessary corridors, helping wildlife species buffer against various disturbances, protecting the valuable gene bank and further maintaining the overall diversity of the ecosystems. Potential corridors are based on the functions of landscape connectivity and population dynamics—such as animal migration patterns and movements for better resources (Moilanen and Hanski, 2001). Haddad et al. (2003) pointed that linkages in the landscape are connected by dispersal routes and facilitate movement and dispersal of individuals, genes, and ecological processes.

However, the current natural environment has been strongly impacted by human activities. Natural landscapes are mostly fragmented due to human disturbing. As known, landscape fragmentation can result in a decrease in habitat availability, and a sharp increase in population density among few suitable habitat patches (May, 1975; Lovejoy et al., 1984). Fahrig et al. (2019) made a great discussion on the relationship between habitat fragmentation and biodiversity. The distance between remnant habitat patches and the degree of landscape connectivity are all important determinants for biotic response to fragmentation (Meurk, 1988). Thus, some individuals in the population would migrate to other habitat patches, i.e., emigration, in order to locally reduce population density (Chetkiewicz et al., 2006). Therefore, it is essential to get clear where could be the migration corridors as well as the habitat patches which could receive the migrating individuals.

Giant Panda (*Ailuropoda melanoleuca*) is a rare and vulnerable mammal species which is categorized as a first-class species for protection (Schipper et al., 2008; Swaisgood et al., 2010). They mainly distribute in six mountainous regions of Sichuan, Shaanxi, and Gansu provinces, China (Hu, 2001; Songer et al., 2012). The 3rd national survey on giant panda population and its habitat showed that there are 273 individuals in Shaanxi (SFA, 2006), with 192 individuals (70% of the Qinling giant panda population) in our studied key distribution area of giant pandas in the Qinling Mountains. This key distribution area includes five nature reserves (NRs): Changqing, Foping, Guanyinshan, Laoxiancheng, and Zhouzhi. Liu and Jin (2008) found out that there are two areas with a high population density of giant pandas, which are located in Changqing NR and Foping NR. Assuming that giant pandas in these two areas keep increasing their local population, some of their individuals would disperse out to the surrounding suitable habitat patches due to competitions on food, mate and space, etc., which gives rise to a natural phenomenon that limits the growth of the wild population of giant pandas (Reid et al., 1991; Gittleman, 1994). Where could be the suitable habitat patches and the potential routes for giant pandas to disperse among those patches? Although the giant panda has been lowdown its status from endangered to vulnerable species (IUCN, 2016), this species is still important to pay attention to since it is the flag species and also umbrella species in wildlife conservation in China as well as in the world.

The Qinling Mountains have experienced commercial logging from 70s to 90s in the last century (Liu et al., 2017b, 2018; Zhang et al., 2019), started the forest restoration after 1998 when the logging was banned. It has made certain forest fragmentation in some areas on the Qinling landscape. With the strengthened natural protection, the giant panda population is increasing according to the national surveys (SFA, 2006, 2015). Therefore, if dispersing of giant panda individuals occurs, they need to find their routes to disperse to the suitable habitat patches which can make them settle down under current fragmented environment. Dispersal is an important factor for the function and dynamic state of the endangered species (Hanski, 2001). Animal individual's dispersing out of the local source patches is also the most appropriate way for giant pandas to obtain suitable habitat, choosing the palatable bamboo as their food, therefore, slowing down the increasing rate of population in one given area (Lu et al., 2001; Pan et al., 2001). Therefore, existence of the dispersing routes for giant pandas and further for human to protect them are crucial, and some necessary restoration efforts can be made to them.

So this study aimed at exploring the potential dispersal routes in the key distribution area of giant pandas in the Qinling Mountains, on the base of identifying the suitable habitat patches as well as the sink patches for receiving the dispersing giant pandas potentially. We tried to achieve our aim by answering the following main scientific questions: (1) What is our modeling approach for identifying the potential dispersing routes for giant pandas? (2) Where are the source and sink patches of giant pandas? (3) Where are the potential dispersal routes among source and sink patches?

MATERIALS AND METHODS

Study Area

Based on the reasons described in the introduction, we selected five giant panda nature reserves (107°17′–107°58′, 33°19′–33°46′) who are neighbored each other: Changqing, Foping, Guanyinshan, Laoxiancheng, and Zhouzhi NRs as the study area (**Figure 1** and **Table 1**), which is the key distribution area of giant pandas with a high density population in the Qinling Mountains.

The five NRs in our study were established in different years according to the conservation progress and steps of China. Guanyinshan NR, originally a commercial logging bureau, was established lastly among these five NRs directly due to the logging ban to be enacted in 1998 in order to protect the forest and restore the habitat for giant pandas. The five NRs have similar environmental and climatic conditions. The summer season has a warm humid climate accompanied by the south-east ward monsoon, which makes the area has a northern sub-tropical floras with rich species composition (Liu, 2001). The study area grows a mixture of forest types including warm-temperate deciduous broadleaf forest and sub-tropical evergreen broadleaf forest. Mountainous terrain showed that vegetation changes with elevation increasing, such as deciduous broadleaf forest at low elevation, beech forest at middle elevation, and conifer forest at high elevation (Liu et al., 2017a). This area provides adequate habitat for wildlife survival (Liu and Li, 2008).

Data

This study used multi sources data including:

(1) Distribution data of giant panda signs (including feces, tracks, feeding signs, and individual occurring sites) from the 3rd national survey of giant panda population and

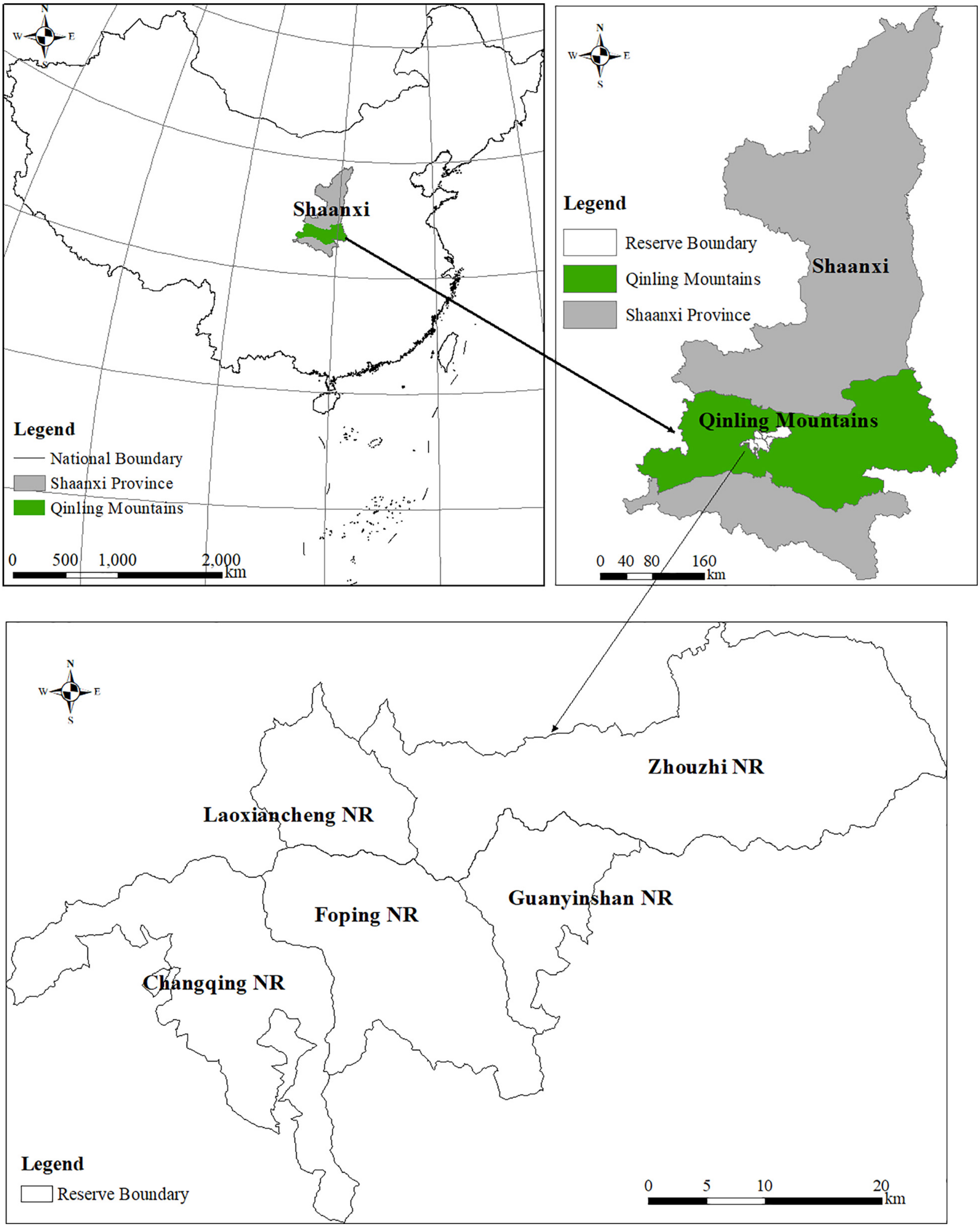

FIGURE 1 | Five nature reserves (NR) in the key distribution area of giant pandas in the Qinling Mountains, China.

TABLE 1 | Basic information of five giant panda nature reserves in the Qinling Mountains, China.

Nature reserve (NR)	Location	Year of establishment	Year assigned a national NR	Area (ha)	Elevation range (average) (m)
Changqing	107°17′∼107°55′ E 33°19′∼33°44′ N	1995	1995	29906	800∼3071 (2271)
Foping	107°40′∼107°55′ E 33°33′∼33°46′ N	1978	1978	29240	980∼2904 (1924)
Guanyinshan	107°51′∼107°58′ E 33°35′∼33°45′ N	2000	2013	11728	1150∼2574 (1424)
Laoxiancheng	107°40′∼107°49′ E 33°33′∼33°46 N	1993	2013	12600	1524∼2904 (1380)
Zhouzhi	107°39′∼108°19′ E 33°41′∼33°57′ N	1986	1988	56393	1196∼2996 (1180)

habitat provided by Shanxi Forestry Department, used for deriving the density map of giant panda signs with a resolution of 30 m × 30 m for later spatial calculation;

(2) Vegetation map with a resolution of 30 m × 30 m provided by Shanxi Forestry Department;
(3) Bamboo distribution maps with a resolution of 30 m × 30 m provided by five nature reserves related to this study;
(4) Terrain data including digital elevation data layer and its derived slope data layer and slope aspect data layer with also a resolution of 30 m × 30 m from Institute of Geographic Science, China Academic Sciences;
(5) Hydrological data with river distribution map from Shanxi Forestry Department, used for deriving the map of distance to rivers with a resolution of 30 m × 30 m;
(6) Human disturbance data including locations of medicinal-herbs collection, lacquer collection, bamboo shoot collection, hunting, road construction, and farming. from the 3rd national survey of giant panda population and habitat provided by Shanxi Forestry Department, used for deriving the map of distance to human disturbance with a resolution of 30 m × 30 m;
(7) Road distribution map provided by Shanxi Forestry Department, used for deriving the map of distance to roads with a resolution of 30 m × 30 m.

We used all these data to analysis habitat suitability, identify important patch areas as source patches where giant pandas dispersing from and sink patches where giant pandas dispersing into, and find potential dispersal routes between source and sink patches.

Software

Linkages Mapper toolbox in ArcGIS was a software program used in our study that needed proper conditions to be applied generally. Linkage design models such as isolation-by-resistance (IBR) model (McRae, 2006), least-cost path (LCP) model (Adriaensen et al., 2003) combine with the Current Theory were widely applied to predict pathways connecting population pairs or gene flow (McRae and Paul, 2007; St-Louis et al., 2014).

Integrative Modeling Approach

The whole modeling approach of our study contained four submodels (**Figure 2**). These submodels were taken to predict the giant pandas' dispersing pattern through analyzing habitat suitability (submodel 1), identifying source and sink patches (submodel 2), calculating the habitat resistance patterns (submodel 3), and final mapping the potential dispersal routes (submodel 4).

Submodel 1: Analyzing Habitat Suitability

An efficient method for modeling the individuals' dispersal was habitat suitability analysis to understand the nature conditions that the species confronted during migrating. The main eight habitat factors used were elevation, slope, aspect, vegetation, bamboo as well as distances to rivers, roads, and human disturbances (**Supplementary Figure 1**), similar with the research work done by Wu et al. (2013). In order to implement the spatial calculation, the same map resolution and projection is required. So, we standardized all GIS data layers in the same spatial projection and resampled these layers into 30 m × 30 m resolution to match with the resolution of vegetation map (30 m × 30 m). To obtain the suitability value, we applied expert assessment approach by which the weight assigning to different habitat factors has been often applied in giant panda habitat assessment, such as Ouyang et al. (2000); Li et al. (2005), Xu et al. (2005), and Wu et al. (2013). For map calculation, we used values of 0, 1, 2, and 3 to represent unsuitable, marginal suitable, suitable, and most suitable (**Supplementary Material**).

To integrate the eight habitat factors, we applied Analytic Hierarchy Process (AHP) which is based on the judgment of importance of each factor. The AHP method was developed by Saaty (1980), and has been often applied, such as Li et al. (2005); Nekhay et al. (2009), and Liu and Sun (2010). We divided the factors into three groups which are biotic factors (vegetation and bamboo), abiotic factors (elevation, slope, aspect, and distance to rivers), and disturbing factors (distances to roads and human disturbances). We then made comparison of importance between every two factors and formed the matrix of importance values. Then the weights of the eight factors were obtained by computing the maximum latent roots and corresponding eigenvectors of the matrix (Liu and Sun, 2010). The weights were 0.492 for bamboo, 0.240 for human disturbances, 0.093 for vegetation, 0.080 for

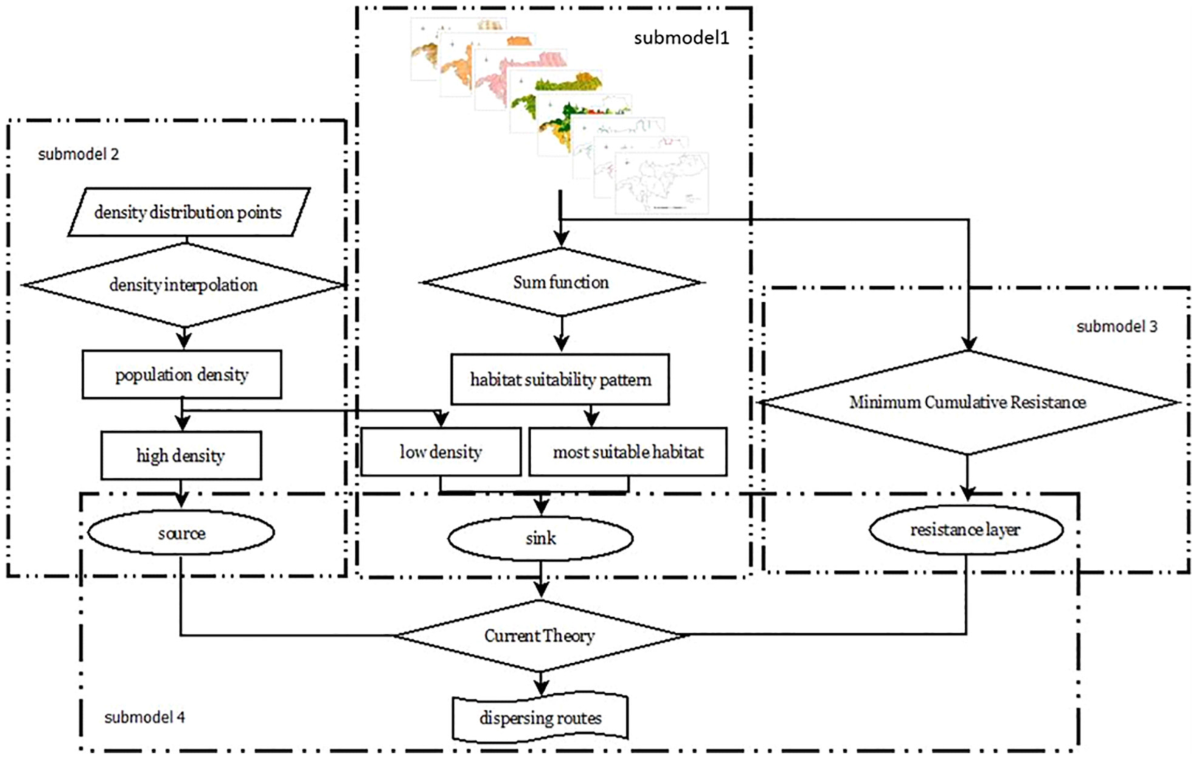

FIGURE 2 | Integrative modeling approach to map the dispersal routes for giant pandas in their key distribution area of the Qinling Mountains, China.

roads, 0.068 for rivers, 0.036 for slope, 0.012 for elevation, and 0.006 for aspect. For creating the final habitat suitability map, each pixel was calculating its suitability value by summing the eight layers through each habitat factor's suitability value multiplied by AHP weights (maintained two numbers behind decimal and then changed to integer by timing 100 for running GIS calculation). This map has a value range from 0 to 835. We reclassified this map into four categories with thresh hold values by using Natural Breaks (Jenks) method: (0∼208.75) as unsuitable, (208.75∼417.5) as marginal suitable, (417.5∼626.25) as suitable, (626.25∼835) as most suitable.

Submodel 2: Identifying Source and Sink Patches

In our research, source patches are the most suitable habitat patches with high-density signs of giant pandas to indicate more animal individuals, where the individuals disperse from and to other habitat patches. Sink patches are the suitable habitat patches with low-density signs of giant pandas, where can receive those dispersing individuals. Linkages between sources and sinks for dispersal have been described as landscape processes, where the matter and energy of source patches can outflow to sinks under viable conditions. Giant pandas disperse and spread to areas with abundant bamboo food, water, and other environment resources for its survival and reproduction.

We first created the density map of giant panda signs and further we used this map to indicate the density of giant panda population. Using the home range of the giant panda, about 6 km^2 (Hu et al., 1985), density maps were calculated using point density tool in ArcGIS with a searching radius of 1.38 km (home range area of 6 km^2). According to Liu and Jin (2008), two high-density areas all have giant panda sings of $\geq$4 sites/km^2. So we maintained to use these criteria to determine source patches. We further defined sink patches with giant panda sings of <4 sites/km^2 and continuous suitable habitat of $\geq$20 km^2.

Submodel 3: Calculating Habitat Resistance by Using MCR Model

When a species moves through various landscapes, it normally encounters obstacles on the way (Gabelli et al., 2006). The Minimum Cumulative Resistance (MCR) model was used for calculating the habitat resistance, which reflects the accessibility and possibility for the species to disperse and find suitable habitat. The MCR model was first proposed by Knaapen et al. (1992) and we applied the formula (1) which was modified by Yu (1998).

$$\mathrm{MCR} = \mathrm{fmin} \sum_{j=n}^{i=m} \mathrm{Dij} \times \mathrm{Ri} \qquad (1)$$

Dij is the spatial distance from source j to landscape unit i. Ri is the resistance of pixel i in landscape. We assigned the resistance in **Table 2** with values of 1, 4, 7, and 10 for eight habitat factors to represent four classes of habitat resistance, i.e., smallest, small, strong, and strongest. We then summed up the resistance values by using AHP weights to obtain Ri for each pixel. Min was the minimum resistance of the assessed pixel to all different sources, and f was the function coefficient between MCR and dispersing

TABLE 2 | Value assignment for habitat suitability classes and resistance analysis for the selected eight habitat factors in the key distribution area of giant pandas in the Qinling Mountains, China.

Factors (weights)	Grade	Habitat suitability/ class value	Resistance/ class value
Elevation (m) (0.012)	<1500	Marginal suitable/1	Strong/7
	(1500–1900)	Most suitable/3	Smallest/1
	(1900–2200)	Suitable/2	Small/4
	(2200–2700)	Most suitable/3	Smallest/1
	(2700–2900)	Marginal suitable/1	Strong/7
	>2900	Unsuitable/0	Strongest/10
Slope aspect (°) (0.006)	N	Unsuitable/0	Strongest/10
	NE	Marginal suitable/1	Strong/7
	E	Suitable/2	Small/4
	SE	Suitable/2	Small/4
	S	Most suitable/3	Smallest/1
	SW	Suitable/2	Small/4
	W	Marginal suitable/1	Strong/7
	NW	Unsuitable/0	Strongest/10
Slope degree (°) (0.036)	(0–5)	Most suitable/3	Smallest/1
	(5–20)	Most suitable/3	Smallest/1
	(20–30)	Suitable/2	Small/4
	(30–40)	Marginal suitable/1	Strong/7
	(40–50)	Marginal suitable/1	Strong/7
	>50	Unsuitable/0	Strongest/10
Vegetation type (0.093)	Coniferous forest	Most suitable/3	Smallest/1
	Mixed conifer-broadleaf forest	Most suitable/3	Smallest/1
	Deciduous broadleaf forest	Suitable/2	Small/4
	Mixed evergreen deciduous broadleaf forest	Suitable/2	Small/4
	Evergreen broadleaf forest	Suitable/2	Small/4
	Shrub	Marginal suitable/1	Strong/7
	Man-made forest	Marginal suitable/1	Strong/7
	Others	Unsuitable/0	Strongest/10
Bamboo types (0.492)	*Bashania fargesii and F. qinlingensis*	Most suitable/3	Smallest/1
	Fargesia nitida	Suitable/2	Small/4
	Fargesia dracocephala	Marginal suitable/1	Strong/7
	No bamboo	Unsuitable/0	Strongest/10
Distance to rivers (m) (0.068)	≤200	Most suitable/3	Smallest/1
	(200–500)	Suitable/2	Small/4
	(500–1000)	Marginal suitable/1	Strong/7
	>1000	Unsuitable/0	Strongest/10
Distance to roads (m) (0.080)	≤100	Unsuitable/0	Strongest/10
	(100–400)	Marginal suitable/1	Strong/7
	(400–1000)	Suitable/2	Small/4
	>1000	Most suitable/3	Smallest/1
Distance to human disturbances (m) (0.240)	≤100	Unsuitable/0	Strongest/10
	(100–400)	Marginal suitable/1	Strong/7
	(400–1000)	Suitable/2	Small/4
	>1000	Most suitable/3	Smallest/1

process. Habitat resistance surface was derived from cost distance toolbox in ArcGIS using resistance layer.

Submodel 4: Predicting Dispersal Routes by Applying the Current Theory

The Current Theory belongs to physics, in which circuits is defined as networks of nodes connected by resistors. When a voltage, V, applied across a resistor, the amount of current, I, flowing through the resistor depends on the voltage applied and the resistance, R (McRae et al., 2008). Nowadays, ecologists are thinking that ecological process like individual movement and gene flow can be related to resistance, current, and voltage in raster grids, which is like what the Current Theory described. Based on the calculated habitat resistance in submodel 3, the Current Theory was applied to predict giant pandas' dispersal routes by using formula (2).

$$I = \frac{V}{R} \tag{2}$$

Longer distance giant pandas disperse, the higher habitat resistance they would encounter. In order to simulate the density of individual movement like the current, the Current Theory was used to simulate the resistance layer. The greater the resistance is, the smaller the current (the dispersing flow of giant pandas) is. We regarded source patches as the starting locations and sink patches as the terminal locations of migration. The habitat resistance determines corridors between any pairs of source and sink patches. The implementation of the Current Theory was applied by the Linkage Mapper Toolkit in ArcGIS.

RESULTS

Reclassified Eight Habitat Factors

Table 2 showed the eight habitat factors and their detailed classes for habitat suitability assigned based on the expert knowledge. Based on this constructed expert knowledge system, the eight habitat factors were all reclassified with four classes: unsuitable, marginal suitable, suitable and most suitable with values of 0, 1, 2, 3, respectively. The eight new maps of these factors were obtained and shown in **Supplementary Figure 2**. They are ready for being used in spatial calculation of habitat suitability of giant pandas.

Suitability Pattern of Giant Panda Habitat

Habitat suitability map (**Figure 3**) showed that the area of the most suitable habitat was 101.8 km^2 in total and shown by three main patches: the largest one 68 km^2, the second largest one 24 km^2, and the third largest one 10 km^2. The most suitable and suitable habitats were distributed in the western part of the study area. The most suitable patches were mainly in Foping, Changqing and Laoxiancheng NRs, while marginal suitable and unsuitable areas were in Zhouzhi NR and the east part of Guanyinshan NR.

Source and Sink Patches

We used the created density map of giant panda activity signs to reflect the density of giant panda population. From this sign density map, we mapped the source patches and the sink patches (**Figure 4**). **Figure 4A** showed that the largest population patches were located in Changqing and Foping NRs, and the highest density of giant panda signs reached 8 sites/km^2. Three identified crucial large source patches contained two in the north of Changqing with areas of 7.5 km^2 and 11.7 km^2, and one in the middle of Foping with an area of 19.0 km^2. Some small source patches appeared separately in the different locations: two of them in Changqing with areas of 2.1 km^2 and 0.7 km^2, and two of them in Foping with areas of 1.5 km^2 and 1.8 km^2. Zhouzhi and Laoxiancheng NRs had one smaller source patch for each with areas of 0.8 km^2 and 1.9 km^2.

Figure 4B showed the identified sink patches and 8 big patches with an area of $\geq$20 km^2 were found in the study area, including three patches in Changqing with areas of 28.7 km^2, 34.8 km^2, 47.5 km^2, one patch in Foping with an area of 22.1 km^2, one patch in Laoxiancheng with an area of 32 km^2, two patches in Zhouzhi with areas of 24 km^2 and 39.1 km^2, and one patch at the junction area of Foping and Guanyinshan with an area of 97.8 km^2. Meanwhile, we found four smaller sink patches with areas all less than 20 km^2 where giant pandas can also potentially disperse to.

The total areas of the source and sink patches are 47.3 km^2 and 325.8 km^2, respectively. The large sink areas indicates that the population of giant pandas in the study area does have the space to increase potentially.

Resistance Patterns for the Dispersal of Giant Pandas

The final resistance cost pattern calculated by MCR, to indicate the difficulty for giant panda to pass through the landscape, was shown in **Figure 5** in which each pixel reflected the cost of migration to the nearest habitat sources. It shows that there exists less cost for giant panda to disperse in the west part of the study area, while the high resistance occurs in the eastern part such as Zhouzhi. Based on this resistance patterns, it was possible to identify areas where giant pandas would potentially disperse to.

Dispersal Routes for Giant Pandas

Figure 6 showed the spatial distribution of our predicted dispersal routes by the Current Theory model. We found the potential dispersal routes between three large source patches and eight large sink patches where the least distance and cost exist. Between source and sink patches, we found 14 routes in the study area in the key distribution area of giant pandas in the Qinling Mountains. Based on three large source patches, the most important potential dispersal routes for giant pandas were from the east of Changqing to the west, to the middle, to the south of Changqing, to the west of Foping and to the northeast to Laoxiancheng. The second-most important routes were from Foping to the west of Foping, to the southwest of Changqing,

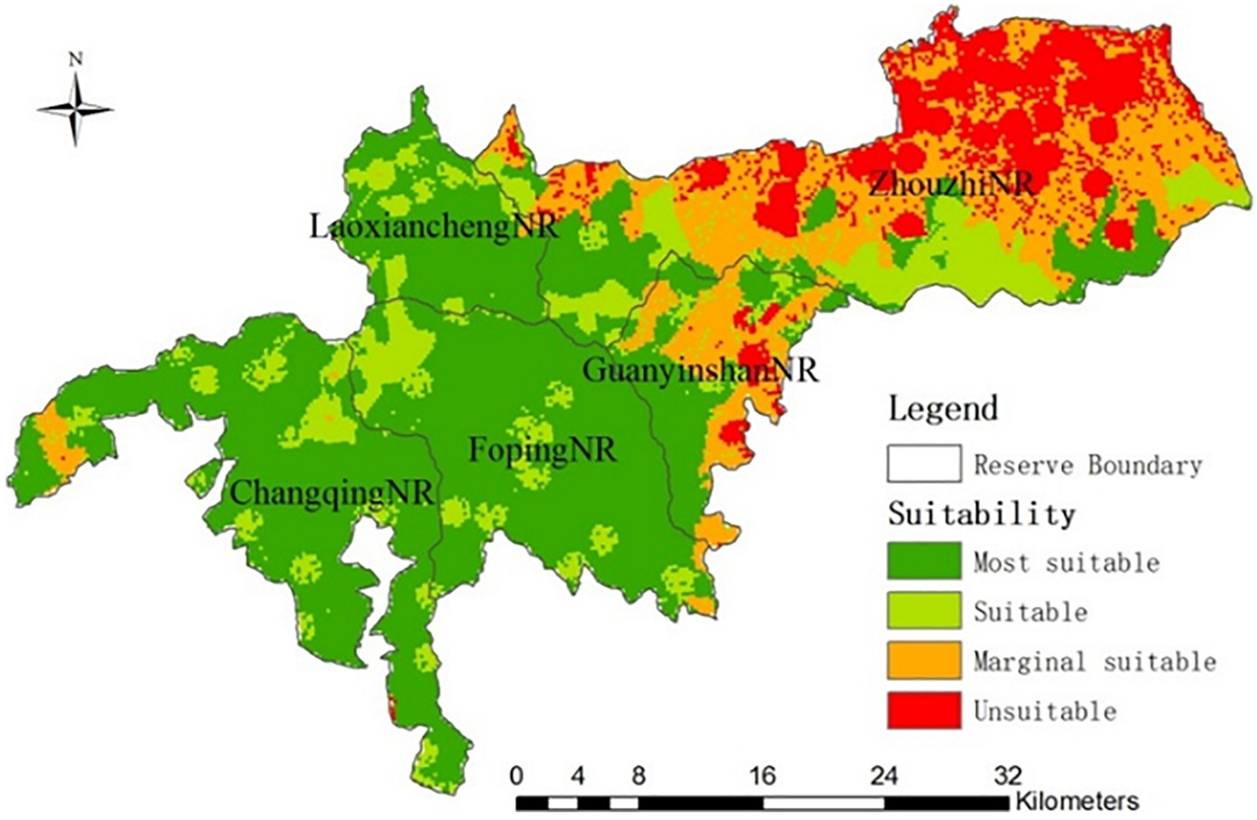

FIGURE 3 | The suitability map of the key distribution area of giant pandas in the Qinling Mountains, China.

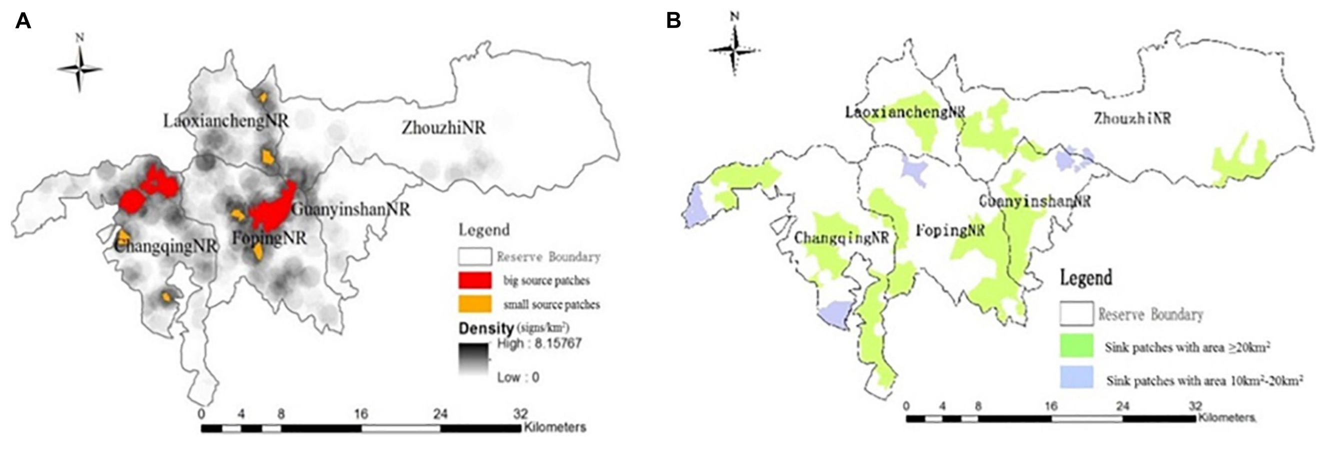

FIGURE 4 | Maps of source patches **(A)** and sink patches **(B)** in the key distribution area of giant pandas in the Qinling Mountains, China.

to the junction area of Foping and Guanyinshan, to the south of Laoxiancheng, and to the west of Zhouzhi, to the west of Guanyinshan and further to the east of Zhouzhi. The center part (with blue color in **Figure 6**) of the predicted potential dispersing routes has the high "current with circuits" with an ecological meaning of that giant pandas are easy to disperse in these center parts. This showed the possible intensity of giant pandas' dispersal in the corridors with blue and orange representing high and low intensity of animal dispersing, respectively.

DISCUSSION

We obtained three major findings: (1) an integrative modeling approach established with applying three submodels to predict giant pandas' dispersal routes; (2) the three large source patches and eight sink patches mapped by this integrative model; and (3) the 14 dispersal routes identified by the Current Theory model. We reached our proposed three research objectives.

Importance of Predicting the Potential Dispersal Routes for Giant Pandas

Fragmentation generally results in a discontinues landscape that consists of remnant areas of native vegetation surrounded by a matrix of agricultural or human developed land (Saunders et al., 1991). As known land use change can lead to conversion of ecological processes and reduction of biological diversity (Graham et al., 2006). Human disturbances changed the landscape of our research area, where there were increasingly more human residents in the northeast Zhouzhi and there was a national-level road (G108) in the east of Guanyinshan. So the resistance value was high in the east part of study area. Along with the essential dispersal route (from the source of Foping NR to the east sink in Zhouzhi NR), human disturbances have an impact in both sides of this route, thus, a necessity for conservation and restoration such as decreasing traffic flow, conducting more tunnels or ecological corridors in giant panda habitat should get more attention.

Dispersal route construction has been proposed as a measure to enhance the long-term genetic diversity (Schonewald-Cox et al., 1983), as well as viability of the regional panda population growth (Yin et al., 2006). Establishing, enlarging, and networking among nature reserves, and strengthening supervision and management in the predicted potential dispersal routes with populations of giant pandas were essential for decision-makers (Diamond, 1975; Diamond et al., 1976; Xu et al., 2006, 2014). From findings of our study, government planning departments should find out the low resistance dispersal routes especially in the boundary regions of NRs (like the junctions of Laoxiancheng-Foping-Zhouzhi and Foping-Laoxiancheng-Changqing), and further strengthen the effort of bamboo restoration and continuous supervision.

Rather than find corridors by adding linkages among sinks and sources, it is necessary to compare relative conservation priority of all linkages through conservation planning research (Possingham et al., 2000). Other researchers only found the cost of dispersal throughout different habitats and a linear path for giant pandas (Li et al., 2010). However, we found 14 polygon dispersal routes, where more complex spatial suitability analysis model and the physical theory were applied to effectively weight the importance of each route. Through these efforts, the influence from disturbing factors can be minimized (Zeller et al., 2012), and the structural and functional quality of ecosystem could be improved (Crooks and Sanjayan, 2006).

Conserving regional habitat connectivity could facilitate recovery and reproduction for many biological population (Bian and West, 1997; Carroll et al., 2012). Thus, we can implement ecological restoration of the damaged and threatened ecosystem; therefore, enhance the capacity and stability of the ecological system (Liu et al., 2015). More nature reserves and conservation stations should be established in the north and east of Changqing, meanwhile, we must reduce the human disturbance in Zhouzhi. Furthermore, improving habitat quality shouldn't be ignored because this measure could get higher conservation returns than only increase the size and optimized the components of patches (Prugh et al., 2009).

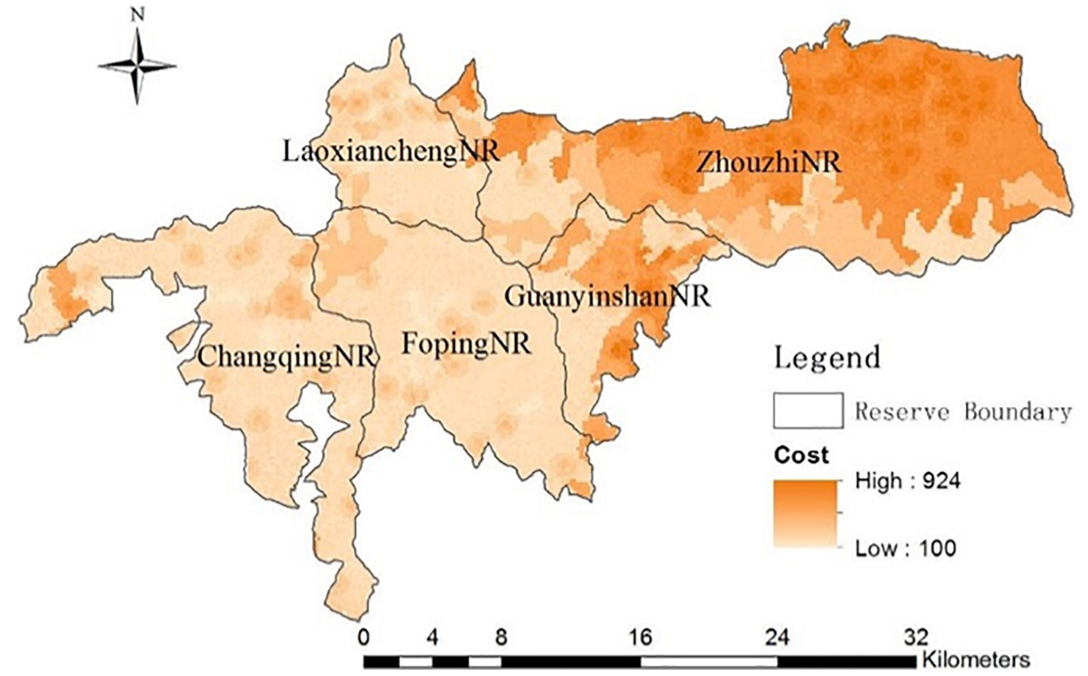

FIGURE 5 | The summed minimum resistance cost pattern in the key distribution area of giant pandas in the Qinling Mountains, China.

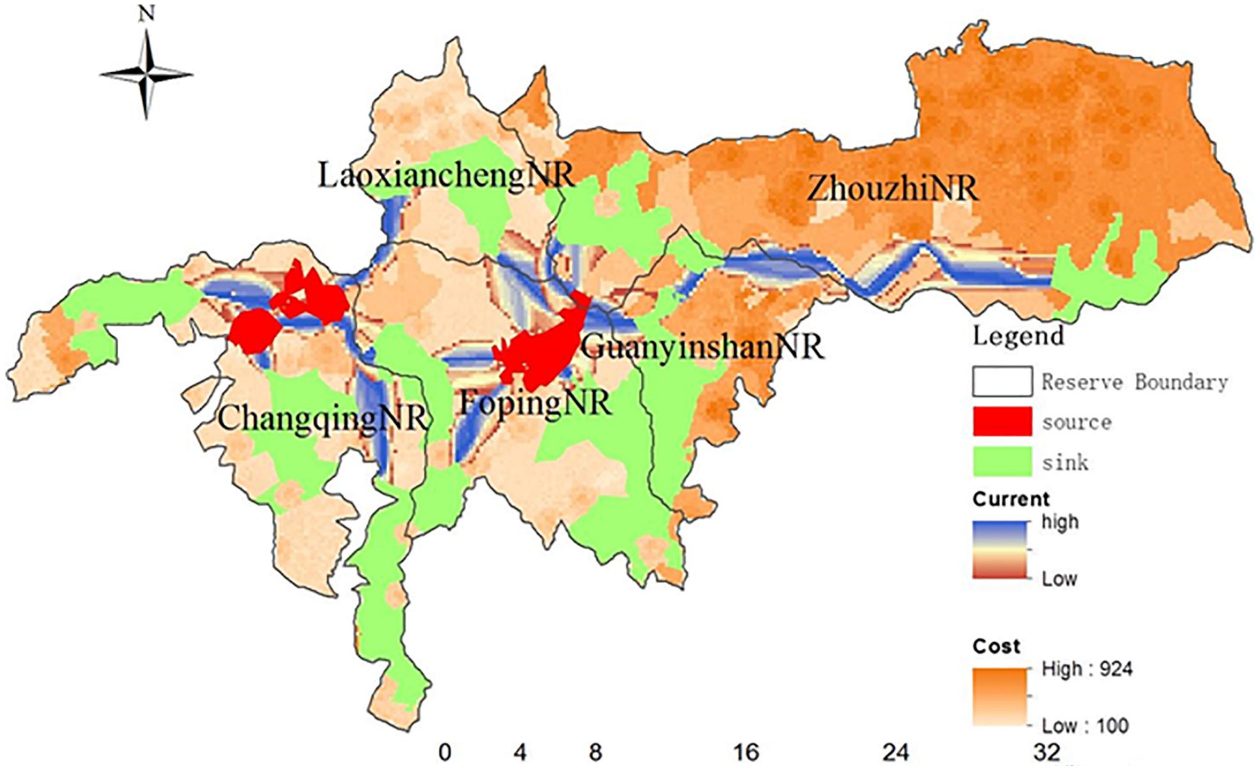

FIGURE 6 | Giant pandas' dispersal routes in the key distribution area of giant pandas in the Qinling Mountains, China.

Key Work in Predicting the Dispersal Routes

Source patches, sink patches, and resistance are necessary to be defined based on empirical environmental data. Source patches represent the starting locations of an animal's movement, which can be expressed in GIS as discrete points, lines and polygons (Oh and Jeong, 2007; Liu and Li, 2008). Sink patches have overall good habitat suitability, and can act as potential sites for occupancy of animals. Resistance can be reflected through calculation of cost, which is quantified by ranking the pixels in GIS.

The MCR model, a way to calculate cost, has been applied in a number of fields, such as landscape eco-planning, landscape ecological suitability assessment (Yu et al., 2005; Liu et al., 2010), landscape pattern analysis (Nelson et al., 2009), and landscape accessibility analysis (Wang et al., 2007; Gan and Hu, 2008). Liu and Li (2008) used an applied least cost paths model, similar to the MCR model, to make a functional division for Laoxiancheng NR. MCR model was also applied to calculate the amount of ecological land that meets the demand of socioeconomic development and ecological protection (Li F. et al., 2015). The results of our study illustrated the initial dispersing directions with a low resistance cost, whereby they stop dispersing further when encountering areas with high resistance (Sawyer et al., 2011). So MCR model is aiming at quantifying multiple environmental factors and find an optimal solution for conservation or restoration of migration corridors.

For two sub-models' processing, i.e., submodel 1 and submodel 3, we applied AHP approach to develop a system for classifying the habitat factors in order to evaluate the suitability and also the resistance of the habitat. AHP model is a very experienced approach and has been applied in many different fields which tried to calculate the weights based on the eigenvalues (Liu and Sun, 2010) for various indicators or factors through comparison the importance between any two indicators. While we admit that such comparison could be a subjective process, experienced experts will guarantee the robustness of the results as only two factors were included in the comparison. To invite more knowledgable experts might further improve the model results and give a proper pattern of giant panda dispersal routs, whereas trade-off needs to be considered between the model output and extra time cost.

The Current Theory is a reliable, efficient method to identify, further protect, restore, and construct connectivity among landscapes (Lacher and Mares, 1996). It can simulate the random movement of population by taking into account routes between patches through a connectivity parameter called resistance distance (McRae et al., 2008; Walpole et al., 2012). Qing et al. (2016) created corridors among Xiaoxiangling Mountains, which research combined the Maxent distribution model and the Current Theory and took spatial distribution of giant panda into consideration. Wang et al. (2014) conducted least-cost and circuit models to identify giant panda dispersal paths among Huangbaiyuan NR and Niuweihe NR, and compared the dispersal cost under different scenarios. Comparing with previous study, we not only identified corridors among the patches as well as reserves, but also predicted possible intensity of dispersal in the corridors.

Limitations From Small Habitat Patches for Animal Dispersal

From all source patches obtained, we easily found six small source patches (**Figure 4A**), which were not able to calculate out the optimal linkages between sources and sink patches. Two reasons are (1) the source patches were too small to react to any changes in the landscape; in addition, negative calculations confirmed that the least cost paths and corridors between small source and sink patches were unobtainable, (2) habitat and resistance around small source patches have a low spatial heterogeneity, and consequently no suitable corridors occur among sources and sink patches. Therefore, giant pandas' capability and probability of moving among these six small habitat patches was unfortunately limited. These two reason were found and explained for the first time.

The Evidence of Giant Panda Using the Predicted Potential Dispersal Routes

Data from the 4th national survey of giant panda provided a very strong evidence on giant pandas' using our predicted potential dispersal routes (**Supplementary Figure 3**). From this spatial pattern, dispersal trend could be revealed through comparing distribution in two periods of the 3rd and 4th national surveys. The 7.6% signs from the 4th national survey in the Qinling Mountains (Unpublished) appeared in the identified dispersal routes. This indicated giant pandas used to minimalize the resistance in their dispersal process and tried to control the distance they move and the energy they spend. From the signs occurred eastward in the dispersal routes in **Supplementary Figure 3**, the 38% signs appeared in the long distance routes, which evidenced they had used this long distance route from source patches in Foping NR and headed to sink patches in the east of Zhouzhi NR. So the 4th national survey's data helped us verify the utilization of dispersal routes. Lack of distribution data, further researches by applying the infrared cameras are necessary to record the giant pandas' activity patterns and so to provide strong proof to their utilization of dispersal routes. Due to limitation of environment data, giant pandas' habitat environmental maps can be supplemented in the future by remote sensing inversion models developed to provide spatial continuous, high-resolution environmental layers (Li et al., 2013; Li Z. et al., 2015).

CONCLUSION AND MANAGEMENT IMPLICATIONS

This study successfully applied MCR and Current Theory models to predict giant pandas' potential dispersal routes on the southern slope of the Qinling Mountains. The results showed that giant pandas in high-density areas may disperse multi-directionally to neighboring sink patches from the source patches. The three large sources, eight sinks, and 14 dispersal routes between sources and sinks were identified among five NRs. We showed the potential linkages between five NRs, and mapped the intensity and direction of giant pandas' dispersing.

Our research revealed possible directional patterns for giant panda dispersal in the key distribution area of the Qinling Mountains. This can provide the scientific support to facilitate planning and managing of giant panda NRs, encourage them to reduce the impacts from human disturbance directly on the predicted dispersal corridors and sink patches, for instance, either planting suitable bamboos in the sites where need more food resources for giant panda or thinning the bamboo stems in the places where provide some space for giant panda to pass and get new bamboo shoots. In these cases, more suitable habitat can be maintained for giant pandas.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because since the elevation-related data are not allowed to share publicly. Requests to access the datasets should be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

XL, LmL, and LnL completed the research and the manuscript drafting. XL kept editing on the manuscript. XJ has provided us the valuable dataset and some ideas on the giant panda dispersing. MS helped with the manuscript quality improving. 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/fevo.2021.636937/full#supplementary-material

Supplementary Figure 1 | The raw data layers used for modeling: **(A)** elevation, **(B)** slope degree, **(C)** slope aspect, **(D)** vegetation, **(E)** bamboo types, **(F)** rivers, **(G)** roads, **(H)** human disturbances.

Supplementary Figure 2 | The reclassified data layers with suitability: **(A)** elevation, **(B)** slope degree, **(C)** slope aspect, **(D)** vegetation, **(E)** bamboo type, **(F)** distance to rivers, **(G)** distance to roads, **(H)** distance to human disturbances.

Supplementary Figure 3 | The eastward giant pandas' dispersal routes used by giant panda based on data from the 4th national survey.

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Limestone Quarry Waste Promotes the Growth of Two Native Woody Angiosperms

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Limestone quarrying is an active mining practices generating bulk of solid remains and altering the habitat by the removal of plants; however, the utilization of such waste for the growth of plants has not been investigated much. The present study aimed to evaluate the effects of limestone quarry waste on the growth of two native plants by analyzing its physicochemical properties and utility for plantation purposes, while determining whether mitigation measures would be required for the habitat restoration of quarry site. Two species, *Acacia modesta* and *Adhatoda vasica* were selected from the quarry site habitat. These plants were grown in different proportions of quarry waste, and garden soil was used as a control. Growth was assessed by recording plant height, number of branches per plant, root and shoot length, and total biomass. We also analyzed the N, P, K, Na, Ca, and Mg contents of the root and shoot tissues of both species. We found a significant increase in plant height (1.24- and 1.19-fold greater than controls for *A. modesta* and *A. vasica*, respectively). Differences in the number branches, root, shoot length, and biomass were also found. A significant and positive relationship was found between the mineral content in roots and the total plant biomass across both species. We conclude that (1) the mining solid waste contained the necessary minerals for the studied plant species and no amelioration would be required for restoration of such sites with the selected indigenous plants; and (2) the quarry waste promoted the growth of the two selected species. The results of the present study can be used to plan habitat restoration in limestone mining areas that have lost plant cover.

Keywords: *Acacia modesta*, calcium, mining, habitat restoration, biomass, mineral uptake

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INTRODUCTION

Mineral deposits are finite and will eventually be exhausted (Jowitt et al., 2020). Mining of minerals is a temporary land use change that alters the original soil strata and produces large amounts of soil remains (Johnson et al., 1994; Basommi et al., 2016). The increasing demand for minerals is causing expansions in mining areas; at present, 57,277 km^2 is being used for mining operations on a global scale (Maus et al., 2020). In many mining operations, waste production, and its disposal can cause extensive and long-lasting disturbances on the natural ecological processes such as changes in species composition, primarily due to unstable substrates for plant growth (Ballesteros et al., 2014; Virah-Sawmy et al., 2014; Reta et al., 2018; Sonter et al., 2018). On a large scale, mining operations impact both the abiotic and biotic components of particular ecosystems (Hester et al., 1994; Millennium Ecosystem Assessment, 2005). The abiotic impacts include changes in soil profile, nutrients, texture, and other physicochemical properties such as pH electrical conductivity and production of particulate matter due to crushing of rocks. The assessment of the physicochemical properties of solid waste is essential to understand its fertility status. Khan et al. (2020) and Okereafor et al. (2020) found that some mining operations can release toxic elements such as arsenic, lead, and nickel, which can pollute the soil and water. Mining can impact on ecology through habitat loss and fragmentation (Gajic et al., 2018). Ntshane and Gambiza (2016) reported 20–30% habitat loss due to mining in South Africa. Sonter et al. (2015) found that a significant amount of carbon emissions ascribed to deforestation was linked with charcoal mining. Similarly, mining in Indonesia resulted in a sixfold increase in habitat loss (Paull et al., 2006).

The utilization of large amounts of mining waste for establishing vegetation in mining areas depends on its physicochemical properties. As a general rule, only a few stress-tolerant plant species are able to grow in postmining substrates (Zhang et al., 2017). This is mainly due to high concentration of minerals, scarce availability of organic matter, and moisture and disruption of soil strata (Zeleznik and Skousen, 1996; Gorman et al., 2001; Grant and Koch, 2007; Skousen and Zipper, 2014). Furthermore, the mining areas can also be inhabited by some exotic species, such as Monty et al. (2019), who recorded the significant invasion of alien plants on limestone quarry wastes, which resulted in indigenous species habitat loss. Additionally, limestone quarries can cause soil erosion and dereliction of mined sites (Langer, 2001). A rapid solution for avoiding soil erosion and plant invasion is the plantation of native species for rehabilitating postmining landscapes. Native plant species can repopulate these postmining landscapes and eventually restore native vegetation.

The social and legislative context in many parts of the modern world means that some form of postmining land use and natural ecosystem reestablishment goals will be set before the permission is granted for a new mine (Skousen et al., 1994; Skousen and Zipper, 2014). Species reestablishment and sustainability are the major factors that determine the success of ecological restoration (Rodríguez-Seijo and Andrade, 2017; Li et al., 2018; Song, 2018). Species selection for restoration can be based on the chemical analysis of plant tissues, which can be indicative of species capacities to uptake the minerals in the solid waste of mining sites. Species more apt at mineral uptake can be effective in site restoration and more easily established (Marcus et al., 2018) such plant-tissue analyses that can be helpful in predicting plant growth. Minerals in mining waste can have positive or negative impacts on plant growth, e.g., plant height and branch sprouting (Jim, 2001; Gajic et al., 2018).

Restoration actions should aim to reestablish ecosystem services through species diversity and survival (Montoya et al., 2012). Appropriate measures, such as the possible solid waste amelioration with fertile soil and the selection of suitable species for mineral uptake, should be taken for the utilization of mining solid waste to revegetate the mining site. These cannot only reduce the impacts of mining on such transformed habitats but also increase the population sizes of the selected species (Macdonald et al., 2015; Gentili et al., 2020). Such species are suitable for ground stabilization and to green a barren anew (Bengson, 1995; Yirdaw and Luukkanen, 2003). Furthermore, being adaptive to local environmental and edaphic conditions, these native species can be established as self-sustaining plant communities. Therefore, the use of native plant species for landscape restoration in mining areas or to replace exotic plants can help to reverse the trend of species loss (Richards et al., 1998; Román et al., 2015).

Pakistan has extensive deposits of limestone in the provinces of Punjab, Sindh, Balochistan, and northern areas. These deposits are located in geological formations that range in age from the pre-Cambrian to the Eocene (Hamid et al., 2012). The presence of these deposits attracts mining companies, resulting in accelerated habitat change for the indigenous plants (Drewes et al., 2007). In the limestone quarry, *Acacia modesta* forms a bi-species climatic climax community with *Olea cuspidata*, while *Adhatoda vasica* and *Dodonea viscosa* both are understory shrubs (Champion et al., 1965). All of these species are valuable sources of livelihood for the local community as they are a source of traditional medicines, fodder, and animal grazing and control soil erosion (Khan, 2013; Khan et al., 2019). Considering the ongoing acceleration of mining impact on natural vegetation, there is a need to utilize the mining solid waste. As the quarry sites with waste heaps become barren, revegetation may begin by planting more productive species such as herbs and shrubs of the area, capable of using the existing postmining solid waste (Swanson et al., 2010). The present study was designed with the following objectives:

1. To analyze the physicochemical properties of solid waste from the limestone quarry.
2. To assess the effects of this waste on the growth of selected plant species.

As the restoration of an abandoned site with limestone waste may follow the natural succession, we hypothesized that the shrub *A. vasica* being the early colonizer may accumulate more minerals in its tissues than *A. modesta*.

MATERIALS AND METHODS

Study Site and Quarry Waste

The study was carried out in the limestone quarry of Tobar, in the Jhelum District of Pakistan, located in the salt range (**Figure 1**). This site is 9 km away from the chemical production facility of a multinational company, where limestone is one of the raw materials used in the manufacturing process. The quarrying operation produces a large amount of solid waste at a rate of 88.18–132 tons/day (Hayyat, 2008). Solid waste from limestone quarrying has a variety of uses, ranging from the manufacturing of

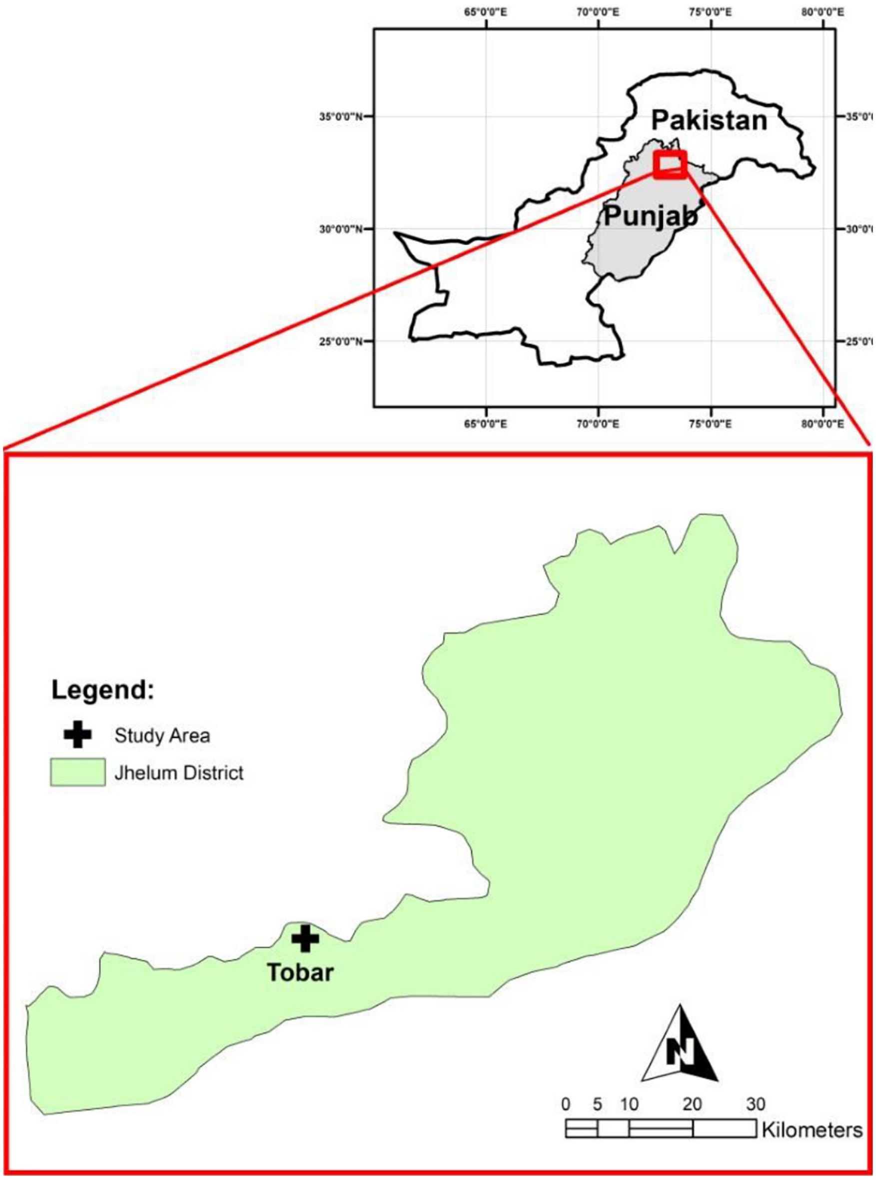

FIGURE 1 | The location of study site in the Tobar area, Punjab, Pakistan.

masonry blocks to cement production (Felekoglu, 2007; Turgut, 2008). In Pakistan, limestone is cheap and its transport expensive; therefore, the use of limestone quarry waste is limited. The average annual production of limestone is 9.95 tons in Pakistan. Mining has a significant potential for the employment of local people, but the related policies are to be redesigned for sustainability (Government of Pakistan, 2004; Ali and Rehman, 2020).

Waste Material

Solid waste was collected from the mining quarry sites located in Tobar, Punjab, Pakistan (**Figures 2a,b**). Ten different 30-kg samples of waste were collected randomly from different locations of the waste heap, avoiding particle size >3.0 mm. The samples were mixed to form a composite sample, which was then used for physicochemical analyses.

Physicochemical Analysis of Soil and Plant Tissues

In the laboratory, solid waste samples were crushed in a grinding mill. The particle size of solid waste from the quarry was determined by sieve, passing 0.25–2.25-mm-diameter particle sizes (McLean and Ivimey-Cook, 1952). To ensure the availability of solid waste in the treatments, the material retained on the sieve was reground until the entire sample passed through the sieve. The textural class of the soil was

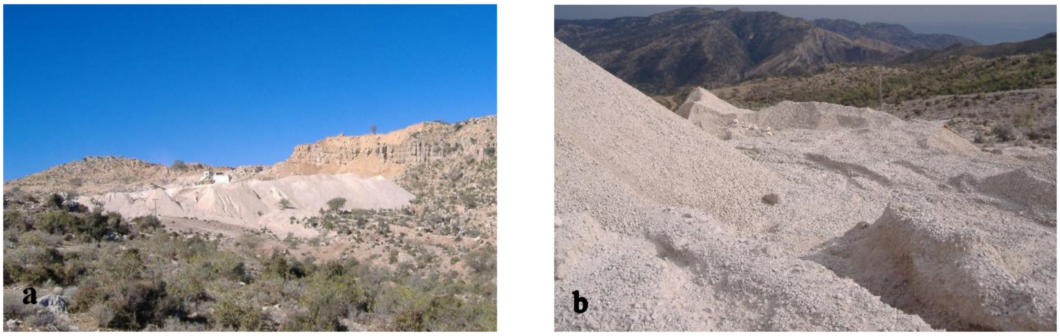

FIGURE 2 | Mining site broader view **(a)**; close view of the waste heaps **(b)**.

determined using a hydrometer according to the method described by Bouyoucos (1962). Garden soil was used to prepare different concentrations of solid quarry waste for the various treatments. A soil:water suspension (1:1) was prepared (He et al., 2012) to determine the pH using a pH meter (inoLab, Germany). A soil saturation extract was prepared for further analyses. The electrical conductivity was measured using an EC meter (SEnsoDirect Con 200, Netherlands). The nitrogen (N) percentage in the samples was determined according to Jones (1991) using the Kjeldahl method. To estimate the phosphorus content (P), a UV-VIS spectrophotometer (SpectroScan 80 D, Cyprus) was used to measure absorbance at 410 nm, as described by Olsen and Sommers (1982). Calcium (Ca) and magnesium (Mg) were determined by titration, while sodium (Na) and potassium (K) were quantified using flame photometry (AFP 100, United Kingdom).

Experimental Setup

The experiment was carried out in ceramic pots (30 cm in diameter) filled with various garden soil/solid waste mixtures, prepared at the Botanic Garden, GC University, Lahore, Pakistan (**Table 1**). Five treatments for each species and five replicates of each treatment were prepared. Seeds of *A. modesta* and cuttings of *A. vasica* were collected from the study area and raised at the nursery at the Botanic Garden, GC University. Eight-week old plants of uniform height 24 cm (±0.47) for *A. modesta* and 15 cm (±0.79) for *A. vasica* were used for the experiment. One plant of each species was grown in each pot and growth data, that is, plant height (cm) and number of branches per plant were measured every 15 days and harvested after 165 days.

TABLE 1 | Preparation of various waste/soil mixtures for treatments.

Sr.	Treatment	Concentrations	Solid waste	Garden soil
1.	T_0	Control	00	100
2.	T_1	25%	25	75
3.	T_2	50%	50	50
4.	T_3	75%	75	25
5.	T_4	100%	100	00

Plants Harvesting and Biomass Assessment

After 165 days, all the plants from both species were carefully extracted from the pots, relieved from excessive soil, placed in labeled zipper bags, and brought to the laboratory for further analyses. The parameters recorded for each plant included the following: plant height (cm), number of branches, root length (cm), and dry weight (g) of above- and belowground parts. To obtain the dry weight, the plants were oven-dried to a constant weight at 78°C. Before chemical analyses, plant materials were passed through a stainless-steel grinder with a 20-mesh sieve, and then mixed thoroughly. Mass-based chemical analysis of plant shoot and root tissues was conducted to determine N, P, Na, P, Ca, and Mg contents, as described in the "Physicochemical Analysis of Soil and Plant Tissues" section mentioned above.

Statistical Analysis

Treatment means, standard errors, and least significant differences were calculated for various parameters. One-way analysis of variance (ANOVA) was conducted using the software package COSTAT, version 3.03, to determine the significance of differences among treatment means $P < 0.05$. Sigma Plot v.14

TABLE 2 | Physicochemical analyses of solid quarry waste and garden soil.

Attributes	Solid quarry waste	Garden soil
Particle size		Sand: 79.50%
≥2.00 mm	44.75 ± 7.7%	Silt: 10.0%
≥1.00 mm	10.65 ± 1.0%	Clay: 10.5%
≥0.25 mm	10.65 ± 3.8%	
≤0.25 mm	33.05 ± 12.7%	
Texture	Sandy-gravel	Loamy sand
pH	8.16 ± 0.01	8.23 ± 0.00
EC (dSm^{-1})	0.06 ± 0.00	0.01 ± 0.00
N (%)	1.53 ± 0.00	8.2 ± 0.05
P (%)	0.01 ± 0.00	0.01 ± 0.00
K (ppm)	2.95 ± 0.06	3.4 ± 0.1
Na (ppm)	3.25 ± 0.16	6.95 ± 0.15
Ca^{++} (%)	2.37 ± 0.00	0.11 ± 0.00
Mg^{++} (%)	0.02 ± 0.00	0.07 ± 0.00

was used to generate the graphics. SPSS v. 13 was used to analyze the effects of treatment and their different duration on the growth of both species. Plant growth was considered a response variable, while treatment and duration were considered factors.

RESULTS

Physicochemical Analysis of Solid Waste and Garden Soil

The physicochemical analysis of quarry waste and garden soil showed that the particle size of solid waste can be divided into four different classes i.e., $\geq$2.00, $\geq$1.00, $\geq$0.25, and $\leq$0.25 mm. In the quarry waste used in the present study, the most abundant class was the $\geq$2.00-mm class; 44.75 ± 7.77% of the quarry waste had this particle size. The second most abundant was the $\leq$0.25-mm-size class (33.05 ± 12.79%). There were almost equal percentages of particles in the $\geq$1.00- and $\geq$0.25-mm-size classes, but greater variations in the percentage of particles in the latter size class. The texture of the solid waste was sandy-gravel, while that of the garden soil was loamy-sand. The pH of the solid waste was slightly lower than that of the soil. The electrical conductivity of the solid waste was higher than that of garden soil. The soil contained higher levels of N, P, K, Mg, and Na than the solid waste. The solid waste had a higher Ca content than garden soil (**Table 2**).

Effect of Quarry Waste on Plant Height and Number of Branches per Plant

After 165 days of growth, significant differences in the total plant height and number of branches per plant were measured among the different treatments for both species. The maximum height per plant was in T_4 (76.66 ± 1.85, 52.31 ± 1.73) and the minimum in T_0 (52.0 ± 0.91, 30.1 ± 1.06) for both *A. modesta* and *A. vasica*, respectively. Similarly, the maximum number of branches was also in T_4 (8.30 ± 1.17) and the minimum in T_0 (6.20 ± 0.47) for *A. modesta*. *A. vasica* did not exhibit significant differences in its branch number (**Figure 3**). The changes in the total plant height and number of branches for both species at intervals of 15 days are shown in **Supplementary Figures 1–4**. Furthermore, the mixed-model analysis showed that the solid waste treatment, number of days, and the interaction of solid waste treatment with the number of days had a significant effect on the total plant height for both species (**Table 3**).

Effect of Quarry Waste on Aboveground, Belowground, and Total Biomass per Plant

There were significant differences in the aboveground biomass in all treatments from T_1 to T_4 compared with T_0. The lowest aboveground biomass was observed in T_0, while the highest aboveground biomass was observed in T_4. However, the belowground biomass of T_1 and T_2 was not significantly different from T_0, but a significant difference was observed between T_3 and T_4 as compared with T_0. The total biomass of *A. modesta* was significantly different from that of T_1 to T_4 in comparison with that of T_0 (**Figures 4A–C**). For *A. vasica*, the aboveground biomass was significantly greater in T_4 than in all other treatments. There were significant differences in the aboveground biomass between T_0 and T_2, T_3, and T_4. The belowground biomass was lowest in T_0 and highest in T_4. The root biomass tended to increase as the percentage of quarry waste in the soil matrix increased. However, significant differences were observed between T_3, T_4, and T_0. The total biomass of *A. vasica* was significantly greater in the T_2, T_3, and T_4 than T_0 (**Figures 4D–F**).

Chemical Analyses of Shoot and Root Tissues of *A. modesta* and *A. vasica*

For both species, the highest nitrogen content was observed in T_4. There were significant differences among the different treatments in terms of mass-based N content percentage (%). Roots showed higher N content than shoots; this pattern was observed in all treatments. The highest P content was in T_4 and the lowest in T_0, with significant variations among the other treatments. The same pattern was observed for K (highest in T_4, lowest in T_0, with significant differences among others). Na content was highest in T_0 and lowest in T_4, and there were significant differences among the other treatments. In both roots and shoots, the highest Ca concentration was observed in T_4 and lowest in T_0, with significant differences among the others and a lower Ca content in the roots than in the shoots. The Mg concentration was highest in T_4 and lowest in T_0, but the difference between T_4 and T_3 was not significant. The magnesium concentration was lower in the roots than in the shoots in all treatments (**Tables 4**, **5**).

Correlation of Minerals With Total Plant Biomass

In the studied treatments, a significant and positive relationship was found between the total biomass of *A. modesta* and *A. vasica*, respectively, with the N content (R^2 = 0.82 and 0.90), P (R^2 = 0.89 and 0.96), K (R^2 = 0.89 and 0.57), Ca (R^2 = 0.97 and 0.70), and Mg (R^2 = 0.80 and 0.67) in roots, while the significant and inverse relationship with R^2 = 0.84 and 0.70 was found between the Na concentration in roots and total biomass across both *A. modesta* and *A. vasica*, respectively. For the relationships between total biomass and P, Na, and Mn the slope was higher for *A. vasica* than for *A. modesta* while the slope of relationship between total biomass and K was higher for *A. modesta* than for *A. vasica*. However, both species had similar slopes for their relationship with Ca content and total biomass (**Figure 5**).

DISCUSSION

Our results showed the enhanced growth of the two selected species grown in the mining waste which provides novel information about habitat restoration by utilizing the two selected woody species *A. modesta* and *A. vasica* on mining wastelands. Furthermore, our hypothesis regarding the comparative mineral uptake between the two species was partially supported. The biomass of *A. vasica* accumulated more Mg, P, and Na and less N and K than *A. modesta*, while both species accumulated similar amounts of Ca. Such species-specific mineral uptake behavior improves our understanding of the ecological restoration of mining sites with varying mineral concentrations. The enhanced growth of both species in the quarry waste, could be due to the high Ca content (2.37%) along with other nutrients such as N, P, K, and Mg and their uptake by the plants, as shown by their significant correlation with the total biomass. Furthermore, the presence of gravel in the mining soil can lower the substrate water-holding capacity, which could prevent the invasion of *Prosopis juliflora* (Khan et al., 2019).

Although mining changed the original soil strata inhabited by these species, the solid waste did not have an adverse impact on plant growth, and the treatments seemed likely to have fertilization effect. The treatment efficiency in the long terms was also observed on the growth of both species, indicating the suitability of both species for restoration of solid waste with the mentioned physiochemical properties of soil. Our findings support Richardson and Evans (1986), who utilized grasses for the restoration of limestone quarrying landscapes. They also found that the waste did not contain any toxic elements and promoted the growth of the selected species. Furthermore, our study also revealed that the solid waste areas can be converted into green patches using indigenous species without ameliorating the existing soil; some other exotic species capable of growing in soils with high Ca content could be planted to establish vegetation. These findings can help improve ecosystem restoration in limestone mining activities where habitats have been altered due to excavation.

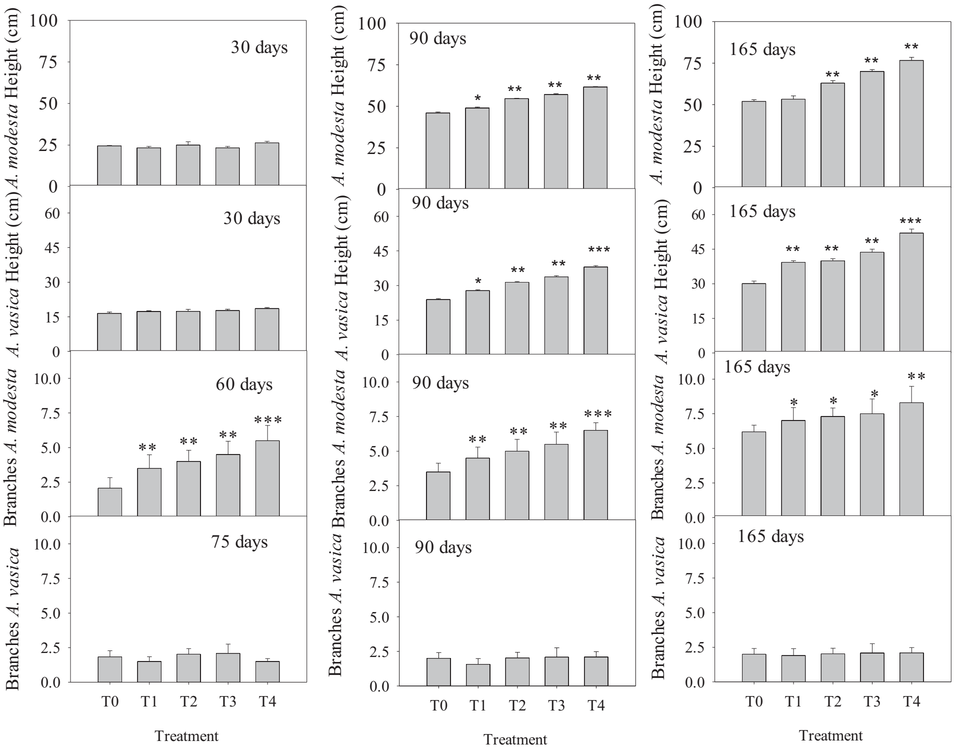

FIGURE 3 | Effect of quarry waste on plant height (cm) and number of branches per plant in *Acacia modesta* and *Adhatoda vasica* during the initial months, middle months, and before the harvest. The asterisk indicate the significant difference of treatment means with the control (T_0): *$P < 0.05$, **$P < 0.01$, and ***$P < 0.0001$.

TABLE 3 | The effect of solid waste treatment, duration of days, and their interactions on the growth of *Acacia modesta* and *Adhatoda vasica*.

Species	Source	Type III SS	*df*	Mean sum of square	*F*-value	Significance
Acacia modesta	Treatment	1173.12	4	293.29	51.94	0.000
	Days	11805.01	2	590.50	1045.36	0.000
	Treatment days interaction	564.09	8	70.51	12.48	0.000
Adhatoda vasica	Treatment	754.03	4	188.50	14.91	0.000
	Days	3942.76	2	1971.38	156.01	0.000
	Treatment days interaction	336.25	8	42.03	3.32	0.008

For the models of both the species R^2 was >0.90.

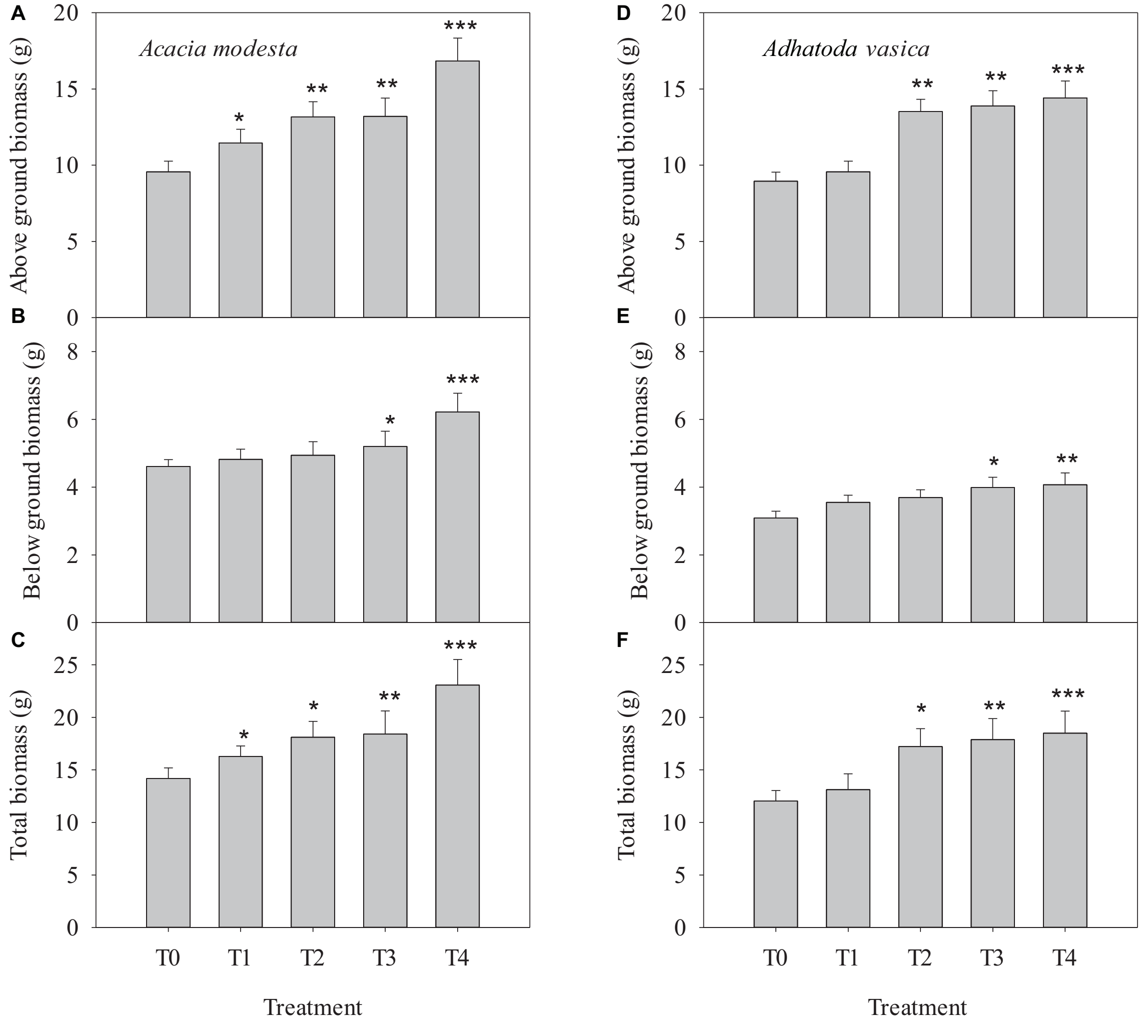

FIGURE 4 | Effect of quarry waste on above ground biomass, below ground biomass, and total biomass in *Acacia modesta* **(A–C)** and *Adhatoda vasica* **(D–F)**. The asterisk indicate the significant difference of treatment means with the control (T0): $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.0001$.

Our results are also consistent with prior ones reporting that limestone quarry waste is mainly composed of calcium carbonate, which could promote plant growth (Jim, 2001; Elsayed et al., 2017; Marcus et al., 2018). Calcium is a necessary micronutrient and is linked with various ion movements in the plasma. Its uptake can also regulate photosynthesis, carbohydrates, nitrogen assimilation, and the enzymes involved in it (Singh et al., 2018), which can enhance not only the performance of cellular mechanisms but also stress tolerance (Marschner, 1995; Konno et al., 2002; Matthew et al., 2011; Saito and Uozumi, 2020). Ecologists have classified plant species into calcifuges, which occur in soils with low Ca content, and calcicoles, which grow on calcareous soils (Lee, 1999). *A. modesta* and *A. vasica* are indigenous to the study area and have the potential to grow better in calcareous soils. However, we found that the Ca content was not uniform in both above- and belowground organs, as the roots had less Ca than shoots, which could be due to the utilization of calcium in the aerial parts for various metabolic processes (Clarkson, 1984).

Our results were consistent with those of Fu et al. (2004), in which *Pteroceltis tatarinowii* seedlings were grown in Hoagland nutrient solutions with three Ca concentrations (5, 10, and 15 mmol L^{-1}) or without Ca (control). Their results showed that the Ca content in the roots, leaves, and bark of *P. tatarinowii* increased with increasing Ca concentrations, and higher Ca content was found in leaves than in roots (Marschner, 1995). Kuznetsova et al. (2010) reported that indigenous *Pinus sylvestris* grew better with high Ca concentrations, and could be a candidate species for mining sites with high calcium content. The inverse correlation of total biomass with sodium concentration supports the findings of Bethke and Drew (1992) and Karim et al. (1993). As in non-halophytic species, high concentrations of sodium ions can reduce plant growth by disturbing plant water relations, unbalancing plant nutrition, and affecting several plant physiological and biochemical processes, which lead to a

TABLE 4 | Chemical analyses of shoot and root tissues of *Acacia modesta* grown in different concentrations of quarry waste.

Treatment	**Shoot tissues**						**Root tissues**					
	N (%)	**P (%)**	**K (ppm)**	**Na (ppm)**	**Ca (%)**	**Mg (%)**	**N (%)**	**P (%)**	**K (ppm)**	**Na (ppm)**	**Ca (%)**	**Mg (%)**
T_0	10.90 ± 0.85e	2.30 ± 0.01d	432.00 ± 2.83d	9.41 ± 0.07d	0.56 ± 0.00e	0.07 ± 0.00c	14.15 ± 0.35d	1.92 ± .01d	426.00 ± 2.12e	10.65 ± 0.07a	0.36 ± 0.00e	0.02 ± 0.00e
T_1	14.83 ± 0.03d	2.55 ± 0.04c	451.00 ± 2.12c	9.38 ± 0.08c	0.57 ± 0.00d	0.07 ± 0.00bc	18.05 ± 0.25c	1.95 ± 0.02d	437.00 ± 0.71d	10.71 ± 0.01ab	0.38 ± 0.00d	0.035 ± 0.00d
T_2	18.05 ± 0.35c	2.63 ± 0.02b	460.00 ± 0.71b	9.35 ± 0.06b	0.63 ± 0.00c	0.07 ± 0.00b	20.81 ± 0.84b	1.99 ± 0.01c	447.00 ± 2.02c	10.53 ± 0.03bc	0.48 ± 0.00c	0.043 ± 0.00c
T_3	20.86 ± 0.49b	2.67 ± 0.07b	469.00 ± 1.41a	9.28 ± 0.02ab	0.75 ± 0.00b	0.09 ± 0.00a	23.85 ± 0.61a	2.06 ± 0.02b	453.00 ± 0.71b	10.35 ± 0.02c	0.50 ± 0.00b	0.06 ± 0.00b
T_4	22.98 ± 0.39a	2.77 ± 0.02a	473.00 ± 2.83a	9.12 ± 0.01a	0.77 ± 0.00a	0.09 ± 0.00a	25.14 ± 1.10a	2.13 ± 0.02a	461.00 ± 1.41a	10.15 ± 0.07d	0.70 ± 0.00a	0.06 ± 0.00a
LSD	1.90	0.07	6.59	0.05	0.01	0.01	2.11	0.04	1.96	0.17	0.01	0.004

Different letters in the same column are significantly different at P = 0.05; LSD, least significant difference.

TABLE 5 | Chemical analyses of shoot and root tissues of *Adhatoda vasica* grown in different concentrations of quarry waste.

Treatment	**Shoot tissues**						**Root tissues**					
	N (%)	**P (%)**	**K (ppm)**	**Na (ppm)**	**Ca (%)**	**Mg (%)**	**N (%)**	**P (%)**	**K (ppm)**	**Na (ppm)**	**Ca (%)**	**Mg (%)**
T_0	–	2.71 ± 0.02e	371.00 ± 0.71	13.30 ± 0.06a	0.43 ± 0.00e	0.10 ± 0.00e	8.00 ± 0.28c	2.18 ± 0.03e	361.0 ± 2.82d	13.31 ± 0.28a	0.28 ± 0.00e	0.06 ± .00d
T_1	8.50 ± 0.07cd	2.89 ± 0.04d	375.50 ± 0.70	13.05 ± 0.05a	0.49 ± 0.00d	0.12 ± 0.00d	9.70 ± 0.84b	2.34 ± 0.04d	367.0 ± 1.41c	13.15 ± 0.07a	0.30 ± 0.00d	0.06 ± 0.00cd
T_2	9.45 ± 0.08c	2.98 ± 0.01c	380.50 ± 0.80	12.85 ± 0.06a	0.51 ± 0.00c	0.13 ± 0.00c	11.20 ± 0.42b	2.60 ± 0.02c	370.0 ± 1.70c	12.90 ± 0.14ab	0.34 ± 0.00c	0.06 ± 0.00bc
T_3	12.91 ± 0.11b	3.12 ± 0.04b	389.00 ± 1.41	12.15 ± 0.29b	0.58 ± 0.00b	0.14 ± 0.00b	13.45 ± 0.49a	2.73 ± 0.02b	377.0 ± 1.41b	12.50 ± 0.14b	0.47 ± 0.00b	0.07 ± 0.00ab
T_4	14.80 ± 0.99a	3.31 ± 0.02a	408.00 ± 2.83	10.95 ± 0.30c	0.61 ± 0.00a	0.15 ± 0.00a	14.0 ± 0.57a	2.85 ± 0.01a	404.0 ± 2.82a	11.75 ± 0.35c	0.57 ± 0.00a	0.07 ± 0.00a
LSD	1.33	0.03	4.16	0.47	0.007	0.005	1.63	0.09	5.48	0.54	0.002	0.004

Different letters in the same column indicate significant differences among the means at P = 0.05; LSD, least significant difference.

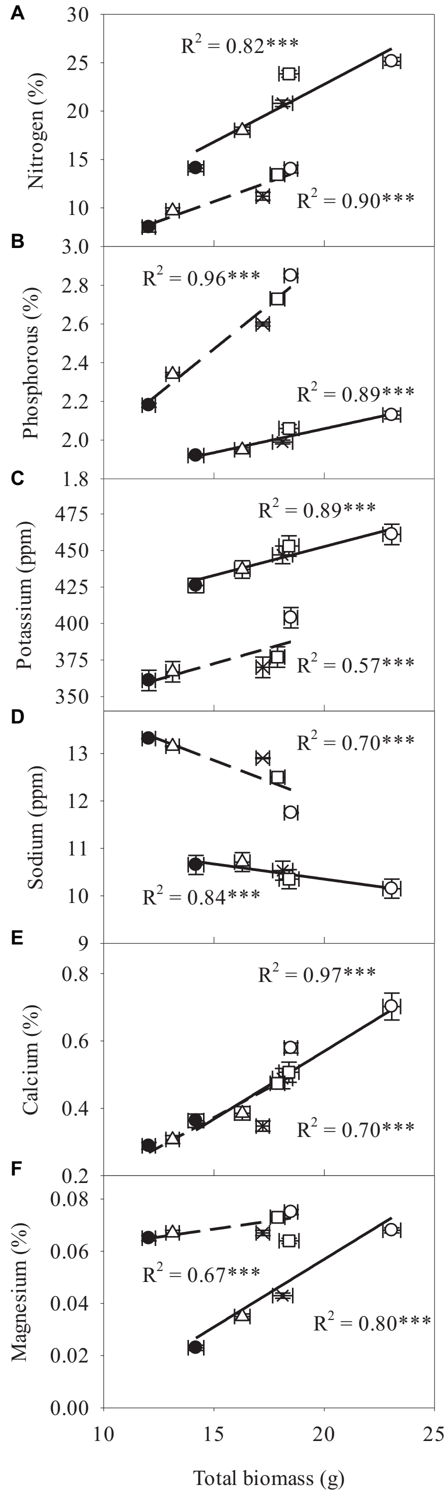

FIGURE 5 | Relationship of total plant oven-dried biomass with nitrogen **(A)**, phosphorus **(B)**, potassium **(C)**, sodium **(D)**, calcium **(E)**, and magnesium **(F)** in the roots of *Acacia modesta* (solid lines) and *Adhatoda vasica* (dashed lines) in T_0 (filled circles), T_1 (empty triangles), T2 (multiplication symbol), T3 (empty squares), and T4 (empty circles). Each symbol indicates the mean ± SE. ***$P < 0.0001$, all the relationships were significant. Linear function was fitted for all the relationships.

reduction in plant growth (Misra et al., 2006; Taffouo et al., 2009). Furthermore, the garden soil had more sodium than the solid waste, hence, the decrease in sodium content with the decrease in garden soil in the three treatments, resulted in increased biomass.

Compared with *A. modesta*, *A. vasica* absorbed higher amounts of all minerals from the mining waste, as shown in **Figures 5A–F**. Kasowska et al. (2018) reported some species that could uptake comparatively more minerals from mining waste. *A. vesica* being the shrubby species and considered to be the initial colonizer could have the potential for higher uptake of minerals, except calcium, as both species had similar uptake of Ca. Although an inverse relationship was found between the biomass and the Na uptake, *A. vasica* had a larger uptake of Na than *A. modesta* in a given treatment, indicating its potential to uptake the growth-reducing minerals more than the later colonizers such as trees. The results of the present study show that both *A. modesta* and *A. vasica* will be helpful for establishing vegetation on limestone quarry sites with high calcium content.

CONCLUSION

Both native species (*A. modesta* and *A. vasica*) showed increased growth in limestone quarry waste compared with the control. Adaptive to the mining substrate, both of these species can be utilized for the restoration of such mined landscapes without any soil amelioration. Planting these species will not only provide an ecological solution for the disposal of the limestone quarry waste but will also create opportunities for other environmental goods and services, such as timber production, habitat formation, carbon sequestration, erosion control, and natural ecosystem functioning.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

MH, ZS, and AK designed the experiment. MH and ZS did the field work. MH and RM conducted the laboratory analysis. MH, ZS, AK, and K-FC analyzed and interpreted the data. All authors contributed the manuscript writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.637833/full#supplementary-material

Supplementary Figure 1 | Effect of quarry waste on plant height (cm) of *Acacia modesta* over time. The asterisks indicate the significant difference of treatment means with the control (T_0): $^*P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.0001$.

Supplementary Figure 2 | Effect of quarry waste on number of branches per plant in *Acacia modesta* over time. The asterisks indicate the significant difference of treatments means with the control (T_0): $^*P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.0001$.

Supplementary Figure 3 | Effect of quarry waste on plant height of *Adhatoda vasica* over time. The asterisks indicate the significant difference of treatments means with the control (T_0): $^*P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.0001$.

Supplementary Figure 4 | Effect of quarry waste on the number of branches per plant in *Adhatoda vasica* over time.

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Critical Dependence of Butterflies on a Non-native Host Plant in the Urban Tropics

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Increasing urbanization in the tropics has led to the loss of natural habitats and local extirpations and the introduction of non-native plants in urban centers. Non-native plants can have widespread positive and negative ecological implications on native fauna including butterflies. In the small tropical urbanized city-state of Singapore, *Aristolochia jackii* (Aristolochiaceae), a native host plant of the nationally threatened Common Birdwing *(Troides helena)* and Common Rose *(Pachliopta aristolochiae),* is considered extirpated, but their shared non-native host plant *Aristolochia acuminata* is a cultivated ornamental in urban habitat. We conducted systematic surveys from years 2010 to 2014 and collated sighting records from 1999 to 2019 to map the distribution of *T. helena* and *P. aristolochiae,* and their host plant *A. acuminata*. We utilized machine learning models (i.e., random forest algorithms) to establish the relationships between various habitat (managed and natural tree cover, waterbody and impervious surface cover) and life-history parameters (minimum distance from the nearest larval host plant and population source derived from expert knowledge) that are associated with the butterfly distributions. Response curves were generated for each species and projected spatially across Singapore's landscape to estimate occupancy. We found that both butterflies had clustered distributions with a greatly reduced probability of occurrence further away from identified population sources and non-native *A. acuminata*. Both study species had similar spatial niche and similar species occurrence responses though there were differences in habitat preferences and temporal niche. Both species showed positive dependence on managed tree cover (Rose more than Birdwing) but the Birdwing also had high positive dependence on natural tree cover, unlike the Rose. We report novel findings that a non-native host plant can provide positive ecological benefits and critically sustain tropical butterfly populations. While there will be a need to evaluate the full ecological impacts of non-native plantings, we suggest using them as a secondary strategy when re-establishment of the native plants has failed, particularly in highly urbanized tropical landscapes.

Keywords: Lepidoptera, species distribution model, Singapore, Asia, urbanization, exotic species, introduced species

INTRODUCTION

Most conservation efforts for tropical butterflies are directed toward habitat protection (New et al., 1995; Bonebrake et al., 2010; Scriven et al., 2019), often due to the lack of species-level data sets that are necessary in formulating species-specific conservation strategies. Yet, as habitat loss continues, many tropical butterflies continue to face a precarious future (Jain et al., 2018; Theng et al., 2020). Many rare tropical insects cannot maintain their populations and need intervention for the species to recover their numbers—just maintaining their native habitats or resources is not sufficient (Schultz and Chang, 1998; Schultz and Dlugosch, 1999; Xing et al., 2019).

Lessons from management strategies devised for temperate butterflies are usually of limited relevance as they are specific to a particular habitat type or ecosystem such as a grassland (Crone and Schultz, 2003; Baguette et al., 2011). Population recovery studies in the tropics have rarely looked beyond documenting the loss and recovery of butterflies due to natural cataclysmic events like forest fires and droughts (Cleary and Mooers, 2004; Dunn, 2004). Therefore, there is a need to design and test strategies for tropical butterflies to restore populations for conservation management. Designing such a strategy is complex because *a priori* knowledge of the species is needed; such as knowledge of species biology, habitat range and dispersal, habitat requirements and an understanding of species survival in potential enrichment locations (Schultz et al., 2008). Species distribution modeling is increasingly being applied to aid such efforts, however, studies tend to lack clear links to ecological interactions that affect the model's translatability to specific conservation management strategies.

Another dimension to consider is the increasing global urbanization that has not only led to the loss of natural habitats but has introduced a large number of non-native plants with mixed impacts on native fauna (Reichard et al., 2001; McKinney, 2006; Schlaepfer et al., 2011; Trentanovi et al., 2013; van Kleunen et al., 2015; Jain et al., 2016). This phenomenon may increase the reliance of native insects including butterflies on non-native host plants (Graves and Shapiro, 2003) and nectar plants (Jain et al., 2016). With rapid urbanization bringing non-native plants to tropical areas, the reliance of butterflies on non-native host plants can be expected. The positive benefits of non-native plants are seldom discussed and remain poorly understood particularly for the restoration of tropical butterfly populations.

In this study, we evaluated the dependence of two threatened but phylogenetically related butterflies in Singapore (both in family Papilionidae)—Common Birdwing (*Troides helena,* hereafter "BW") and Common Rose (*Pachliopta aristolochiae,* hereafter "CR") on their non-native host plant *Aristolochia acuminata*. To do this, we mapped the butterfly and host plant distributions and estimated the occupancy of the butterfly species in Singapore. We also identified the species habitat dependence (forests, urban parks and private gardens), establish relationships between various habitat and life-history parameters (such as distance from larval host plant, % natural tree cover, % managed tree cover, % impervious surface cover) and investigated spatial and temporal niche overlap between the two species. The BW and CR are listed as nationally "vulnerable" (Singapore Red Data book version 2: Davison et al., 2008). CR was voted as the people's choice of the national butterfly of Singapore in 2015 (Zengkun, 2015).

METHODS

Host Plants of the Study Species

BW and CR butterflies use the non-native *Aristolochia acuminata* (**Figure 1**) as their host plant in Singapore (Tan and Khew, 2012; A. J. pers. obs.) as *Aristolochia jackii* (the only known *Aristolochia* species native to Singapore) is considered nationally extirpated. Its last known wild habitat, i.e., Jurong swamp in Singapore was destroyed in the 1930s. *A. acuminata* is believed to be introduced for its ornamental value with earliest records from the Botanic Gardens in 1918 (Chong et al., 2009; Singapore Herbarium Online, 2020) and in the past decades has been mainly planted by butterfly enthusiasts. BW and CR are believed to have utilized *A. jackii* as their native host plant in Singapore in the past and are hypothesized to have survived extirpation by relying on the introduced *A. acuminata* post extirpation of their native host plant (Jain et al., 2019).

Data Collection for Habitat Mapping

We consulted 30 local butterfly experts (including A. J.) about areas where the BW and CR have been sighted in Singapore since the year 1999. These consultations yielded 61 locations between the years 1999 and 2009 that were mapped to a 20 m × 20 m resolution. The survey effort at each location as estimated by the experts was also recorded. Because BW and CR are large and conspicuous butterflies, we assumed that local experts could identify them reliably in the wild.

Butterfly surveys were conducted across 125 locations between the years 2010 and 2014 (**Figure 1a**) ranging from forested areas to urban parks and private gardens. Our survey locations included areas where the two species have been previously sighted, or locations with a high perceived likelihood of BW or CR sightings (**Supplementary Figure 1**), i.e., proximity to known host plants and/or perceived appropriate habitat conditions (e.g., medium to high canopy cover, multi-tiered urban plantings or a complex habitat structure). The western catchment forest and Pulau Tekong (in the east) could not be sampled because they are restricted military areas. However, experts were asked to include sightings from these locations.

All locations were visited at least five times, with most locations visited more than 10 times on days of clear weather (no cloud or rain conditions); each visit lasted at least an hour or more. Visits were spaced out over time with each location visited typically once every 3–6 months. The minimum distance between two locations was 400 m. Existing trails were walked in forests and urban park locations. Additionally, transects of 100 m length and 2.5 m width on both sides of transect locations were established in forested sites in the Bukit Timah and Central Catchment Nature Reserves, which are the largest forest patches in Singapore. The number of transects

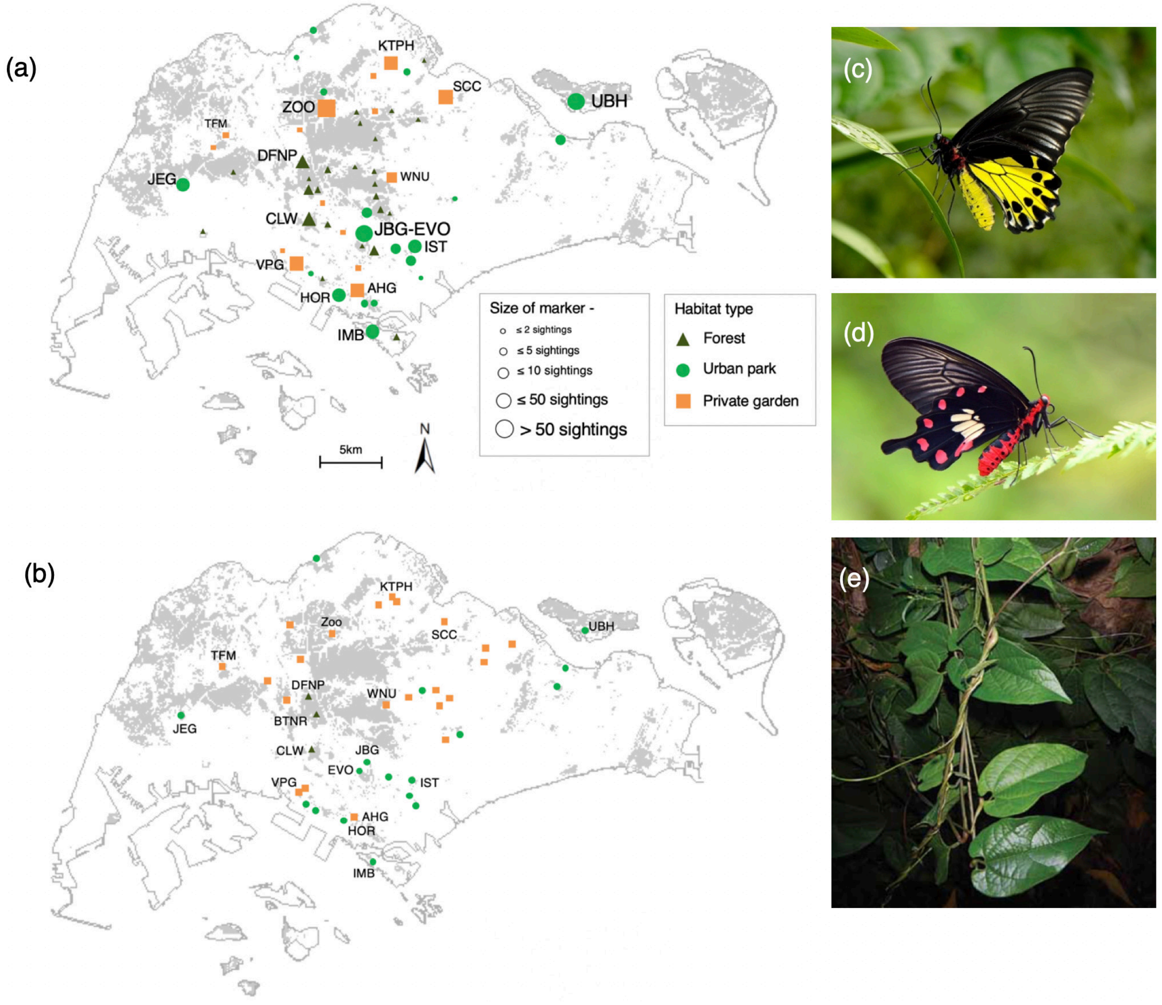

FIGURE 1 | (a) Combined sightings of Common Birdwing (BW) and Common Rose (CR) butterflies, **(b)** Larval host plant locations across habitat types in Singapore from years 1999 to 2019. Gray areas in the map refer to forested areas. Abbreviations refer to source locations identified by experts (see **Supplementary Table 1** for details). **(c)** Common Birdwing, **(d)** Common Rose, **(e)** *Aristolochia acuminata* larval host plant. Photos **(c,d)** by Tea Yi Kai, **(e)** by Amy Tsang.

per patch varied depending on the patch size, with larger forest patches (> 100 ha) having 8–10 off-trail transect locations. Private gardens were searched as exhaustively as possible each visit, in lieu of establishing transects.

The abundance of BW and CR was recorded during each visit at every location. One hundred and nineteen locations with a total of 6,294 h of survey effort were retained in the analysis (**Table 1**). Locations with less than 5 h spent were deemed insufficient to detect the study species and were discarded. The 2010–2014 surveys included 51 locations that overlapped with locations surveyed between 1999 and 2009. Overall, 72% of survey effort and 84% of butterfly sightings occurred between the years 2010 and 2014. Additionally, sightings of BW or CR and locations of their host plants were checked between the years 2015 and 2019 on www.inaturalist.org for all of Singapore. Three new sighting locations were discovered during this time that were not raised by the experts or recorded between the years 1999 and 2014.

Known locations of the host plant *A. acuminata* ($n = 41$) between years 1999 and 2019 were compiled with the help of local butterfly and plant experts, relevant personnel from the National Parks Board (Singapore) and Singapore Botanic Gardens Herbarium records (Singapore Herbarium Online, 2020). These locations were mapped to a 20 m × 20 m resolution. The majority (> 80%) of locations were ground-truthed between the years 2013 and 2014, with additional locations (where adults were sighted between 2015 and 2019) ground-truthed in year 2019–2020 to confirm if *A. acuminata* was still found there (**Figure 1b**). All except four sites were found to (still) have the host plant.

Source Population Consultations

A.J. consulted 30 experts who have monitored and studied BW and CR over the years (some since the year 1999) to identify likely (or certain) source populations for BW and CR based on the consistency of butterfly observations during their field visits.

They identified 14 potential source population locations (see **Supplementary Table 1**).

Models to Examine Habitat Preference and Spatial Occurrence

To establish the relationships between various land-use and life-history factors that can contribute to the distributions of the two butterfly species, we took a geospatial approach utilizing random forest models. Specifically, we implemented conditional random forests, which is a machine learning technique that relies upon a series of conditional inference trees (n = 999) and the permutation of variables (mtry = 7) to assess the relative contribution of each variable (Hothorn et al., 2006; Strobl et al., 2007). Conditional random forest models were chosen owing to their ability to handle and reduce the effects of overfitting, selection bias, and collinearity (Hothorn et al., 2006). Besides being able to provide accurate predictions, random forest models are also able to generate variable importance values that denote the degree of influence each variable had on improving its performance (indicated as variable importance in **Figure 3**), by covering the impact of each explanatory variable individually as well as in multivariate interactions with other explanatory variables. The variable importance values in random forest models do not represent the directionality between explanatory and response variables and instead represent the degree of importance. Positive variable importance means that the model performance improves with the inclusion of the explanatory variable in the model. Negative variable importance means that removing a given variable from the model improves the performance. It can be inferred that such variables do not have a role in the prediction and are not important.

These models were constructed based on each butterfly species' distribution data (presence or absence), and the associated land-use and life-history conditions within the 100 m surrounding that species locality (i.e., data from each 100 m raster cell resolution). Land-use variables considered here were obtained from Gaw et al. (2019), which is based on land-cover from 2003–2018 and included classifications that reflected managed and natural tree cover, managed and natural shrub/grassland cover, bare ground cover, building cover, waterbody and impervious surface cover (see Gaw et al., 2019 for details). Time period was based on the month and year of data collection. Dependence on life-history variables was estimated by utilizing sampling results and constructing maps representing minimum distance from the nearest larval host plant and potential population source in meters (as identified by experts).

Data was randomly split into testing (75%) and training (25%), and bootstrapped 50 times to account for potential uncertainties (reported as 95% confidence intervals in **Figure 3**). We then projected the averaged model across Singapore's landscape to predict the potential occurrence of both butterfly species. Owing to the complexities of random forest models, and the inability of variable importance values to denote directionality between explanatory and response variables, we secondarily generated response curves by using the random forest model (formed by the "party" package) to predict the effect of increasing values of the five most important explanatory variable for each species (e.g., distance from source, managed tree cover) on the response variable (probability of occurrence) to elucidate more precise relationships.

All analyses were performed in R version 3.6.0 (R Core Team, 2019), utilizing the package "party" (Hothorn et al., 2006; Strobl et al., 2007) and "raster" (Hijmans et al., 2019).

Seasonality

Seasonal patterns for BW and CR were inferred based on sighting records across months that were aggregated over the study period. We also collated records of BW and CR larvae in consultation with experts and during surveys and ground-truthing of the host plants. However, larval records were not included in the species distribution models.

RESULTS

Abundance Across Habitat Types

Overall, ~55% of locations surveyed had the presence of BW or CR (**Table 1**). Urban parks had the highest abundance of both butterfly species. Private gardens had the highest proportion (22/33 locations) of host plant locations but the lowest abundance of BW among the three habitats (**Table 1** and **Figure 1**). A greater percentage (29%) of BW sightings were in forest habitats than CR which had only 8% of sightings in forest habitats. CR abundance was higher in private gardens than forested areas.

There was considerable variation in survey effort (average = 52.9 ± 35.5 h) per location. However, correlations

TABLE 1 | Abundance (number of sightings) of Common Birdwing (BW) and Common Rose (CR), presence of host plants and source locations across habitat types between years 1999 and 2019.

Habitat types	Survey effort (h)	Total abundance of BW	Total abundance of CR	Total locations surveyed	Locations with host plants	Source locations (suggested by experts)	Locations with BW	Locations with CR	Mean abundance ± std. dev BW	Mean abundance ± std. dev CR
Forest	2554	107	38	55	3	2	26	11	4.1 ± 5.5	3.5 ± 4.0
Urban parks	1550.5	162	121	31	16	5	15	10	10.8 ± 19.7	5.1 ± 4.5
Private gardens	2189.5	56	61	33	22	7	15	12	3.7 ± 2.99	12.1 ± 15.4
TOTAL	6294	325	220	119	41	14	56	33	5.8 ± 11.2	6.7 ± 9.6

between survey effort and BW presence (Pearson's R = 0.035, p = 0.71, n = 119) as well as survey effort and CR presence (Pearson's R = 0.16, p = 0.095, n = 119) were not significant.

Spatial Occurrence

Based on the area under the receiver operating characteristic curve (AUC) value, the accuracy of models for BW and CR was 0.809 ± 0.006 and 0.669 ± 0.02 (95% confidence interval), respectively. Overall, BW tended to possess more areas with a higher probability of occurrence compared to CR. There was a relatively high degree of spatial niche overlap between the two species (Schoener's D = 0.960; I-statistic = 0.999; **Figure 2**) suggesting that they possess similar spatial distributions.

Source Populations

We found that the source population locations identified by experts corresponded to a minimum of 0.3 predicted probability of occurrence for BW, and a minimum of 0.14 predicted probability of occurrence for CR (**Figure 2**). Only 8 of 14 source locations had >0.3 predicted probability of occurrence for CR. Ten of 14 locations reported a minimum of 5 BW individuals whereas only 8 of 14 locations reported a minimum of 5 CR individuals. Our results support the expert opinion and indicate that the presumed 14 locations are likely source populations for BW. However, if the minimum of 0.3 predicted probability of occurrence (as observed for BW) is applied to CR, only 8 locations qualify as CR source populations. Additionally, the importance of locations where BW or CR abundance was low (<5 individuals) may be debated as being a source. The presence of larval host plant was confirmed at all source populations by ground truthing. No additional source populations (not identified by experts) were detected by the species distribution models.

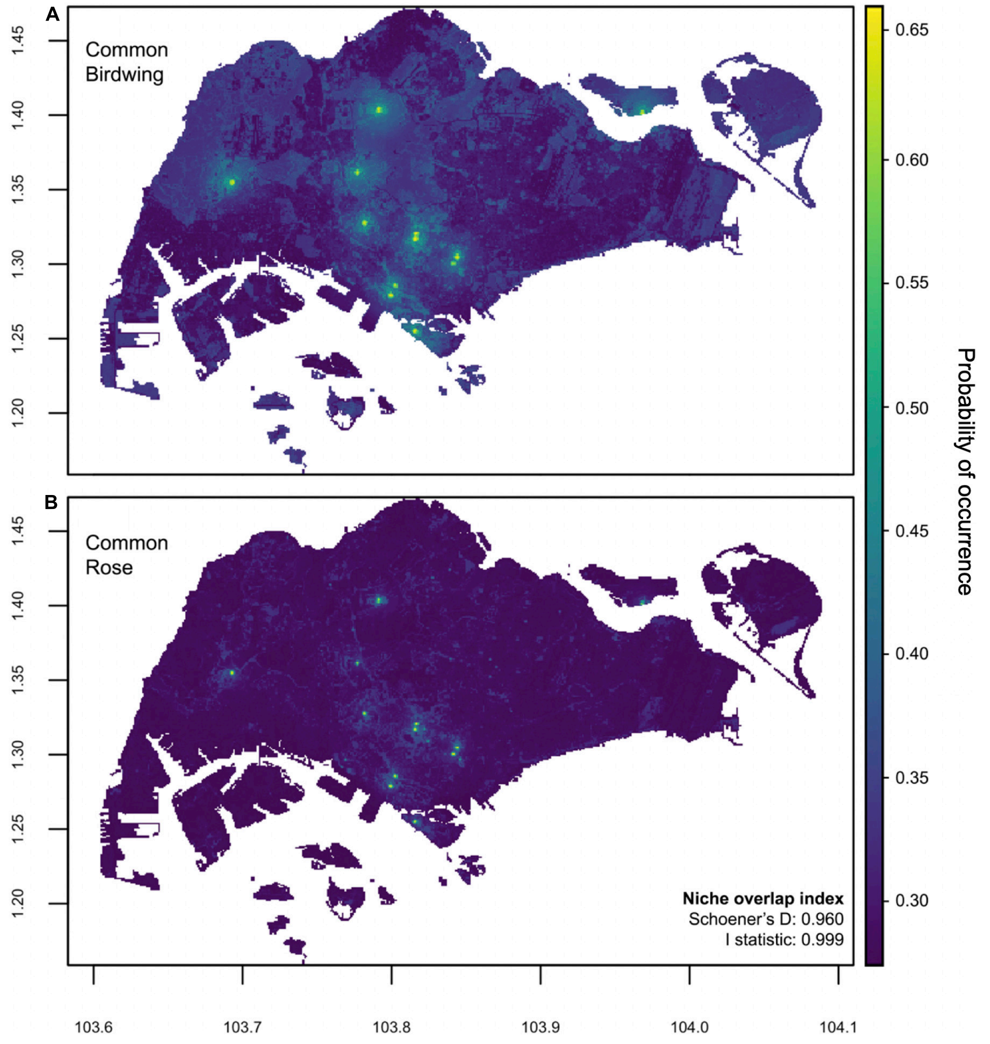

FIGURE 2 | Prediction maps showing the probability of occurrence of **(A)** BW and **(B)** CR butterfly species in Singapore. Both species possess similar predicted occurrence patterns and possess a relatively high degree of spatial overlap, as indicated by the Schoener's D and I-statistic. The latitude and longitude values are shown on the vertical and horizontal axis, respectively.

Relationship Between Butterfly Occurrence and Habitat and Life-History Parameters

The distance from the nearest source population had the highest influence on BW occurrence and this and distance from larval host plant had the highest influence on CR occurrence (**Figure 3**). The probability of occurrence for both species greatly reduced further away from the population source and larval host plant (**Figure 4**). Distance from larval host plant, impervious surface cover, managed tree cover and natural tree cover were also important for the occurrence of BW (**Figures 3**, **4**). Managed tree cover and managed shrub/grassland cover were important and had a positive influence on CR occurrence (**Figures 3**, **4**). Impervious surface cover had negative influence on BW and CR occurrence (**Figure 4**).

Seasonality

Aggregated over the study period, BW and CR adults were recorded in all 12 months of the year across survey locations. CR larvae were recorded in all 12 months but BW larvae were recorded in 9 months of the year with no records in March, May and August. The relative abundance of BW peaked in December with smaller peaks in February, May and July. The relative abundance of CR peaked in June, August and January (**Figure 5**). Typically, CR populations peaked a month after BW populations (**Figure 5**).

DISCUSSION

Critical Dependence on Non-native Urban Plantings

Our results show that the highest abundance and the majority of source populations of BW and CR are found in urban parks and private gardens. Therefore, urban plantings are critical for the survival of these butterflies. This is an unusual situation because BW and CR are forest species that can be found in primary forest and secondary forest habitats throughout Southeast Asia

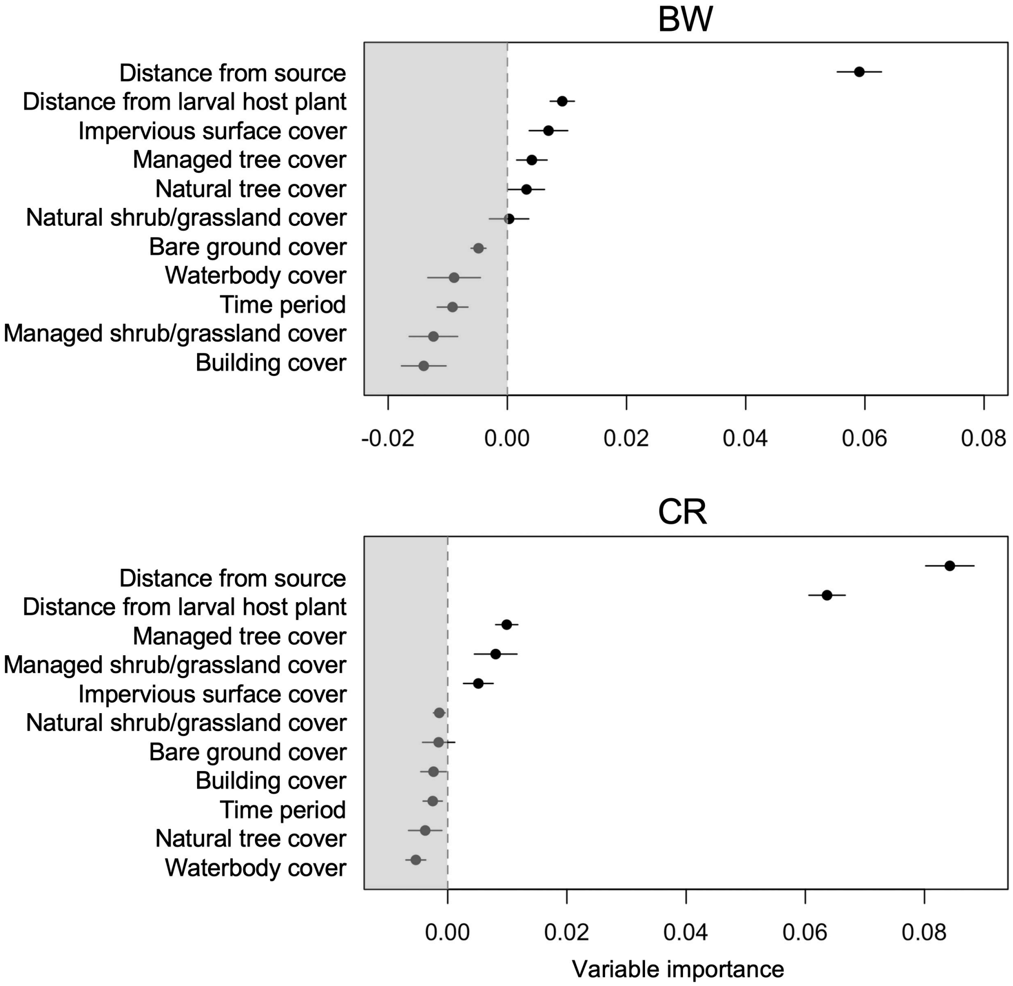

FIGURE 3 | Relative importance of habitat and life-history parameter values on the occurrence of BW and CR butterfly species in the random forest model. Error bars are 95% confidence intervals.

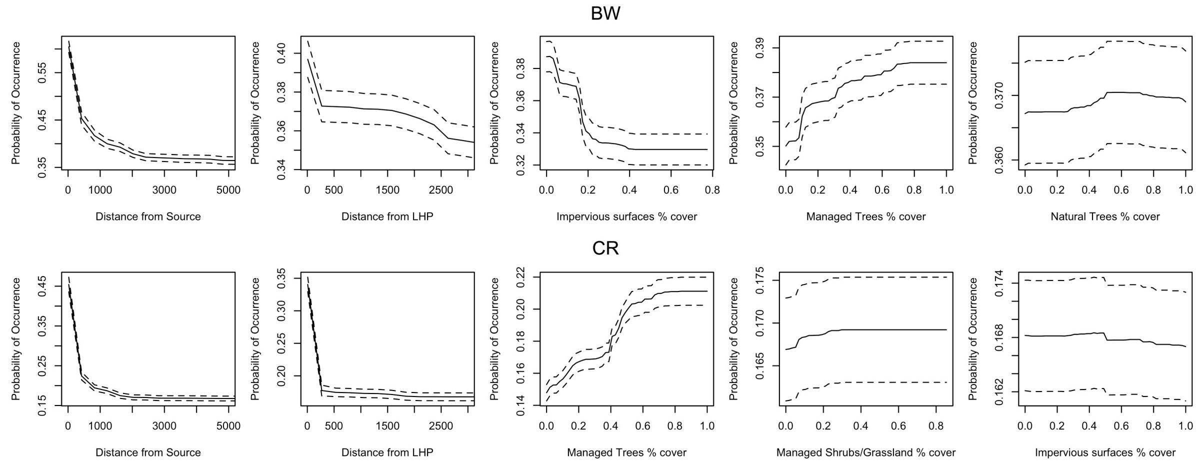

FIGURE 4 | Response curves showing the relationship between the probability of occurrence of BW and CR various habitat and life-history parameters. The order of the response curves is by the importance of the variable. Distances are shown in meters. Habitat variables (e.g., managed tree cover) are shown as percentage values. LHP refers to the larval host plant. The dotted lines are 95% confidence intervals.

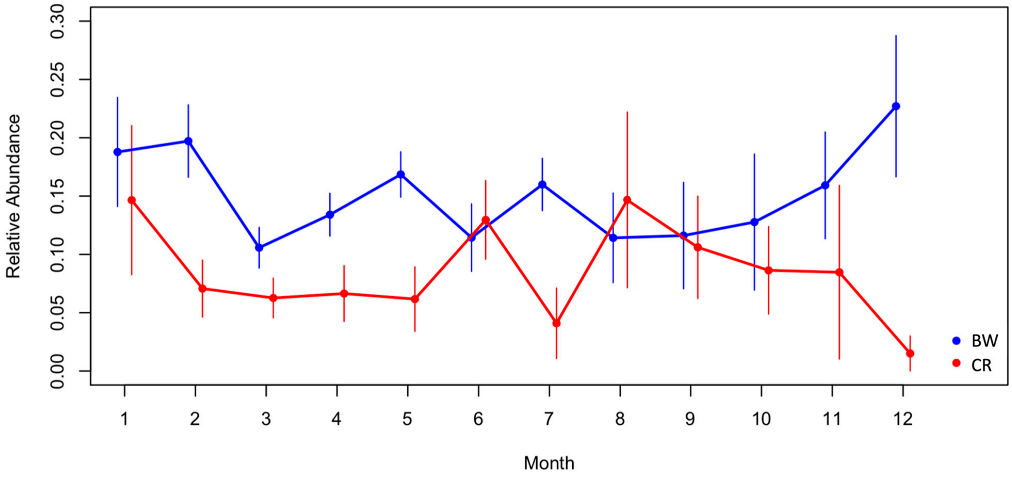

FIGURE 5 | Relative abundance and seasonality BW and CR across months aggregated over the study period. Relative abundance = log(abundance + 1)/survey effort. Error bars indicate standard errors of the mean.

(Hsieh et al., 2010; Corbet and Pendlebury, 2020). The current situation, therefore, presents an unusual case of two forest butterflies that have switched to a non-native host plant and now rely completely on urban plantings after the extirpation of their native host plant.

With a greater prevalence of non-native plants (particularly introduced as ornamentals) across urban centers globally (McKinney, 2006; Trentanovi et al., 2013), the reliance of native butterflies on non-native host plants seems poised to become an increasingly common phenomenon. At least a third of butterfly species in California are known to utilize non-native plant taxa (Graves and Shapiro, 2003) with geographic range and native diet breadth being significant predictors of non-native host use (Jahner et al., 2011). As many native plants face extirpation with loss and fragmentation of natural habitats in urban centers, non-native plants may provide alternative hosts and refuge for butterflies and other native fauna. While some non-native species cause much ecological damage, the potential conservation and ecosystem service value of non-native species is increasingly being recognized in areas where climate and land use are changing rapidly (Schlaepfer et al., 2011).

Habitat Preference and Potential Natal Affinity

BW and CR appear to have similar spatial niches and similar species occurrence responses as they share the same larval host plant and have a preference toward managed tree cover. However, the main difference between the two species appears to be in their preference toward forested habitats. The spatial model confirmed that BW has a higher habitat preference toward natural tree cover than CR, which corroborates with higher BW sightings in forest habitats than CR. Studies on other species of Birdwings (e.g., *Troides aeacus formasanus* in Taiwan, Hsieh et al., 2010) suggest that they prefer inner forest compared with forest trails and road edges.

In contrast, CR occurrence was positively influenced by the managed tree cover and managed shrub/grassland cover in the spatial model. One explanation for this result could be that CR has a stronger natal affinity than BW which limits CR's home range around the planted larval host plants in urban parks and private gardens in Singapore. However, further research on the role of CR's natal affinity in determining its habitat preference is needed. In its natural habitat in western China, *Byasa impediens*, a species with similar life-history characteristics as CR, was observed to prefer open areas and sparse forests, and did not utilize host plants in forests with dense vegetation (Li et al., 2010). CR also exhibits a greater degree of flower specialization compared with BW (Jain et al., 2016). Finally, it should be noted that our results showing model performance for BW, at AUC > 0.8, is considered acceptable whereas the model performance for CR, at AUC = 0.669, is considered relatively poor and has limited predictive power. For this reason, it may be premature to generalize model results for CR. More field surveys are suggested to improve the predictive power and generalizability of the CR model.

The Persistence and Connectivity of Source Populations

Meta-population theory suggests that a butterfly should have a minimum of 20 suitable habitat patches for the long-term survival of the meta-populations (Hanski et al., 1995; Li et al., 2010). The identified BW and CR source population locations in Singapore do not appear to meet the stable meta-population criterion of 20 patches and may be under a high risk of inbreeding and potential extinction. During the study, we observed that BW and CR were sometimes missing in smaller population sources (when ranked by BW or CR abundance) such as SCC and KTPH. This observation agrees with the literature where only large habitat patches were found to be significant predictors of year on year occupancy for the Golden Birdwing (*Troides aeacus)* and local extinctions in small patches were common (Li et al., 2010). It may also be possible that population sources of BW and CR exist in southern Malaysia within the species dispersal range and may be contributing to the persistence of the species in Singapore. Systematic long-term population monitoring at each source population is necessary to determine local extinction rates and better understand long-term metapopulation persistence in Singapore and potential interactions with Malaysian populations.

Connectivity between source populations identified through our study can be understood based on dispersal estimates from the Golden Birdwing (*Troies aeacus*) and *Byasa impediens* as they are species phylogenetically related to and with similar life-history characteristics as BW and CR, respectively. *B. impediens* has been found to disperse up to 5 km in mark-recapture studies (Li et al., 2012). *T. aeacus* was recorded to disperse to 4.3 km in telemetry studies in China (Wang et al., 2019). However, it likely disperses to more than 5 km as it is bigger in size than *B. impediens.* BW and CR can be assumed to disperse to 5 km over suitable habitat as a conservative estimate, however, their dispersal over impervious surfaces and unsuitable habitat remains unknown. Further research is needed to understand the connectivity between various previously identified source populations in Singapore.

Temporal Niche Separation

Our findings that the relative abundance of BW and CR peaks at different months suggests that the two species may have some temporal niche separation. This may be adaptive as the two butterflies share the same larval host plant. The emergence of early instar caterpillars may also be timed with the presence of young leaves on the host plant. Our field observations suggest that the BW tends to use larval host plants with more leaves (i.e., older plants) as BW larvae are bigger and have a more voracious appetite than CR. The temporal niche separation may also be related to BW and CR caterpillar's ability to digest Aristolochic acids in *A. acuminata* leaves which vary with flowering and fruiting cycles (Brown et al., 1980). Additionally, BW caterpillars are sometimes observed to ring-bark their host plant vines, similar to other Birdwing species (*Ornithoptera alexandrae* and *O. goliath* larvae; Parsons, 1992) which leads to withering of the host plant and thereby, rending it unsuitable for a few weeks until plant recovery. The role of ring barking in the context of temporal niche separation of the two species should be investigated in the future.

Implications for Habitat Enrichment

We show that clustered populations of BW and CR have emerged in Singapore shaped by the locations of larval host plantings by butterfly enthusiasts in Singapore. Long-term survival of these threatened butterflies would require a planned habitat enrichment strategy that can increase the size of existing source populations, increase the number of source populations to at least 20 patches for stable metapopulations and increase the connectivity between existing source populations to reduce local extinction risk. The observed habitat preferences of the species can provide important cues in site selection for habitat enrichment.

The planting of host plants in urban parks adjacent to forest habitats may be the most suitable locations for BW enrichment because BW's probability of occurrence increased with natural and managed tree cover. Isolated urban parks and gardens can be utilized for CR enrichment because natural tree cover was not important for CR's probability of occurrence. Habitats can also be enriched with nectar species preferred by BW and CR (Jain et al., 2016) to achieve synergistic effects.

Though urban plantings are currently the only available option for BW and CR management in Singapore (planting of the non-native host plant is not permissible in forest habitats), it should be no surprise that the longevity of urban plantings is limited as they are prone to frequent landscape changes. There have been at least 4 documented locations of breeding populations of BW and CR in Singapore that were wiped out in the past (e.g., Asimont Lane) as a result of a change in garden/park management (van Heezik et al., 2012). In fact, this dependence on a planted resource continues to make the BW and CR particularly vulnerable to extinction. Future studies should also aim to identify if any identified population sources may be ecological traps.

A longer-term strategy with less risk would be to reintroduce *Aristolochia jackii* as the native host plant for the BW and CR. At least three of California's butterfly species have been documented to have lower rates of survival on non-native host plants compared to their native counterpart (Graves and Shapiro, 2003). If *A. jackii* turns out to be an effective host plant for BW and CR, restoration efforts could be united to systematically bring back these butterflies to forest habitats in Singapore.

A coordinated planting effort of (native and non-native) host plants in forests, urban parks and private gardens to expand the size, quantity and connectivity of source populations could be explored in Singapore. In particular, source populations may need to be established in the central and eastern parts of Singapore to connect the western and easternmost (i.e., Ubin) populations. Important lessons can be drawn from the community engagement program for the Richmond Birdwing (*Ornithoptera richmondia*) in Australia in which schools planted the rare native host plant *(Pararistolochia praevenosa)* to restore historical connectivity between the fragmented butterfly populations (Sands, 2008). The success of such an effort also depends on an improved understanding of the study species' micro-habitat preference during the juvenile (egg/caterpillar/pupa) stages across forested and urban areas.

Broadly speaking, the enrichment strategy identified here that introduced (non-native) host plants could be used for butterfly conservation is novel in the context of tropical urban habitats. Caveats involved include possibly lower rates of larval survival on non-native host plants compared to their native counterpart (see Graves and Shapiro, 2003). For this season, we recommend that non-native plants be planted as a secondary strategy only when re-establishment of the native plants has failed. The wider ecological consequences of non-native plantings will also have to be carefully studied before such a strategy can be widely adopted for conservation.

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

AJ designed the study and was responsible for data collection. AJ and YZ analyzed the data. AJ, YZ and EW contributed ideas and drafted the manuscript. 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/fevo.2021.655012/full#supplementary-material

Supplementary Figure 1 | Survey locations for BW and CR butterflies divided by habitat types.

Supplementary Table 1 | Source populations for Common Birdwing (BW) and Common Rose (CR) in Singapore as identified by experts, survey effort and BW and CR abundance recorded as part of our study. BW and CR prediction values represent the probability of occurrence in Singapore based on the random forest models.

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Descriptive Spatial Analysis of Human-Elephant Conflict (HEC) Distribution and Mapping HEC Hotspots in Keonjhar Forest Division, India

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Escalation of human-elephant conflict (HEC) in India threatens its Asian elephant (*Elephas maximus*) population and victimizes local communities. India supports 60% of the total Asian elephant population in the world. Understanding HEC spatial patterns will ensure targeted mitigation efforts and efficient resource allocation to high-risk regions. This study deals with the spatial aspects of HEC in Keonjhar forest division, where 345 people were killed and 5,145 hectares of croplands were destroyed by elephant attacks during 2001–2018. We classified the data into three temporal phases (HEC1: 2001–2006, HEC2: 2007–2012, and HEC3: 2013–2018), in order to (1) derive spatial patterns of HEC; (2) identify the hotspots of HEC and its different types along with the number of people living in the high-risk zones; and (3) assess the temporal change in the spatial risk of HEC. Significantly dense clusters of HEC were identified in Keonjhar and Ghatgaon forest ranges throughout the 18 years, whereas Champua forest range became a prominent hotspot since HEC2. The number of people under HEC risk escalated from 14,724 during HEC1 and 34,288 in HEC2, to 65,444 people during HEC3. Crop damage was the most frequent form of HEC in the study area followed by house damage and loss of human lives. Risk mapping of HEC types and high priority regions that are vulnerable to HEC, provides a contextual background for researchers, policy makers and managers.

Keywords: human-elephant conflict (HEC), spatial pattern analysis, populations at HEC risk, HEC hotspot mapping, trends in spatial risk, types of HEC

INTRODUCTION

Rapid human population growth and over-exploitation of wildlife resources has degraded suitable habitats and threatened the survival of many wildlife species (Tischendorf and Fahrig, 2000; Fahrig, 2003; Rushton et al., 2006). The imbalance between economic development and wildlife conservation is not only causing economic loss but also impacting the day to day lives and personal safety of people (Jadhav and Barua, 2012; Li et al., 2018). Ultimately, this leads to frequent and severe conflicts between humans and wildlife in areas where they interface and where wild animals have easy access to concentrated and reliable food sources (Baruch-Mordo et al., 2008).

Indian Elephants (*Elephas maximus indicus*), a subspecies of Asian elephants (*Elephas maximus*) is a prime example of a species known for the highest wildlife damage in India, causing extensive damages to property and loss of human lives. Nearly 2,381 people and 490 elephants have died in India from 2015 to 2018 (MoEF and CC, 2018) and between 2000 and 2010, 0.5 million households have suffered annual losses due to crop raiding by elephants (MoEF, 2010, 2012). The Indian government has paid compensations of around US$ 19.2 million for damage to crops and property and US$ 5 million for human lives lost due to HEC from 2014 to 2018 (MoEF and CC, 2018). While 60% of the world's elephant population is found in India, only 30% of these elephants survive within large contiguous forests (Naha et al., 2019; Sengupta et al., 2020). The rest depend on small forest ranges under constant pressure from human encroachment. Due to threats such as habitat degradation, human–elephant conflict (HEC), and poaching (Leimgruber et al., 2003; Hedges et al., 2005; Sukumar et al., 2016; Menon et al., 2017), Asian elephants are vested with the highest degree of Wildlife Protection under the Schedule-1 in India. Ongoing conservation efforts are directed toward protecting elephants, but HEC is a serious drawback in finding a tradeoff between anthropocentric development and protection of elephants (Sampson et al., 2019). Thus, effective mitigation of HEC is a top conservation priority for this keystone species, not only in India (Karanth et al., 2012), but also in the world (Chen et al., 2016).

Despite years of research and financial investments on mitigation, we are still lacking knowledge on the fundamentals of HEC (Dickman, 2010; Karanth et al., 2012). This data deficiency is a significant problem affecting the sustainability of HEC mitigation projects. Spatial analysis of HEC patterns is essential for understanding the underlying processes of conflict, and to develop mitigation management plans which prioritize high-risk regions. In general, there is a certain notable relationship between the spatial phenomenon of HEC and the geography of that area. Exploring these significant relationship patterns will not only provide insights about the geographic dispersal of HEC and the underlying drivers, but also allow various stakeholders to detect regions and populations under high risk of HEC, regardless of the area of extent (Huang et al., 2008; Jackson et al., 2009). This study integrated statistical and spatial analyses into human-elephant conflict research for an exploratory pattern analysis and locating the high-risk zones of HEC.

Socio-economic factors such as trust in administration, awareness and education, economic status and religion build communities' tolerance toward elephants while promoting co-existence (Dickman, 2010; Redpath et al., 2015; Nyhus, 2016; Saif et al., 2019). Nevertheless, the competition for limited resources between humans and elephants co-habiting an overlapped landscape remains a leading cause of HEC (Morzillo et al., 2014; Shaffer et al., 2019). In spite of that, very few studies have explored the concepts of spatial distribution of HEC (Sitati et al., 2003; Morzillo et al., 2014; Chen et al., 2016; Kitratporn and Takeuchi, 2020), patterns of crop-raiding and prediction of HEC hotspots (Gubbi, 2012; Acharya et al., 2016; Chen et al., 2016; Naha et al., 2019) except for some studies on compensation distribution patterns (Karanth et al., 2012; Karanth et al., 2013; Sengupta et al., 2020).

Our study is based in the Keonjhar forest division of Odisha province, in eastern India. As per a state government report, Odisha has the highest HEC in India and loses more elephants than other more elephant-bearing provinces. Odisha also recorded the highest number of human deaths due to HEC in 2017–2018, while it only harbors 1,976 elephants, which is less than Assam (∼5,700) and Karnataka (∼6,000) provinces (MoEF and CC, 2018). Keonjhar forest division has evidenced a sharp fall in the elephant population from 112 elephants in 2002 to only 40 elephants in 2017. Such decline in the elephant population is not a consequence of poaching, which is a rare occurrence in the Keonjhar forest division, but as a result of a devastated and fragmented landscape, which has forced elephants to leave their native home range and scatter out into other regions (MoEF and CC, 2017). From 1989 to 2016, 13.7% of the total forest cover in Keonjhar forest division had been lost, mainly due to mining, agriculture and developed areas (Patra and Sethy, 2014; Tripathi et al., 2019). This has led to an escalation of HEC, that took 198 human lives (between 2000 and 2018) and destroyed 20,800 hectares of crop land (during 2005 and 2018). Many researchers who have discussed the issue of HEC in this region have done it from a very human-centric perspective and they have recommended some extremely restrictive measures that disregard the right to natural existence of elephants (Vihar et al., 2012; Thakur et al., 2016; Mohanty and Mishra, 2017).

This study spatially analyzed the distribution of HEC which would facilitate stakeholders to identify high-priority villages for conflict intervention. Thereby, we encouraged mitigation efforts to be focused toward these vulnerable regions and provided suggestions to improve the current mitigation approaches, and to maximize their impacts in a cost-effective manner. Our study aims to: (1) identify significant spatial patterns of HEC distribution, (2) evaluate the number of people under threat of HEC in the clusters using spatial scan statistics, (3) map the hotspots of HEC as well as its different types, and (4) assess the temporal changes in the spatial risk of HEC over the study period.

MATERIALS AND METHODS

Study Area

Human-elephant conflict incidences that occurred in the forest ranges of Keonjhar forest division, East India (**Figure 1**), were the primary data source for this study. The study area is located between latitudes 21°1′ N–22° 10′ N and 85°11′ E–86°22′ E and covers an area of approximately 6,038 km^2. The study area is the mining hub of Odisha province, where minerals like Manganese (Mn), Iron (Fe), and Chromite (Cr) are generally found within forest areas. Nearly 30% of the land is covered by dense forest which mostly include Northern tropical deciduous trees such as, Sal tree (*Shorea robusta*), Asan (*Terminalia elliptica*), Jamu (*Syzygium cumini*), Mahua (*Madhuca longifolia*), Mango (*Mangifera indica*), and Kendu (*Diospyros melanoxylon*). Keonjhar forest division has patchy forests which support 50–60 elephants and act as their movement paths to neighboring states. The study area has around 1,600 villages with a total human population of 1,801,733 people (Census, 2011). About 80% of its residents are classified as rural of which 35% depend on agriculture.

The study area experiences three main seasons; summer, rainy season and winter. The temperature fluctuates depending on the season, with the average temperature during summer being 33–36°C and during winter it is 14–17°C. Rainfall is also highly variable with a mean annual rainfall of around 1,535 mm.

Data Collection and Generation of Spatial Data

We gathered data from all possible sources such as the damage compensation records of the Keonjhar Forest Division, published literature and reports from Indian Ministry of Environment, Forest and Climate Change (MoEF & CC). According to the Wildlife Protection Amendment Rules (2002) (Odisha), compensation shall be paid to the victims for the damages caused by wild animals, after a certain level of verification by the forest and police departments. The scheme encourages the public to voluntarily report losses suffered from wildlife. We collected HEC data recorded by victims from 2001 to 2018, which contains information about the victim's details, village name, date of event, damage caused by elephants to people, property and crops, and the amount compensated according to the loss. The HEC incidences were grouped into three temporal phases such as HEC1 (2001–2006), HEC2 (2007–2012) and HEC3 (2013–2018) for analyzing the trend of HEC pattern over different phases of time in our study area. Although there was no spatial information in the collected data sets, we geocoded the incidents by assigning the centroid coordinate of the village where the incident had happened and prepared a geodatabase for further spatial analysis.

Descriptive Spatial Analysis

The descriptive spatial analysis of HEC incidences was carried out in three steps: (1) pattern detection of HEC distribution by measuring the spatial homogeneity using distance-based Ripley's K-function; (2) neighborhood analysis and investigation of the HEC clusters and; (3) hotspot detection using spatial autocorrelation statistics (**Figure 2**).

Spatial Pattern Detection of HEC Distribution

HEC spatial patterns result from discrete stochastic phenomenon and using inappropriate approaches to analyze the pattern can lead to misrepresentation of the results due to spatial dependency, spatial noise, non-stationarity and heterogeneity (Boots and Getis, 1988; Bailey and Gatrell, 1995; Logan and Martinez, 2018). Our interests lay in the pattern of distribution of conflicts relative to one another, therefore, we preferred a distance-based point pattern analysis. Ripley's K-function was used to interpret the spatial patterns of HEC distribution under the null hypothesis of complete spatial randomness. K-value was calculated using "Kest" function of "spatsat package" in R statistics for the three temporal phases HEC1, HEC2 and HEC3. This function compares the actual value of K (K-true) with expected value of K (K-expected) for assessing spatial regularity (clustering). Edge correction was applied to reduce the bias produced from the non-detectability of points from the random pattern outside the window (Ripley, 1988). The output of this analysis helped us to quantitatively assess whether the cases were driven by chance (random pattern) or some external factors (cluster pattern).

Investigation of HEC Clusters

Spatial-weighted matrix is the key component in constructing spatial autocorrelation statistics. Prior to cluster analysis, a spatial-weighted matrix was executed using higher order queen contiguity, which quantified spatial associations and connectivity among the HEC incidences. The HEC incidences which did not have neighboring incidences were excluded and the resulting matrix was used to construct the spatial autocorrelation (Getis and Aldstadt, 2004).

Although, there are other popular methods for investigating clusters (Kelsall and Diggle, 1995; Duczmal et al., 2006) they were not suitable for our study as they additionally required the geographic information for all non-case data too (Huang et al., 2008). The intention of this investigation was to find out the number of major HEC clusters in the study area. To this end, we used a *K-means* unsupervised clustering algorithm to evaluate the number of HEC clusters "K" in HEC1, HEC2, and HEC3 (James et al., 2013). To find the optimal K for the algorithm, we plotted the number of clusters (from 2 to 15) against the clustering compactness (sum of squares within the corresponding clusters). The algorithm then started randomly assigning each event to the K number of clusters and calculated the mean center of each cluster. Euclidean distance was calculated between each event and the clusters' mean centers. The events were reassigned to a new cluster of closest mean centers and then it recalculated the mean of the new centers. The process was repeated until no points were reallocated to another centroid. The silhouette coefficient (Si) was used to validate the goodness of clustering, where overall positive Si explained the number of clusters in HEC distribution.

Detection of HEC Hotspots

Local indicator of spatial association (LISA) was used to locate hotspots where HEC cases are extreme and geographically homogeneous. LISA uses Moran scatterplot, which is calculated using Local Moran's I and based on Moran scatterplot, all the HEC villages were categorized into four groups: High-High (HH), High-Low (HL), Low-High (LH), and Low-Low (LL). HH-HEC and LL-HEC are positive spatial autocorrelations, where HH represents the clusters center with high HEC cases surrounded by high HEC cases while LL represents the low HEC case clusters surrounded by low HEC cases. HL-HEC and LH-HEC are the negative spatial autocorrelations, which represent the dissimilar values in its neighboring locations (Anselin, 1995). Univariate LISA cluster maps were plotted based on the Moran scatterplot categorization for HEC1, HEC2, and HEC3. Monte Carlo randomization (499 permutations) was implemented to assess the significance. The HEC cases having p-values larger than 0.05 were classified as not significant.

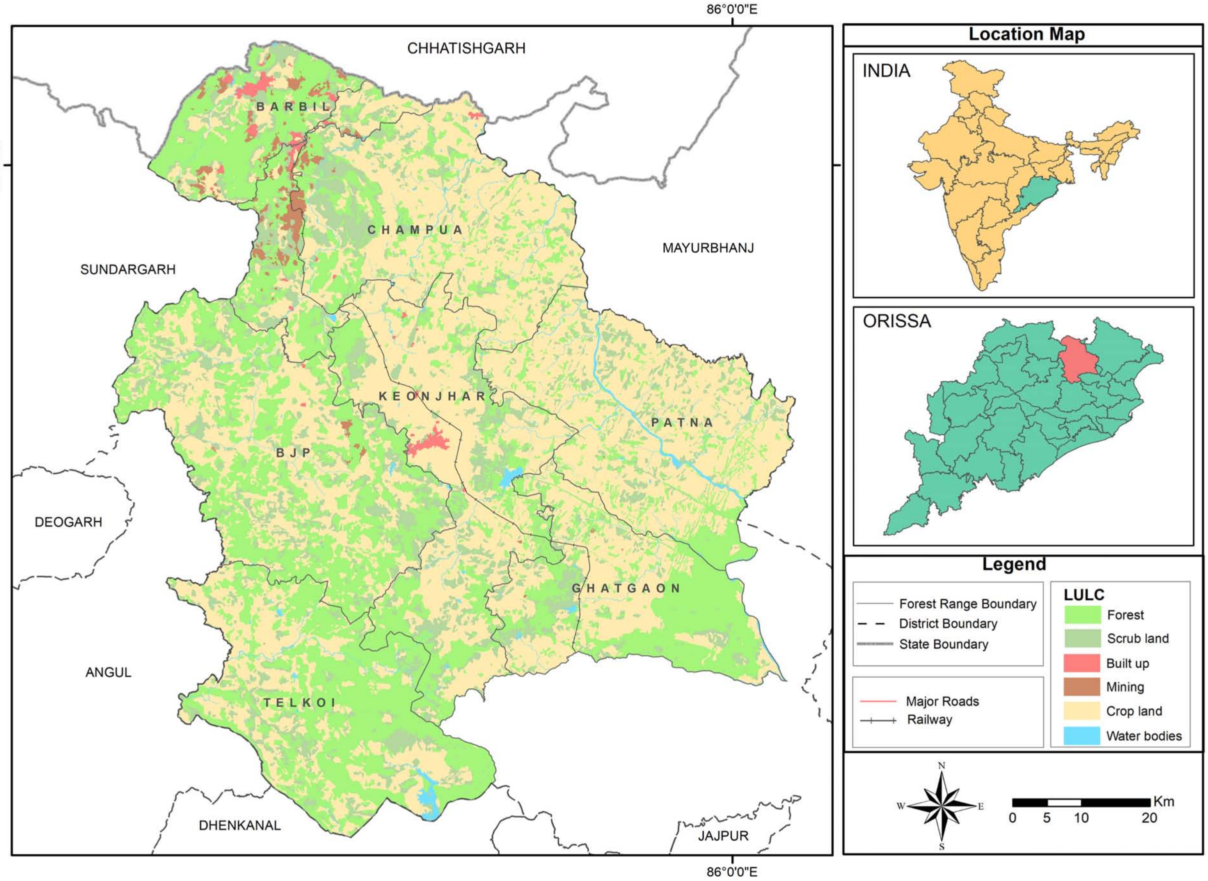

FIGURE 1 | Map showing the land cover and land use of the study area comprising forests, scrub land, built up areas, mining, crop land, water bodies and transportation networks. Keonjhar District has seven-forest ranges: (1) Barbil, (2) Bhui yan-Juang Pihra (BJP), (3) Champua, (4) Ghatgaon, (5) Keonjhar, (6) Patna, and (7) Telkoi. Source: Keonjhar Forest Division.

Mapping Human Populations at Risk

SaTScan a non-parametric spatial scan statistic was used to characterize HEC clusters by scanning with spatial circular windows (SCW). SaTScan uses Kulldorff's technique (Kulldorff, 1997; Kulldorff, 2013) which is the most powerful (Duczmal et al., 2006; Alemu et al., 2013) and widely used method (Zhao et al., 2013; Areias et al., 2015; Ge et al., 2016; Wang et al., 2016) for spatial analysis of irregularly shaped clusters. The scanning position and size of circular window are flexible, which changes for each location of HEC incidence and calculates the number of detected and expected incidences inside the SCW. The size of SCW was determined based on the radius enclosing a minimum of 30% population at risk of HEC. Ma et al. (2016) observed that the windows might be too large to contain the low-risk locations if the window covered 50% of the population, which might lead to a high false positive rate. However, the windows with smaller populations might be too small to detect the real high-risk locations, thereby leading to a high false negative rate. Considering several studies (Ge et al., 2016; Wang et al., 2016; Ma et al., 2016) and the nature of our data we selected the SCW covering 30% of the population at risk and the overlapping SCWs were excluded.

A map of SCW was plotted where each circular window represented significant high risk HEC clusters including the number of people living inside the respective circular windows. SaTScan also calculated the relative risk (RR = ratio of observed HEC counts within the SCW to its expected HEC counts) for each SCW (Kulldorff, 2013), which represented the HEC risk inside the SCWs with respect to outside. The SCWs where the risk within the circular window was twice (RR > 2) that of outside were identified as high-risk clusters (Ge et al., 2016), as the people inside these clusters were more likely to get attacked by elephants than people outside.

Assessing Temporal Trends in the Spatial Variation of HEC Risk

Kernel density interpolation was used to create a continuous surface map of HEC distribution. HH-HEC villages and high-risk SCWs were overlaid on the HEC kernel density map, for better perception of the densest clusters of high-risk HEC regions and its spatial variation over the period of 18 years in the study area.

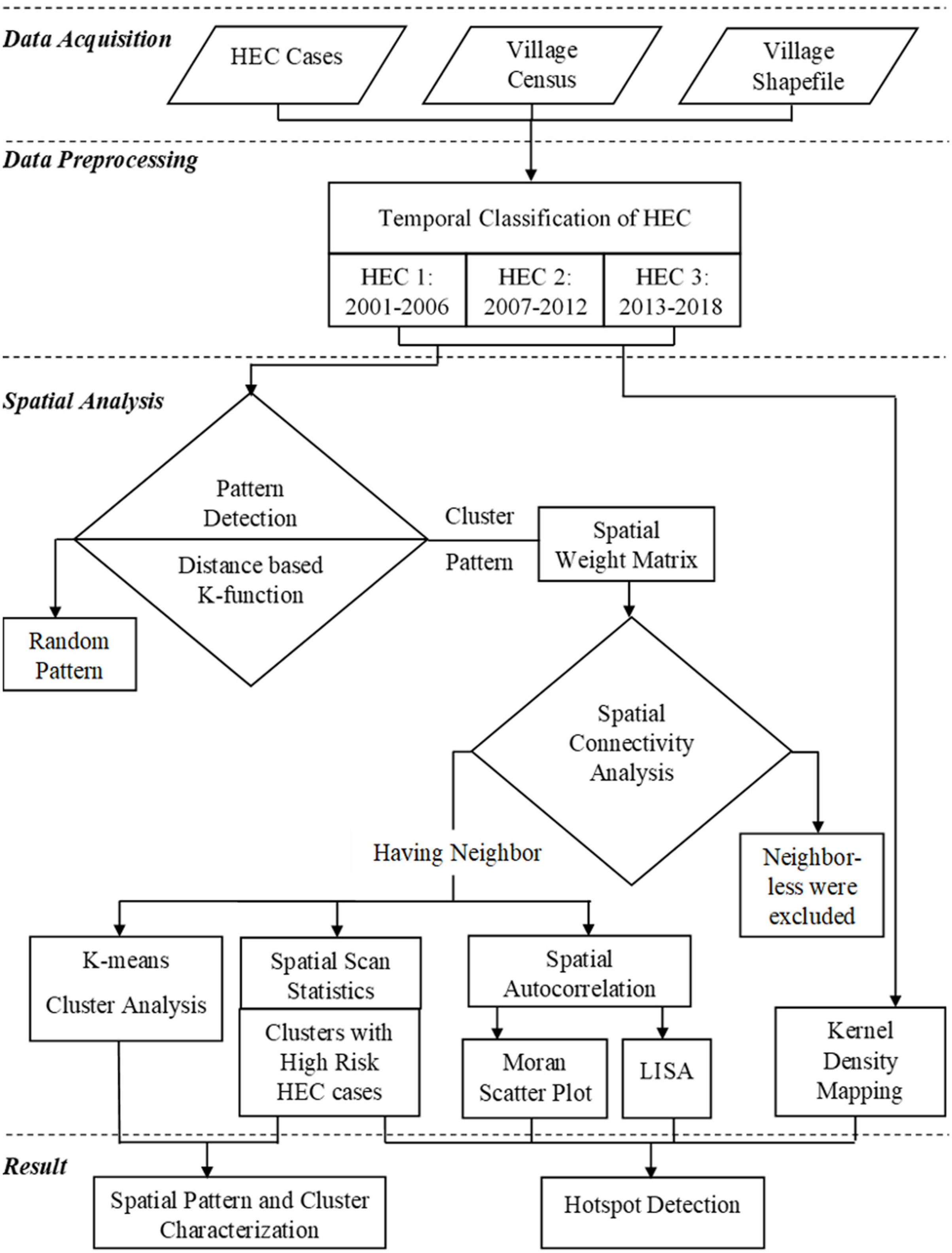

FIGURE 2 | A methodological flowchart for this study.

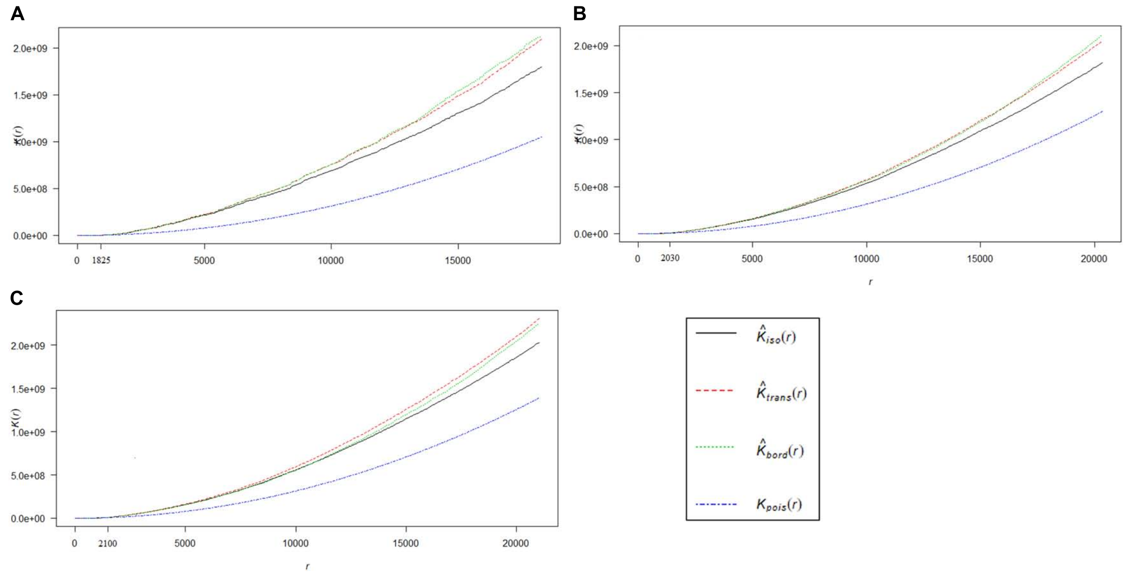

FIGURE 3 | The graph represents the result of inferential analysis of K-function, which is statistically deviating from complete spatial randomness. Distribution of the true values of K [Kpois (r)] for HEC1 **(A)**, HEC2 **(B),** and HEC3 **(C)** incidences (blue line), which is compared to their corresponding expected values [Kiso (r) in black line, Ktrans (r) in red line and Kbord (r) in green line]. HEC incidences are clustered at distances greater than 1.825 km, 2.03 and 2.1 km for HEC1, HEC2, and HEC3 respectively. Note: The isotropic, translate and border corrections are executed by default in the K-function of R.

Spatial Distribution of HEC Impacts on Human Life and Property

To illustrate the distinction and the underlying patterns of severity of HEC impacts on human lives, property and crops, HEC data was categorized into three classes; human casualty (human death and injury), house damage and crop raiding. We extracted the hotspot villages for each type of HEC using Moran scatter plot and LISA (according to the method followed in the section "Detection of HEC Hotspots"). Separate Kernel density maps were plotted for human casualty, house damage and crop raiding. Subsequently, the High-High hotspot villages of each HEC type were overlapped over the corresponding kernel density surface to assess the regions that were highly impacted by human death and injury, house damage and cropland destruction.

Software Tool

The SaTScan^{TM} software (v 9.6, Kulldorff and Information Management Services, Inc.) was used to determine the high-risk clusters and to characterize the SCW. Open GeoDa software (Arizona State University, United States) was used for Moran scatterplots and LISA analysis. ArcGIS (v10.6, ESRI Inc.) was used to plot the HEC kernel density map. R (v3.6.1) was used for pattern detection using *Ripley's K-function* and cluster analysis using *k-means* function.

RESULTS

Spatial Patterns of HEC

Ripley's K-function test provided evidence against the null-hypothesis of complete spatial randomness, i.e., the spatial pattern of HEC1, HEC2, and HEC3 were observed to be significantly clustered (**Figure 3**). We found that HEC incidences in HEC1 (**Figure 3A**), HEC2 (**Figure 3B**), and HEC3 (**Figure 3C**) appeared to be more clustered than expected at distances greater than 1.8, 2, and 2.1 km, respectively.

A summary of spatial weighted matrix of higher order queen contiguity for HEC1, HEC2 and HEC3 are listed in **Supplementary Table 1**. The number of neighbors for each observation is shown in a connectivity histogram (**Supplementary Figure 1**), while the neighborhood structure is shown in connectivity maps (**Supplementary Figure 2**).

Characterization of HEC Clusters

The dissimilarity within the clusters is shown in a group sum of squares chart (**Figure 4**) for selecting the optimal K. The curve is monotonically decreasing, so it was difficult to figure out the point where the curve starts to flatten out. The change in the within-cluster sum of squares was observed to be increasing as the number of clusters reduced from 4 to 3 for HEC1 (**Figure 4A**) and HEC2 (**Figure 4B**) and 5 to 4 for HEC3 (**Figure 4C**).

We set K = 3 for HEC1, K = 3 for HEC2 and K = 4 for HEC3, whose cluster compactness (**Table 1**) was 70.1, 69.8, and 77.6% respectively. Silhouette coefficient supported the evidence that the selected numbers of clusters were optimal as the overall silhouette values were positive (Si = 0.42 for HEC1, Si = 0.44 for HEC2, and Si = 0.40 for HEC3). The aim of this analysis was not to achieve 100% compactness within the clusters but to identify a reasonable number of clusters which could potentially explain a considerable part of the HEC distribution. The cluster centers for HEC1 were located in Keonjhar, BJP, and Ghatgaon forest ranges, for HEC2 in the border of Ghatgaon and Patna,

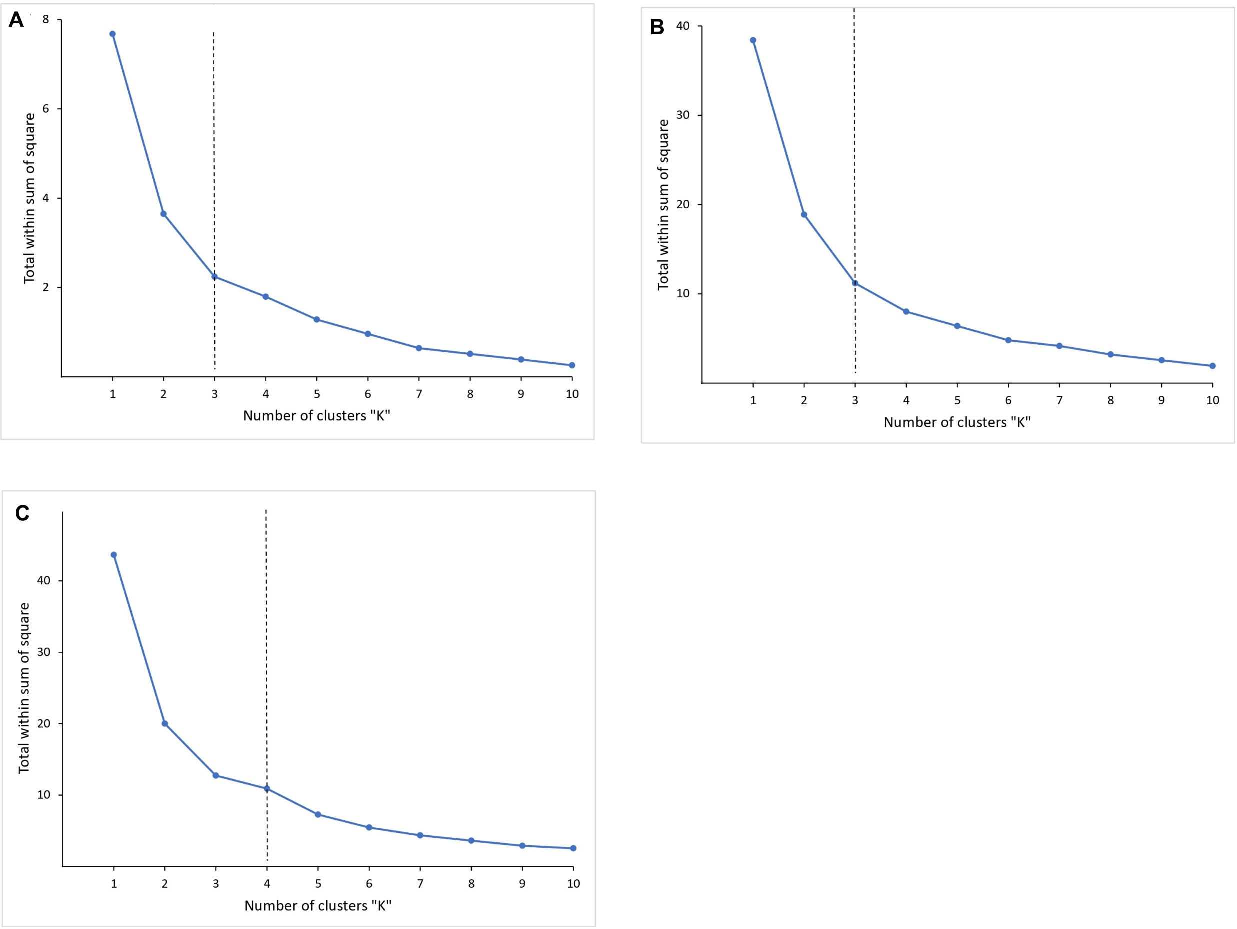

FIGURE 4 | The graph is showing the dissimilarity within the clusters by calculating the within clusters sum of squares for corresponding number of clusters. The curves are not showing an obvious point where the curve starts to flatten out. However, it can be observed from the curves that it is decreasing at k = 3, k = 3 and k = 4, which can be considered as optimal-K for respective HEC1 **(A)**, HEC2 **(B)**, and HEC3 **(C)**.

Champua and Telkoi forest ranges and for HEC3 in Keonjhar, Champua, border of Champua and Patna and Telkoi forest ranges (**Supplementary Figure 3**).

HEC Hotspots

The Moran scatterplot (**Supplementary Figure 4**) represents the linear fit through the standardized HEC values, where the slope corresponds to Moran's I value [HEC1 = 0.112 (**Supplementary Figure 4A**), HEC2 = 0.039 (**Supplementary Figure 4B**) and HEC3 = 0.071 (**Supplementary Figure 4C**)].

The LISA cluster map (**Figure 5**) augments the location of significant HEC hotspots derived from the Moran scatter plot. However, we have only focused on the HH-HEC locations to identify the hotspots. The hotspots during HEC1 (**Figure 5A**) were mainly identified in Keonjhar, Ghatgaon and in the border of BJP and Keonjhar forest ranges. During HEC2 (**Figure 5B**) the hotspots were found in Keonjhar and Champua forest ranges with few HH-HEC clusters in Ghatgaon and Patna forest ranges. These regions were also observed to be hotspots during HEC3 but with a greater areal extent in the Champua forest range (**Figure 5C**).

Populations at Risk Within HEC Clusters

The significant high-risk HEC clusters were represented in SCWs (0.5–10 km radius of blue circles) (**Figure 6**). The RR of significant SCWs (**Table 2**) for the whole study period ranged from 2.708 to 6.682. We found 4 SCWs for HEC1, where $W_1$3 SCW (radius 4.3 km) in Ghatgaon forest range (**Figure 6A**) with a population of ∼5,200 people were recorded as the most vulnerable zone for HEC1. The RR of $W_1$3 SCW was 2.085, indicating that the risk of HEC within the particular SCW was higher than that of outside. Around 10 SCWs were found for HEC2, where ∼13,800 residents (RR = 2.126) living in the $W_2$6 SCW (radius 4.7 km) of the Champua forest range (**Figure 6B**) were exposed to high risk of HEC. In the same period, $W_2$1 SCW (radius 3.9 km) in the Keonjhar forest range was also identified as a highly conflicted region with ∼6,150 people (RR = 3.134) under threat. We observed 12 SCWs for HEC3 (**Figure 6C**) where respective populations of ∼17,500 (RR = 1.971), ∼11,800

TABLE 1 | List of different number of clusters according to within sum of squares with their cluster compactness values (cc%) and silhouette values (Si).

HEC1			HEC2			HEC3		
No of clusters (K)	cc%	Si	No of clusters (K)	cc%	Si	No of clusters (K)	cc%	Si
$K = 3$	70.1	0.42	$K = 3$	69.8	0.44	$K = 4$	77.6	0.40
$K = 4$	75.3	0.40	$K = 4$	76.8	0.39	$K = 5$	80.5	0.32

It shows that K = 3, K = 3, and K = 4 are the optimal K values for HEC1, HEC2, and HEC3.

(RR = 1.923) and ∼16,250 (RR = 1.708) people living within the respective SCWs; $W_3 3$, $W_3 4$, and $W_3 6$ (radius 4.8, 4.6, and 7.01 km) of the Champua forest range were highly vulnerable to HEC. Apart from the Champua forest range, $W_3 2$ SCW (of radius 3.2 km) in the Patna forest range with a population of 3648 (RR = 2.505) was also identified as a major SCW with a significant risk of HEC.

Temporal Trends in the Spatial Variation of HEC Risk

The kernel density map was created where the risk indices were ranging from 0 to 1 and equally divided into five groups: (1) non-risk areas (0–0.2), (2) very low-risk areas (0.2–0.4), (3) mid-risk areas (0.4–0.6), (4) high-risk areas (0.6–0.8) and (5) very high-risk areas (0.8–0.1). The densest clusters of high-risk HEC regions were distinguished by the commonly overlapped areas on the HH-HEC villages and SCWs maps overlaid on the kernel density map (**Figure 7**).

During HEC1, the high-risk HEC regions were spatially concentrated in the border of Keonjhar and Ghatgaon forest ranges (**Figure 7A**), which scattered throughout the study area (**Figure 7B**) during HEC2. Around 20 villages primarily from the Ghatgaon forest range and nearly 30 villages, majorly from Keonjhar forest range were found to be highly affected by elephant attack during HEC1 and HEC2, respectively (**Table 2**). The spatial risk was severely intensified throughout the landscape and concentrated in the northern part of study area during HEC3 (**Figure 7C**), where around 45 villages were found to fall within the high-risk zone of HEC (**Table 2**).

Spatial Variation in HEC Impacts on Human Life and Property

In the seven forest ranges of Keonjhar forest division, 35,900 HEC cases were recorded from approximately 530 villages during 2000–2018. Wherein, the casualty was noted at ∼300 people and additionally hundreds of people were injured by elephants. We observed that human casualty incidents due to HEC had occurred in nearly 50 villages, among which 25 villages were entirely from the Keonjhar district (**Figure 8A**). The highest casualties were reported from villages in the Keonjhar forest range and its border to Ghatgaon and Champua ranges. Analysis of house damage showed that about 30% of total houses damaged by elephant attacks were completely destroyed and the rest were partially damaged. The house damage incidences were spread all over the study area (**Figure 8B**) and spatially concentrated in Keonjhar and Champua forest ranges, where the number of highly impacted villages were 22 and 12 respectively. Moreover, crop damage was the most challenging issue in the study area, with 5,140 hectares of cropland being raided and ruined by elephants. The intensity of crop damage which was experienced all over the landscape, was also very high in comparison to human death and house damage (**Figure 8C**). Champua forest range was the most susceptible to crop damage followed by Telkoi, Keonjhar and BJP forest ranges. Around 35 villages were found to be highly impacted by crop raiding in the Champua forest range, followed by around 25 villages in the Telkoi forest ranges. The Barbil forest range bordering the Champua range recorded the lowest crop raiding incidents in the study area with only a few affected villages.

DISCUSSION

Human disturbance and land use change has limited original habitats of elephants (Leimgruber et al., 2003; Choudhury et al., 2008; Naha et al., 2019; Sampson et al., 2019). Converting habitats to cropland, urban spaces and linear construction (road, railway, channels and bridges etc.) influence the natural patterns of elephant movement (Dasgupta and Ghosh, 2015). Such fragmented habitats cause elephants to come into closer proximity and greater contact with human society as elephants seek to fulfill their nutritional, ecological and behavioral needs (Sukumar, 1990). This overlap in the space use between people and elephants lead to more frequent conflict (Wilson et al., 2015; de la Torre et al., 2021). Although past studies have analyzed spatial variation of HEC, conceptual obstacles still exist due to the complex nature of the relationship between HEC and its occurrence in a specific spatial context. Controlling elephant depredation requires proper understanding of the conflict distribution patterns across time and space scales (Gastineau et al., 2019; Williamson et al., 2020) and spatial risk assessment can be a valuable mechanism in locating the HEC hotspots.

Interpretation of Spatial Trends in HEC Prone Zones

The conflict incidences were concentrated to a few regions in the central part of the study area during HEC1, where ∼15,000 people suffered from damage caused by elephants. During HEC2, conflicts spread all over the landscape, putting ∼23,600 people from the Champua and Keonjhar forest ranges in high HEC risk. Around 1.02% (62 km^2) of the total area was under high risk of conflict during HEC1 and 1.82% (110 km^2) during HEC2, which increased to 5.46% (330 km^2) during HEC3. As a result, ∼85 km^2 within the Champua forest range became the largest

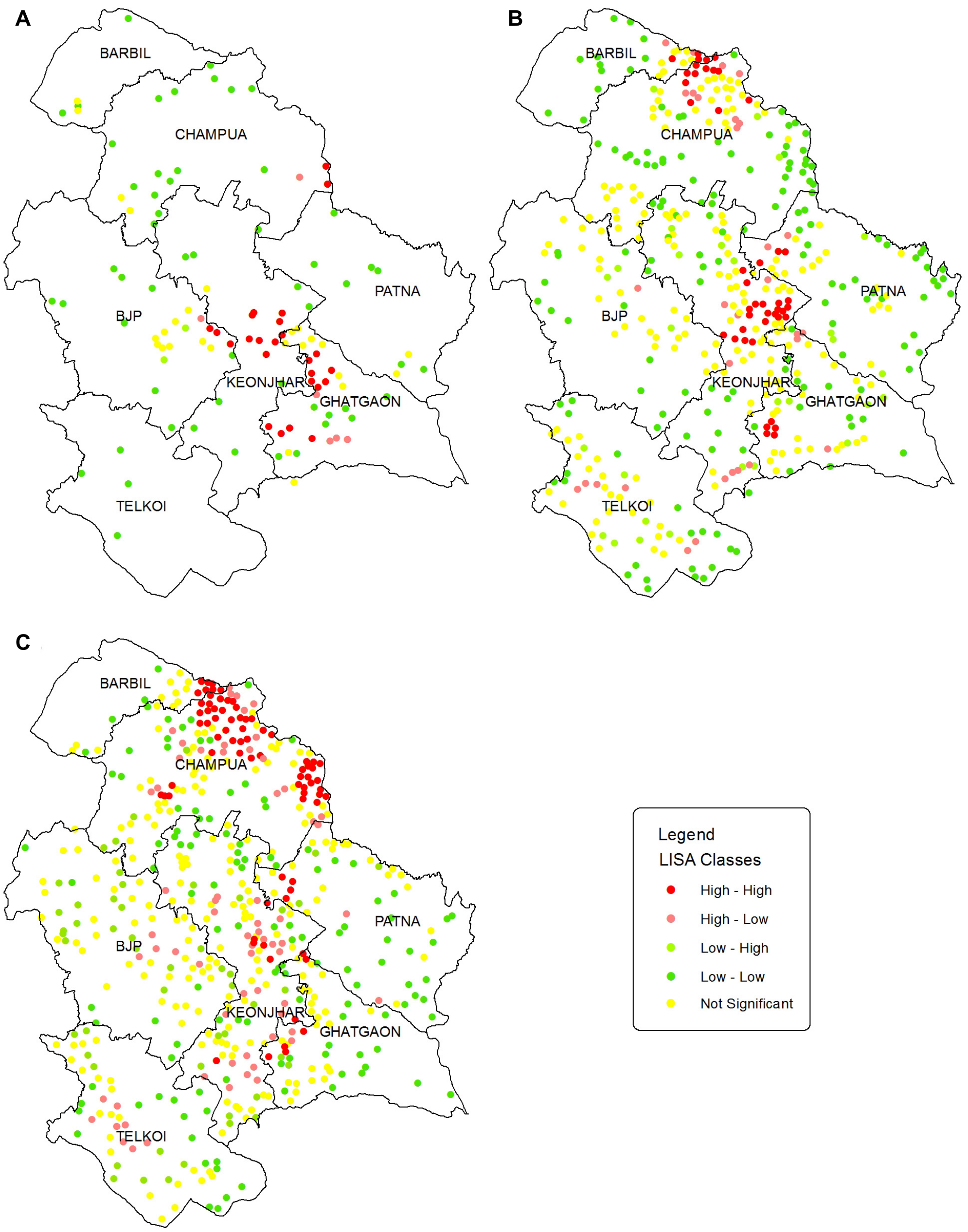

FIGURE 5 | Maps showing the LISA significant point clusters for HEC incidences in Keonjhar district for **(A)** HEC1, **(B)** HEC2, and **(C)** HEC3. LISA cluster maps were classified into 4 classes based on Moran scatterplot categorization. The HEC cases having *p*-values larger than 0.05 were classified as not significant and shown in yellow dots. The dark red and dark green locations are indications of positive autocorrelation (HH; high HEC values surrounded by high, and LL; low HEC values surrounded by low) while, the light green and light red are negative autocorrelation indications (LH; low surrounded by high and HL; high surrounded by low HEC cases).

area under high risk during HEC3, where the vulnerable human population to elephant attack was ∼45,500 people. Besides, Keonjhar, Ghatgaon and Patna forest ranges also have shown a steady rise in conflicts since HEC1. Owing to the periodical movement of elephants from neighboring provinces to the northern parts of the study area (Chatterjee, 2016; Das et al., 2018; Kanga et al., 2018), the indiscernible conflict risk in Champua and Barbil ranges during HEC1 had distinctly heightened by HEC2. Barbil forest has an elephant corridor connecting it to a forest reserve in the neighboring province (Jharkhand), which also happens to overlap with rich mineral resources in this area. The elephant range surrounding the corridor and the elephant movement pathways were encroached by mining and subjected to other biotic pressures from villages such as extraction of fuel

TABLE 2 | Table showing the results from the Kulldorff's spatial scan statistics performed in SatScan and the HH-HEC villages inside each SCW.

Temporal session	Forest range	Spatial circular window (SCW)	Radius of SCW	Human population inside SCW	No. of HH-HEC villages inside the SCW	Relative risk (RR)
HEC1	Keonjhar	$W_1 1$	8.3	4,879	9	1.710
	Ghatgaon	$W_1 2$	4.5	4,268	7	1.995
		$W_1 3$	4.3	5,191	3	2.085
	BJP	$W_1 4$	4.47	386	0	5.900
HEC 2	Keonjhar	$W_2 1$	3.9	6,151	13	3.134
		$W_2 2$	1.2	1,783	0	2.973
		$W_2 3$	3.4	3,589	5	2.289
	Ghatgaon	$W_2 4$	3.1	2,507	5	2.696
		$W_2 5$	1.1	429	0	4.468
	Champua	$W_2 6$	4.7	13,802	6	2.126
		$W_2 7$	1.02	795	0	3.623
		$W_2 8$	0.74	344	0	6.682
	Patna	$W_2 9$	3.03	3,309	2	2.038
	Telkoi	$W_2 10$	3.7	1,579	0	2.291
HEC 3	Patna	$W_3 1$	0.86	296	0	5.893
		$W_3 2$	3.44	3,383	2	2.505
	Ghatgaon	$W_3 7$	3.7	3,363	0	3.581
	BJP	$W_3 12$	2.6	1,777	0	2.370
	Champua	$W_3 3$	4.8	17,476	8	1.971
		$W_3 4$	4.6	11,775	9	1.923
		$W_3 5$	2.03	2,483	4	3.420
		$W_3 6$	7.01	16,255	18	1.708
	Keonjhar	$W_3 9$	5.4	1,387	0	2.760
		$W_3 10$	1.7	1,297	3	3.655
		$W_3 11$	2.02	3,648	0	2.000
	Telkoi	$W_3 8$	5.7	2,304	0	3.498

We estimated the radius of each SCW and the number of people living inside the respective SCWs for each forest range in the Keonjhar district.

wood and other forest products (Vihar et al., 2012; Menon et al., 2017). This in turn has led to a higher degree of HEC.

The conflict scenario in and around the central part of the study area has prevailed throughout the 18-year period. The southern extent of Keonjhar forest range is more likely to harbor permanent herds of elephants because it is in close proximity to the current Asian elephant habitat range (Menon et al., 2017). Therefore, the possibility of conflicts remains high due to increased infringement of elephant habitats by agriculture and rural settlements. The rate of declining forest density in the study area (**Figure 7**) can also be recognized as a factor contributing to the elephant menace due to its impact on shrinking elephant habitats (Vihar et al., 2012). The dense forest cover has been decreased by almost 40% between 1990 and 2000 and by 51% from 2000 to 2012 (Patra and Sethy, 2014; Tripathi et al., 2019), majorly due to mining and agriculture followed by urbanization, timber smuggling (Tripathi et al., 2019), and forest fires. Frequent explosions, transportation of ores and dumping of waste from the mining industry also disturb the tranquility of elephant habitats. Additionally, pollution and drying up of perennial streams (Harichandan et al., 2017) cause elephants to move away from their native territory in search of water. Consequently, elephants are attracted toward easily accessible sources of food and water in the nearby villages, which is leading to frequent conflict with the human society in this landscape.

Interpretation of HEC Impact on Human Life and Property

Crop damage was the most frequent form of HEC, which was spread persistently across the landscape (**Figure 8C**) predominantly in Champua, Telkoi and Keonjhar forest ranges. The forest covers of these respective ranges have been degraded by 9.5, 11, and 23% from 2001 to 2018, with an overall decline in 18% of the forest cover throughout the whole study area. The forests have been majorly converted to cropland and settlements (Vihar et al., 2012; Patra and Sethy, 2014; Tripathi et al., 2019) creating fragmented habitats which elephants continue to use for their sustenance because of their firm loyalty to their traditional home ranges (Baskaran et al., 1993; Cushman et al., 2005). Besides, cropland was dominant over other land use types in the hotspot regions, where paddy crops hold ∼50% share of crop area (Sahu, 2020) and are highly preferred by elephants over natural forage due to its easy accessibility, nutrition and palatability (Sukumar, 1990; Campos-Arceiz et al., 2009). Therefore, the conversion of elephants' traditional home ranges into crop lands, along with dietary preferences of elephants cause frequent crop raiding in these hotspots.

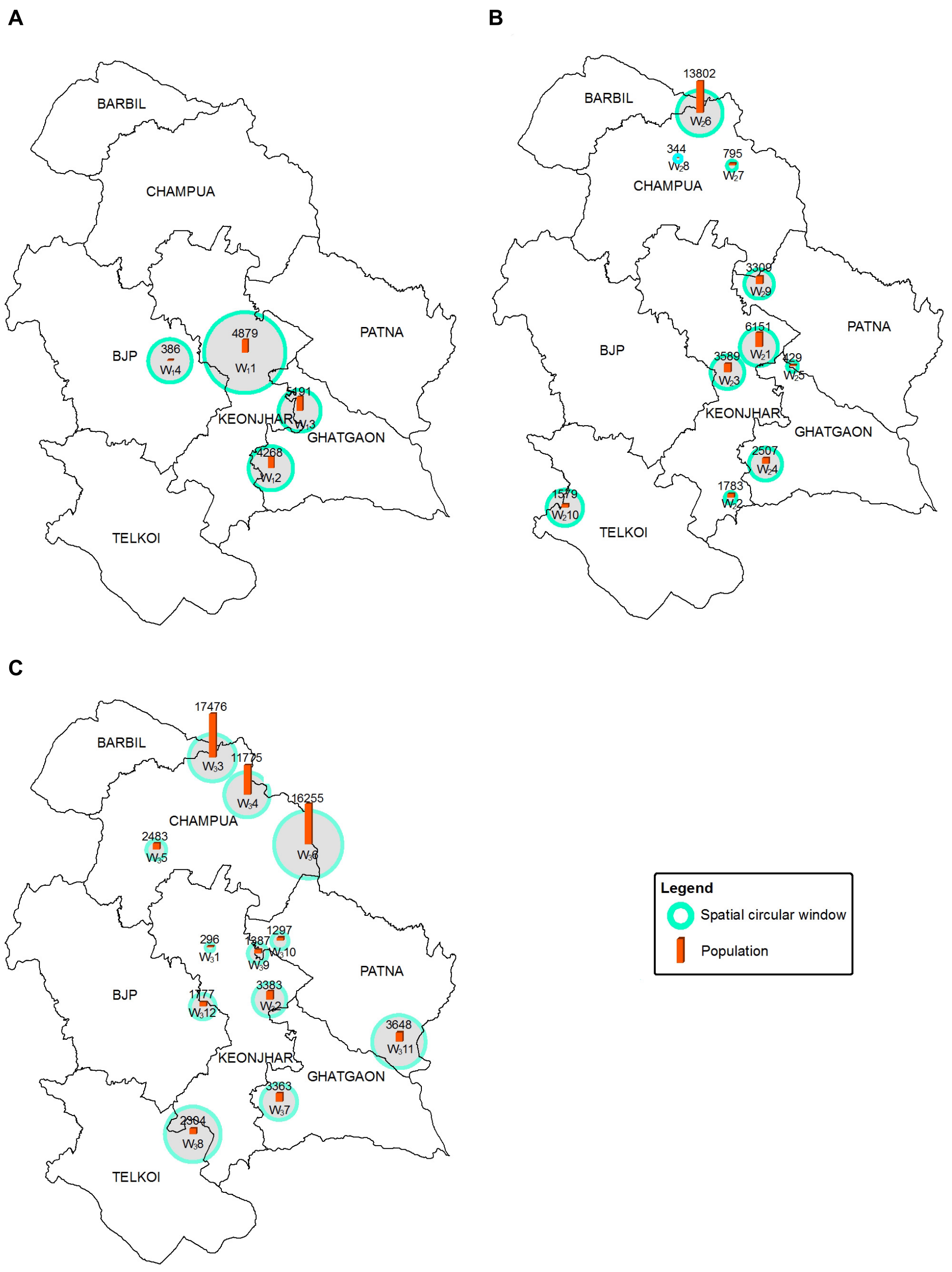

FIGURE 6 | Maps showing the geographical locations of high-risk HEC SCWs for HEC1 **(A)**, HEC2 **(B)** and HEC3 **(C)** where blue circles of radii ranging from 0.5 to 10 km show the SCWs. The red bars plotted within the SCWs show the number of people at risk in each SCW.

The intensity of human casualty was found to be much higher in the central part of the study area (**Figure 8A**) followed by Champua, Patna and Ghatgaon forest ranges with lower intensities. The decline in forest cover due to human intervention has degraded elephant habitats leading to increased clashes between elephants and people. The higher casualties in the central region can be attributed to high human density (settlements) surrounding the elephant range. However, while the settlements in Patna are dispersed, and its highly fragmented forest patches which are too small to host elephant herds, thereby reducing the chance of casualties due to HEC in that area. Elephant attacks are mostly accidental in nature and driven by the lack of awareness of local residents, who either venture into the forest or settle and cultivate in elephant ranges (Sukumar, 2003; Sahu and Das, 2012; Mishra et al., 2015; Chatterjee, 2016). Also, there seems

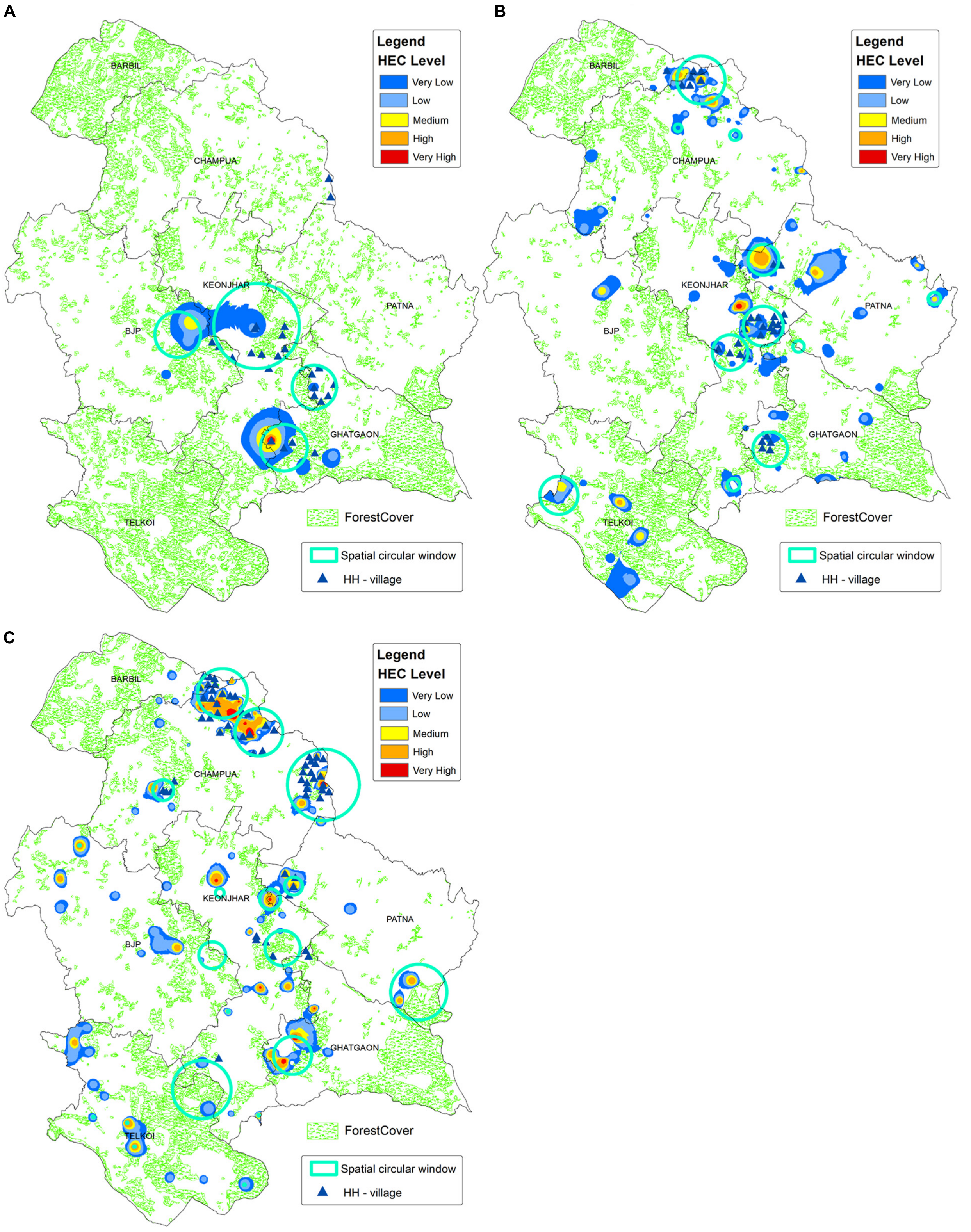

FIGURE 7 | The descriptive map showing the regions highly affected by HEC, which was generated by overlaying high-high HEC and SCWs over kernel density map, for **(A)** HEC1, **(B)** HEC2, and **(C)** HEC3. The kernel density layer is showing the smooth surface map of HEC cases, where the shades of red regions have the highest density of HEC cases. Forest cover data for 2006 **(A)**, 2012 **(B)**, and 2018 **(C)** is given in the background, which is showing a decreasing trend in forest cover from HEC1 to HEC3.

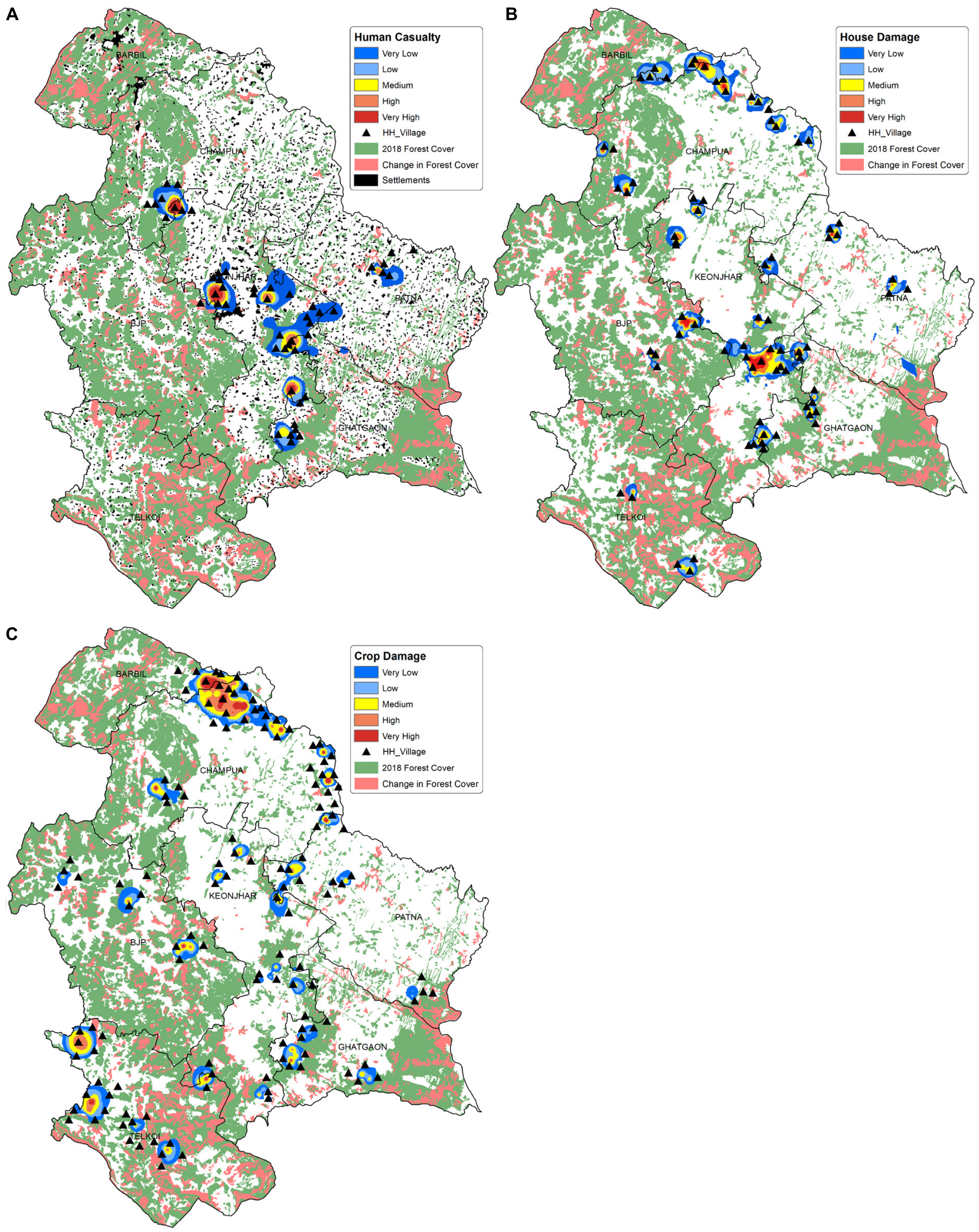

FIGURE 8 | Map illustrating the spatial distribution of HEC impacts on human life and property where **(A)** Human casualties (death and injury), **(B)** House damage and **(C)** crop damage in the study area. The smooth surface layer in the map is showing the intensity of conflict and the triangle-dots are representing the highly impacted villages. The forest cover map of year 2018 is projected in green, while the change in forest cover between 2001 and 2018 is shown in pink. The human settlements are shown in black patches in **(A)** (Source of Human settlement and forest cover data: Keonjhar Forest Division).

to be a high recurrence of house damages in Keonjhar and Champua forest ranges compared to other areas. **Figure 8B** illustrated that the distribution of house damages was majorly concentrated in the fringe zone closer to the forest border. Based on literature, it is more likely that houses located within 200m to 1km of a farmland, water source and/or elephant habitat range are frequently raided due to the higher and easy availability of stored grains, kitchen food and local brew (Chartier et al., 2011; Wilson et al., 2015; Gross et al., 2021).

Strengths and Limitations of the Study

In similar studies, significant variables were used to predict the probability of conflicts by employing grid-based geostatistical method (Sitati et al., 2003; Chen et al., 2016) and machine learning techniques (Maxent) (Naha et al., 2019). Taking the scale of study area and limited availability of high-resolution variables into consideration, we used a flexible scan statistic along with Moran's I and kernel density to identify the risk prone zones to elephant attack. This upgrades the conventional method of evaluating the number of villages in HEC affected areas proposed by Gubbi (2012), by combining SCWs and LISA cluster map, in addition to assessing the human population vulnerable to elephant attack in these hotspots. While studies usually considered either overall HEC (Gubbi, 2012; Naha et al., 2019) or a particular type of HEC (Sitati et al., 2003; Wilson et al., 2015; Chen et al., 2016) to analyze the spatial aspect, we derived hotspots for overall HEC as well as different types of HEC, separately.

A major limitation of this study is reliance on compensation data as it might not reflect actual intensity of conflict (Karanth et al., 2018). All the victims of HEC might not have claimed compensation and there could also be instances where damage due to other wildlife are reported as damage from elephants. These instances can lead to a false estimation and mislead the interpretation outcome. Also, compensation schemes vary on factors like; economic status of the country, political scenario, degree of awareness, literacy and sometimes also gender, religion etc. (Agarwala et al., 2010; Karanth et al., 2012, 2013, 2018; Manral et al., 2016; Johnson et al., 2018), which could restrict voluntary reporting by victims. To overcome this, future studies can include surveys to compare the actual scenario with the estimations obtained from the hotspots as well as in the least/not affected regions. The absence of HEC spatial locations was another limitation, which might have led to some spatial error in estimating hotspot zones, resulting in a small degree of variation on the ground level. However, as the study objective was to map the HEC hotspot regions/villages, the precise location of HEC incidences were not required. Additionally, to overcome this spatial error in future studies it is advisable to conduct a preliminary survey to collect the actual locations of HEC for error estimation. Although, compensation records are prone to the above-mentioned errors, in the absence of primary data they are a faster and effective way for assessing the levels of conflict intensity (Sengupta et al., 2020) of a landscape. It also helps to address the lack of primary data availability since there is barely any published information in the study area at the village scale.

Implications and Recommendations

Analyzing spatial patterns of HEC and identifying high risk areas is important for policy formulation, HEC management and planning. It provides better context of the risks associated with the identified hotspots which helps to maximize the effectiveness and minimize the cost of HEC management, by ensuring efficient resource allocation to these zones. Finding hotspots for different types of HEC helps in devising streamlined compensation policies, whilst expanding the scope of mitigation measures. For instance, human casualty hotspots can be prioritized over property or crop damage hotspots when mitigation funds are scarce, as the cost of human casualty precedes cost of property or crop damage (Gulati et al., 2021). Furthermore, outcomes of this study will help forest administrations to develop location-based strategies and determine suitable locations to implement mitigation plans such as early warning systems, bio or non-lethal fencing, and restoration of wildlife habitats and corridors. Formulation of spatial baseline data on HEC hotspots, as demonstrated in our study, could contribute to improvement of regional databases which may further help in catalyzing larger analyses and collaborations.

This study makes the following recommendations based on the interpretations of its outcomes. The limitations of this study have brought to our understanding that having access to a detailed long-term dataset is key to a more dynamic analysis. Therefore, we recommend upgrading and strengthening HEC data collection protocols by adding the geolocation and other relevant information such as time of incidence and characteristics of species etc., which improves the utility of collected data in resolving conservation issues. Also, the data collection procedures should be reviewed and validated periodically by conducting ground-level surveys. As a proactive conflict management strategy toward coexistence, it is important to spread awareness on the compensation and insurance schemes (Merkle et al., 2011), which will also increase the reporting rate of HEC incidences by the victims. Apart from compensation schemes, we advocate for government collaborations with the forest division in promoting more community-based initiatives such as village response teams in vulnerable regions.

Before initiating any mining/industrial projects effective land-use planning should be carried out, where the changes in the land-use type and its consequences on elephant movement behavior along with their routes are considered. The hotspot map developed in our study can be considered as a baseline for such land use planning activities and it can also be used by the wildlife authorities in prioritizing different areas for promoting elephant conservation initiatives in this landscape. Future mitigation plans should focus on assessing elephant habitat utilization and reconfiguring their movement pathways to avoid further encounters with human society. Given the increasing trend in HEC and factors influencing elephant movement behavior (Chiyo et al., 2005) there is scope for future research in determining the significant factors affecting HEC distribution. Conservationists can further probe into factors (landscape characteristics, proximity between the conflict sites and elephant habitats etc.) that influence a site's vulnerability to HEC. Future studies can also focus on potential inequalities in HEC by examining the socio-demographic status of people living within the identified high-risk zones compared to people outside.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because with the permission of District Forest Department we can share the data. Requests to access the datasets should be directed to Divisional Forest Officer, Wildlife Division, Keonjhar, Govt. of Odisha - India, Email: rti-ori@nic.in Phone: 91- 674-2391356 Fax: 91- 674-2390818.

ETHICS STATEMENT

The animal study was reviewed and approved by the Mr. Santosh Joshi (Indian Forest service), District Forest Officer, Keonjhar Forest Department, Odisha, India.

AUTHOR CONTRIBUTIONS

BT developed the theory. XL supervised the finding of this work and manuscript improvement. XL, BT, and NC conceived the framework and methodology of the study. BT, SK, and WW provided a factual review and helped write the manuscript. BT, SK, WW, and KM performed data collection, pre-processing, spatial analysis, and validation. MS, LK, and BT did a major discussion of results and recommendation. All the authors have given their contributions in many ways and provided essential feedback to shape the research.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.640624/full#supplementary-material

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Novel Quantitative Method for Assessing Driving Forces of Landscape Succession: Case Study From Yancheng Coast, China

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Variations in landscape patterns can provide key information on the effects human activity has on landscapes, and consequently, have received increased attention in recent years. This paper mainly deals with the spatio-temporal variation and driving force of the landscape pattern on the Yancheng coast using remote sensing and GIS. The results indicate the following: (1) The landscape was mostly farmland from 1984 to 2008, not wetlands. The landscape matrix changed from a situation in which the natural landscape was equal to the artificial landscape in 1984, while the latter was dominant between 1990 and 2008. The area of natural landscape decreased considerably—the proportion of natural landscapes was 51.07% in 1984, while it decreased to 28.82% in 2008. Artificial landscapes increased significantly—the majority of the increased artificial landscapes were farmland and aquaculture ponds. (2) The changes in these landscapes showed a trend, changing from natural landscapes to artificial landscapes. Salinity is the decisive factor of this fixed route o the landscape successions of the coast. (3) Although Yancheng wetland nature reserve was established in 1984 and was designated as a National Nature Reserve in 1992, anthropogenic activities on the Yancheng coast continue apace, and the trend of natural landscape loss has not changed. (4) According to the analysis of the landscape transition rate of the Yancheng coast during each phase, we concluded that the main driving force of coastal landscape succession was anthropogenic activities. Our method provides a novel quantitative method to assess the driving forces behind landscape successions.

Keywords: landscape pattern, driving force, natural landscape, artificial landscape, Yancheng coast, landscape succession, nature reserve

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INTRODUCTION

Landscape pattern variations can provide crucial information on the effects of anthropogenic activity on landscapes, and this topic has consequently received much attention in recent years (Baus et al., 2014; Currin et al., 2015; Skilodimou et al., 2018). The coast is an ecotone with interactions between marine effects, land, and atmospheric processes, biological effects, and anthropogenic activities (Noble et al., 2003; Lee et al., 2006). It is also a fragile ecotone that is sensitive to environmental changes (Rosenberger et al., 2008; Kong et al., 2015). The coast is a suitable habitat for many endangered waterfowl used for breeding and wintering, and plays a significant role in environmental regulation and biodiversity conservation. On the other hand, anthropogenic activities have become the main factors of coastal landscape succession. With population increases and rapid economic development, coastal resources have been over-developed by tideland reclamation, coastal projects, and so on (Lei and Zhang, 2005; Chen et al., 2017), which can lead to the invasion of alien species and coastal pollution.

The Millennium Ecosystem Assessment shows that the coast suffers more interference. In particular, natural habitats have decreased significantly, which poses a serious threat to biodiversity on the coast [Millennium Ecosystem Assessment [MEA], 2005]. All around the world, coastlines are subjected to the contradiction between resource exploitation and environment protection, which is the main reason that integrated coastal management has become a global hot topic in recent years (Farmer and Parent, 1997; Hu and Xiao, 1999; Falcucci et al., 2007; Garza, 2008; Schwemmer et al., 2008). Therefore, the analysis of landscape spatial changes and its driving forces during different periods of the coast has become the latest trend, and is important for better understanding the evolution of the regional environment and changes in the global environment (Wang et al., 1996; Xiao et al., 2001; Li et al., 2002; Ou and Yang, 2003; Hu et al., 2004; Wang and Li, 2006; Zhang et al., 2009). It is also an issue that needs to be studied urgently to promote better conservation.

The analysis on the driving forces of landscape change is a sort of directional study, and therefore there is no specific method or framework. Statistical analysis is helpful in identifying correlations between landscape changes and driving forces. Some studies have only qualitatively analyzed the causes of natural habitat changes in coast (Cheng et al., 2019). Some studies try to use landscape pattern change to analyze driving factors (Plieninger et al., 2016; Yan et al., 2019). The problems of management and conservation policy are widely known, but quantitative information about the driving force of deterioration is deficient. Although most current achievements do not fully explain the causal relationship and driving mechanism between factors and changes, they lay a good foundation for the future of research in this field.

Some natural coastal ecosystems are being continuously altered, transformed, or destroyed. Can the development of nature reserves prevent the change in landscape patterns? Although nature reserves are generally believed to be the cornerstones of biodiversity conservation and the safest strongholds of wilderness (Noss, 1996), human encroachments and threats are still very common in many nature reserves. Liu et.al found that Wolong Nature Reserve, located in the mountains, has become more fragmented and less suitable for giant panda habitation after the reserve's establishment (Liu et al., 2001). It is not clear whether protected coastal areas are effectively protected because there is little research comparing ecological degradation after the protected areas were established.

This study evaluated landscape changes of the coastal ecosystems at the Yancheng coast from 1984 to 2008. With landscape pattern changes at the Yancheng coast, certain ecological problems have emerged, such as wetland degradation and habitat loss. The quantitative analysis of landscape changes is necessary to solve the ecological problems resulting from landscape changes. The main goals of this study are: (1) to analyze the route of landscape succession at the Yancheng coast, (2) to identify the conservation effectiveness of a nature reserve, and (3) to evaluate the main driving forces of landscape succession.

STUDY AREA

The Yancheng coast is a typical muddy beach with accretion and is located in the central coastal areas of Jiangsu, which is an underdeveloped region in the Yangtze River Delta region. The coast has been strongly influenced by human activities, especially in the last 30 years. A series of ecological problems, such as large-scale land reclamation, pollution, over-exploitation, and biological invasion (Wang et al., 2007) have significantly impacted biodiversity conservation. The natural landscape area has been gradually reduced, and the landscape patterns have changed dramatically. The quality of the habitat for endangered birds has decreased. Experts have carried out extensive research, but quantitative analysis on spatiotemporal variation and the driving mechanisms of landscape patterns on the Yancheng coast have been lacking.

The benign climate and favorable natural environment of the Yancheng coast have led to the development of rich biological resources. It is not only an important migration route for East Asia-Australasia migratory birds, but it is also the world's largest wintering ground for red-crowned cranes—listed as Chinese first-class protected wild animals. In 2002, it was designated as a RAMSAR site.

To analyze the dynamic changes in the landscapes in different years, we set the study area to the same as the boundaries of the Yancheng Wetland National Nature Reserve, which is the main part of the Yancheng coast. We selected the 1992 west, south, and north boundaries of the Reserve and the east boundary as it was adjusted in 2006.The area covers 5,515km^2 and includes five counties of Yancheng, namely, Xiangshui, Binhai, Sheyang, Dafeng, and Dongtai (**Figure 1**).

MATERIALS AND METHODS

Data Collection

We combined expert classification and supervised classification methods to extract the land cover information of the study area and corrected the classification result using ground survey data in ERDAS Imagine 8.5 and ArcGIS 9.3. We then obtained four landscape pattern figures of the study area.

We devised a generalized classification scheme of the landscape which includes 10 types: reed fields (*Phragmitesaustralis*), *Suaeda* fields (*Suaeda salsa*), *Spartinaalterniflora* fields, mudflats, river, sea, aquaculture

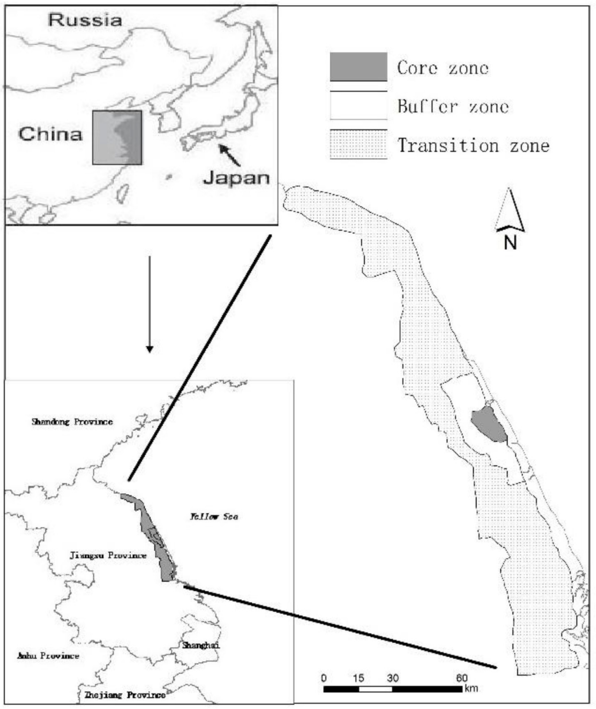

FIGURE 1 | Study area.

ponds, salt ponds, farmland, and residential areas. To eliminate the influence of tides, we selected the border of the land area covered by the maximum extent on each image as the eastern boundary of mudflats. The area to the east of the mudflats was classified as the sea.

Regarding landscape classification, most studies divided the study area into many landscapes by the land-use/land-cover method or divided the coast into wetland and non-wetland landscapes, and then divided wetland landscapes into natural wetlands and artificial wetlands (Wang et al., 1997; Li et al., 2006; Ding et al., 2009; Hao et al., 2010). To reveal the driving mechanism of landscape changes more effectively, this study divided the area into natural and artificial landscapes. The natural landscapes include reed fields, *Suaeda* fields, *Spartinaalterniflora* fields, mudflats, rivers, and the sea. The artificial landscape includes aquaculture ponds, salt ponds, farmland, and residential areas.

Methods

To explore the structure and the change of landscape patterns during 1982–2008, we calculated the landscape transfer matrix of the Yancheng coast in three phases. We then calculated some parameters in different steps, such as the dynamic transfer rate of single land use (Wang and Bao, 1999), the retention rate of the landscape, the contribution rate of a specific landscape transfer process, and the contribution rate of major landscape transfer processes (Zeng et al., 2003; Liu et al., 2009).

The dynamic transfer rate of single land use was calculated to reveal the changes in the type of land use within a specific time in the study area. It is calculated as:

$$K = \frac{U_b - U_a}{U_a} \times \frac{1}{T} \times 100\% \tag{1}$$

where K is the dynamic transfer rate of single land use during the study period, U_a and U_b are the quantity of a type of land-use at the beginning and end of the study period, respectively, T is the length of the study period (when the time period of T is set as year), and the value of K is the annual transfer rate of single land-use in the study area.

The retention rate of the landscape was used to analyze the stability of the main landscape in different periods. It refers to the ratio of the area of a single landscape that had not been transferred at the beginning and end of the study period.

$$BR_i = BA_i / TA_i \tag{2}$$

where BR_i is the retention rate of the ith landscape in a certain period, TA_i is the area of the ith landscape at the beginning of the study period, and BA_i is the unchanged area of the ith landscape during the study period.

The contribution rate of a specific landscape transfer process refers to the proportion of the transfer area of a transfer process to the total amount of transfer occurring in the landscape. It can be used to compare the importance of several specific landscape transfer processes.

$$T_{pi} = A_{ij} / A_t \tag{3}$$

where T_{pi} is the contribution rate of a specific landscape transfer process, A_{ij} is the area transferred from the ith landscape to the jth landscape, and A_t is the total area of landscape transfer occurring in time t.

The contribution rate of the major landscape transfer process can describe the distribution of the area reduction of the dynamic transfer processes of major landscapes in the study area.

$$OR_{ij} = A_{ij} \Big/ \sum_{j=1}^{n} A_{ij} \tag{4}$$

where OR_{ij} is the contribution rate of the transfer from the ith landscape to the jth landscape, A_{ij} is the area of the ith landscape transferred to the jth landscape, and n is the number of types transferred from the ith landscape.

RESULTS

Landscape Characteristics

Table 1 shows the landscape of the Yancheng coast in 1984, 1992, 2000, and 2008 (**Figures 2–5**). Unexpectedly, the primary landscape type has always been farmland, not wetlands. In 1984, the natural landscape proportion was similar to that of the artificial landscape, but the natural landscape had a slight advantage. Its area was 280,000c, accounting for

TABLE 1 | Area statistic of landscape types in Yancheng coast.

Landscape type		CA(hm^2)				PLAND(%)			
		1984	1992	2000	2008	1984	1992	2000	2008
Natural landscape	1	48316	44142	9356	9314	8.76	8.00	1.70	1.69
	2	33759	19797	9788	3260	6.12	3.59	1.77	0.59
	3	66	1068	6892	12524	0.01	0.19	1.25	2.27
	4	147256	126144	114802	83950	26.70	22.87	20.81	15.22
	5	9260	7915	8084	6705	1.68	1.44	1.47	1.22
	6	43001	43126	43234	43212	7.80	7.82	7.84	7.83
	Total	281659	242192	192155	158966	51.07	43.91	34.84	28.82
Artificial landscape	7	23618	39416	68644	86583	4.28	7.15	12.45	15.70
	8	39376	43443	42768	37464	7.14	7.88	7.75	6.79
	9	206759	225944	246666	265511	37.49	40.97	44.72	48.14
	10	127	544	1305	3015	0.02	0.10	0.24	0.55
	Total	269879	309346	359382	392572	48.93	56.09	65.16	71.18

CA, Class area; PLAND, Percentage of Landscape; 1, reed fields; 2, Suaeda fields; 3, Spartinaalterniflora fields; 4, mudflats; 5, river; 6, sea; 7, aquaculture ponds; 8, salt ponds; 9, farmland; 10: residential area.

51.07% of the study area (**Tables 1**, **2**). In 2008, the natural landscape area was 160,000 hm^2, accounting for 28.82% of the study area. The artificial landscape area increased annually and became the dominant landscape. Farmland and aquaculture ponds were the major landscape types in 2008. The majority of the artificial landscapes are aquaculture ponds and farmlands.

The natural landscape area continued to decline with 281,700 hm^2, 242,200 hm^2, 192,200 hm^2, and 159,000 hm^2 in

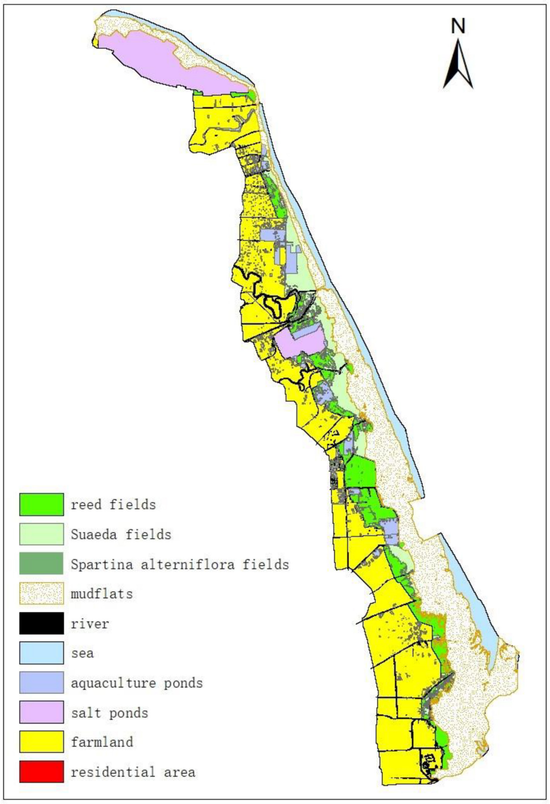

FIGURE 2 | Landscape map of Yancheng coast in 1984.

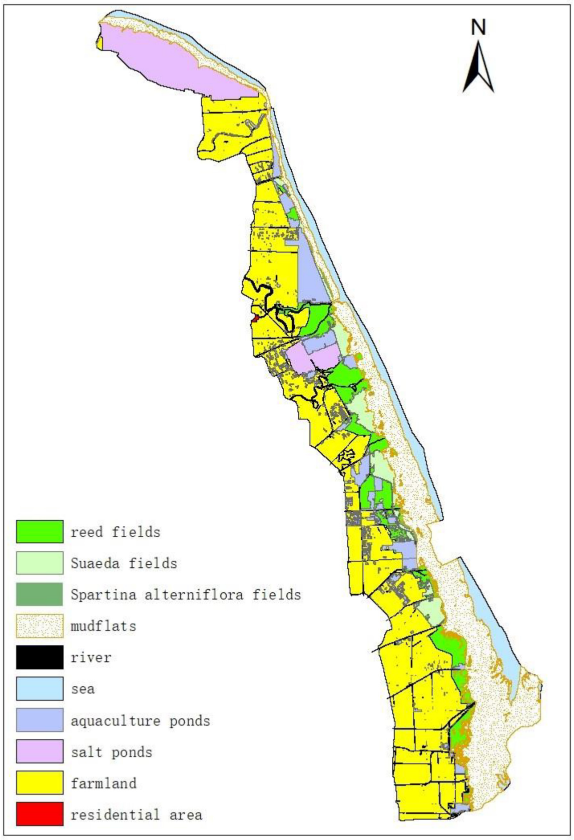

FIGURE 3 | Landscape map of Yancheng coast in 1992.

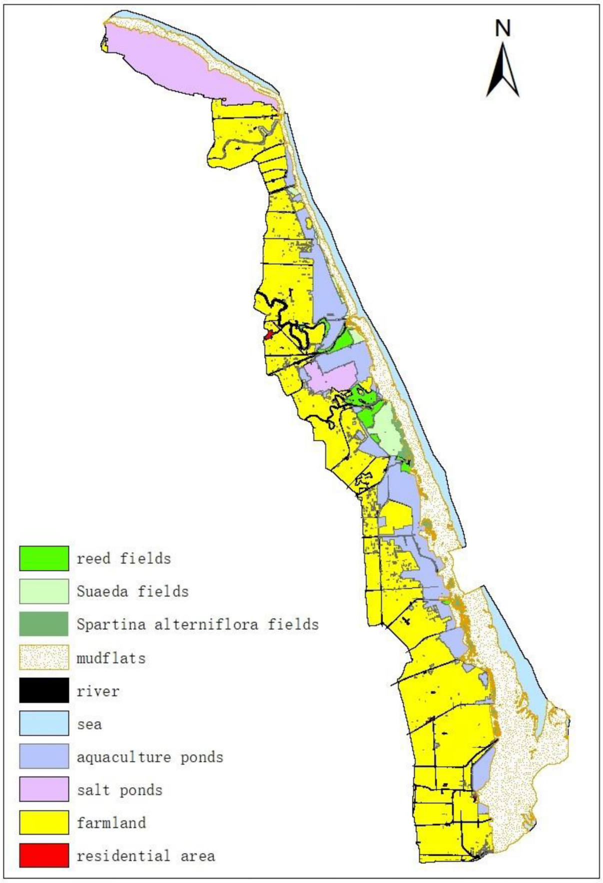

FIGURE 4 | Landscape map of Yancheng coast in 2000.

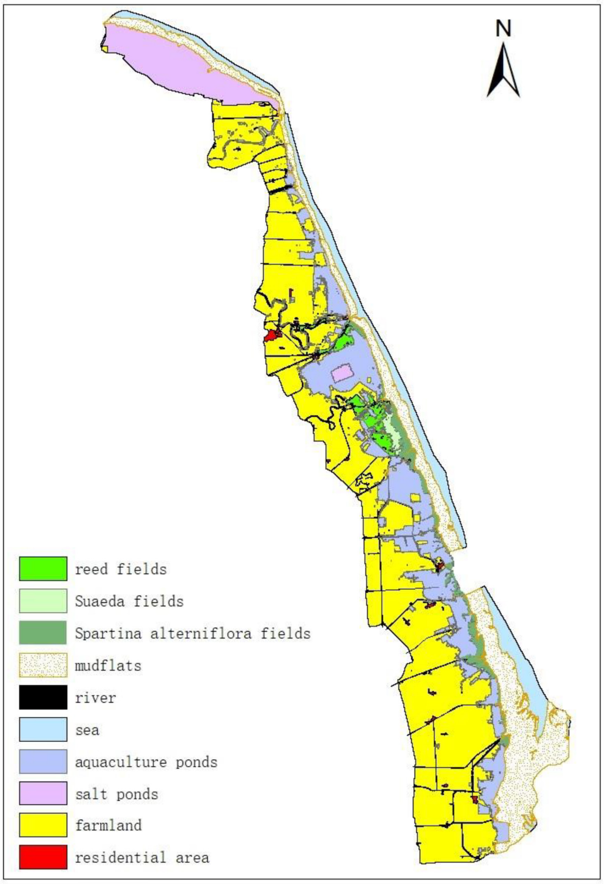

FIGURE 5 | Landscape map of Yancheng coast in 2008.

1984, 1992, 2000, and 2008, respectively. Throughout the three phases, the area of natural landscape was reduced by 39,500 hm^2, 50,000 hm^2, and 33,200 hm^2, and declined by 122,700 hm^2 in total. The proportion of the natural landscape in the study area was reduced from 51.07% to 28.82%. The rest of the natural landscape showed a downward trend, except for the area of *Spartinaalterniflora* fields, which showed an increase of 189 times because it is an alien invasive species (**Table 1**). Mudflats had the maximum amount of reduced area, with a decrease of more than 60,000 hm^2, and a decline of 42.99%. The area of reed fields declined drastically, especially in the phase of 1992–2008. The extent of reed fields dropped from third (8.76%) to seventh place (1.69%), and the area shrunk to 1/5 of the original area, with a decline of 80.72%. The total decrease accounted for 28.40% of the total negative flow area. The area of *Suaeda* fields dropped from seventh place (6.12%) to ninth place (0.59%), the largest extent of the decline. The *Suaeda* field area shrunk to less than 1/10 of its original extent, with a decline of 90.34%.

The proportion of artificial landscape areas has continued to rise. The extent of the artificial landscape displayed a significant growth trend, except for the salt ponds, which showed a slight decrease. The area of the aquaculture ponds was promoted from eighth (4.28%) to second place (15.7%), with the maximum amount of area growth (62,965 hm^2). The total growth accounted for 11.42% of the study area. Farmland always constitutes the largest landscape type in this region. The total growth in farmland accounted for 10.65% of the entire study area. From 1984 to 2008, the farmland area grew by 58,753 hm^2, an increase of 28.42%. The residential area expanded from 126.72 hm^2 (1984) to 3,014.55 hm^2 (2008), an increase of 22.79 times.

The Relationship of Spatial-Temporal Variation of Landscape

By analyzing the transfer matrix of the Yancheng coast landscape in 1984 and 2008, we found the spatial-temporal variation in landscape types. Reed fields were converted to farmland (31,322 hm^2) and aquaculture ponds (13,233 hm^2). *Suaeda* fields were converted to aquaculture ponds (16,665 hm^2), farmland (10,146 hm^2), and *Spartinaalterniflora* fields (5,216 hm^2). Mudflats were generally converted to aquaculture ponds (37,857 hm^2) and *Spartinaalterniflora* fields (12,166 hm^2) and then converted into farmland (5,779 hm^2) and salt ponds (3,881 hm^2). Rivers were primarily converted into farmland (2,193 hm^2). There was little change in the extent of seawater. Aquaculture ponds and farmland were converted into each other, but conversion to farmland dominated (11,315 hm^2). Salt ponds were mainly converted to aquaculture ponds (6,223 hm^2). The growth of residential areas was primarily caused by changes in the agricultural landscape, with a net transfer area of 2200 hm^2.

Considering the changes in landscape patterns in the study area, the transition rates of the landscape were 17.46% (1984–1992), 16.57% (1992–2000), and 15.03% (2000–2008), respectively. The results showed that the change in the overall landscape patterns was large, but the rate of change was stable, with the highest rate of change in the first phase.

According to a comprehensive analysis of the characteristics of the transfer matrix of landscape areas in the three different phases (1984–1992, 1992–2000, 2000–2008), the changes in main landscape of the Yancheng coast showed a fixed route, from natural landscapes to artificial landscapes (**Figure 6**). First, mudflats were converted to *Spartinaalterniflora* fields, salt ponds, *Suaeda* fields, reed fields, and aquaculture ponds. Second, *Spartinaalterniflora* fields and salt ponds were converted into aquaculture ponds. Third, *Suaeda* fields were converted into aquaculture ponds and reed fields. Fourth, reed fields were converted into aquaculture ponds and farmland. Fifth, aquaculture ponds and rivers are converted to farmland. Sixth, farmland was converted to residential areas.

Investigation found that salinity is the decisive factor of the fixed route for landscape successions of coast. In the early stage of reclamation, a large number of soil salinization was caused by water evaporation, and the soil with higher salinity could only be used for Mariculture or salt field development. Due to rain shower deposition and the introduction of fresh water by irrigation, the salinity of the tidal-flat area was reduced. Land can be used for large-scale farmland cultivation and freshwater aquaculture.

Landscape Temporal Change Analysis Process

During 1984–2008, the reed fields and *Suaeda* field landscape retention rate was always low. During 1992–2000, there

TABLE 2 | Dynamic transfer rate of land-use in Yancheng coast.

Landscape type		Transferring area percent (%)					Transfer rate per year (%)		
		1984	1992	2000	2008	Total	Phase 1	Phase 2	Phase 3
Natural landscape	1	8.76	8	1.7	1.69	−7.07	−1.08	−9.84	−0.07
	2	6.12	3.59	1.77	0.59	−5.53	−5.17	−6.34	−8.33
	3	0.01	0.19	1.25	2.27	2.26	225.00	69.74	10.20
	4	26.7	22.87	20.81	15.22	−11.48	−1.79	−1.13	−3.36
	5	1.68	1.44	1.47	1.22	−0.46	−1.79	0.26	−2.13
	6	7.8	7.82	7.84	7.83	0.03	0.03	0.03	−0.02
	Total	51.07	43.91	34.84	28.82	−22.25	−1.75	−2.58	−2.16
Artificial landscape	7	4.28	7.15	12.45	15.7	11.42	8.38	9.27	3.26
	8	7.14	7.88	7.75	6.79	−0.35	1.30	−0.21	−1.55
	9	37.49	40.97	44.72	48.14	10.65	1.16	1.14	0.96
	10	0.02	0.1	0.24	0.55	0.53	50.00	17.50	16.15
	Total	48.93	56.09	65.16	71.18	22.25	1.83	2.02	1.15

1: reed fields; 2: Suaeda fields; 3: Spartinaalterniflora fields; 4: mudflats; 5: river; 6: sea; 7: aquaculture ponds; 8: salt ponds; 9: farmland; 10: residential area.

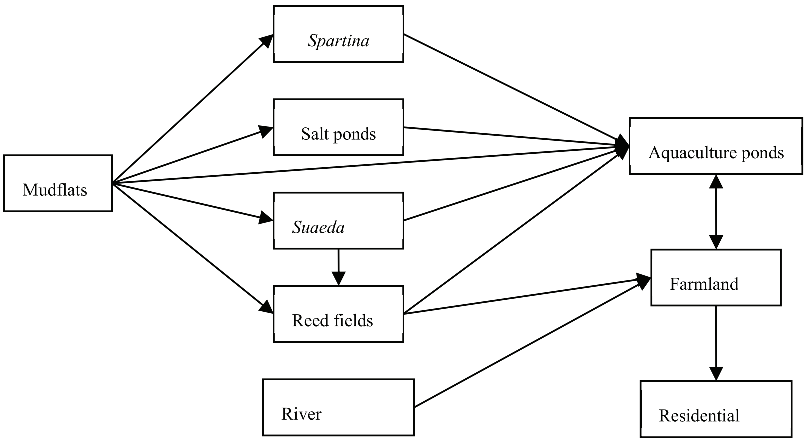

FIGURE 6 | Succession of main landscapes in Yancheng coast.

were more reed field changes, and its landscape retention rate was 18.20%. In contrast to other natural landscapes, *Spartinaalterniflora* spread quickly into the mudflats. On the other hand, reclamation, expansion of ponds, and other human activities occupy part of *the Spartinaalterniflora* fields. Its retention rate in the landscape was higher in the first phase but lower in the second and third phases. Compared with natural landscapes, the retention rate of artificial landscapes is higher and has good stability. The retention rate of the aquaculture pond landscape was over 50% in three phases, and the retention rate of the landscape of farmland, salt ponds, and residential area was over 85% (**Figure 7**).

Table 3 shows the changes in the advantage transfer type of the Yancheng coast in three phases. In the first phase, where the cumulative contribution rate of the transfer process of natural landscape reclamation was 31.03%, reed fields were mainly converted to farmland, *Suaeda* fields changed to reed fields, and *Suaeda* fields and reed fields changed to aquaculture ponds. In the second phase, in which the cumulative contribution rate of the transfer process of natural landscape reclamation was 53.48%, there were three dominant transferring processes: reed fields were converted to aquaculture ponds and farmland, *Suaeda* fields changed to aquaculture ponds, and aquaculture ponds changed to farmland. In the third phase, where the cumulative contribution rate of the transfer process of natural landscape reclamation was 32.48%, the major transfer process was mudflats converted to aquaculture ponds, aquaculture ponds to farmland, and mudflats to *Spartinaalterniflora* fields. It is evident that the human reclamation effects on the natural landscapes are significant in all three phases. In particular, the interference influence of natural landscape reclamation was the greatest in the second phase.

The overall landscape change rates are 17.46%, 16.57%, and 15.03% in 1984–1992, 1992–2000, and 2000–2008, respectively. These percentages indicated that while the landscape pattern changes were relatively great, the rate of change steadily decreased, with the highest rate in the first phase.

This finding indicates that, Yancheng wetland nature reserve was established in 1984 and designated a National Nature Reserve in 1992, but anthropogenic activities on the Yancheng coast continue apace, and the trend of natural landscape loss did not change. Although the regulations on nature reserves

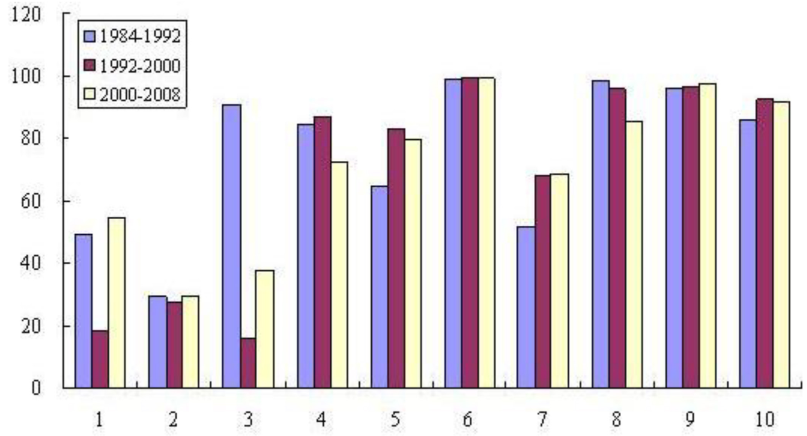

FIGURE 7 | Retention rate of main landscapes on Yancheng coast.

TABLE 3 | The dominant transfer process and its contribution rate.

1984-1992		1992-2000		2000-2008	
Transfer type	**Contribution rate (%)**	**Transfer type**	**Contribution rate (%)**	**Transfer type**	**Contribution rate (%)**
1→9	12.12	1→7	18.81	5→7	23.89
7→9	11.26	1→9	14.44	7→9	23.71
2→1	10.60	2→7	13.66	5→3	11.16
2→7	9.78	7→9	13.08	8→7	6.78
1→7	9.13	5→3	6.93	9→7	5.07
5→1	8.79	5→7	6.57	3→7	4.99
5→2	7.28	9→7	4.78	2→1	3.78
9→7	6.59	1→4	4.31	2→7	3.61
Cumulative contribution rate%	75.54		82.58		82.98

1: reed fields; 2: Suaeda fields; 3: Spartinaalterniflora fields; 4: mudflats; 5: river; 6: sea; 7: aquaculture ponds; 8: salt ponds; 9: farmland; 10: residential area.

stipulates that nature reserves are strictly protected and prohibits reclamation, it has not been seriously implemented.

The Driving Mechanism of Landscape Succession

Driven by endogenous and exogenous factors in different spatial and temporal scales, the landscape is always in a state of dynamic change (Cheng et al., 2019). Recent research has focused on the reasons behind the landscape changes and the "driving forces" have been developed into a fundamental concept (Plieninger et al., 2016). It can be divided into specific natural driving forces and anthropogenic driving forces (Pearsell and Mulamoottil, 1994; Day et al., 2000; Fu et al., 2006).

The natural driving forces mainly include dynamic marine conditions, sediment supply, and *Spartina* proliferation, which drive landscape succession as natural factors. Between 1984 and 2008, the natural driving force was reflected in the mudflats converting to *Suaeda* fields (first phase), mudflats to *Spartinaalterniflora* fields (the second and third phases), *Suaeda* fields to reed fields (first and third phases), and mudflats to reed fields (first phase). This finding suggests that *Suaeda* occupied part of the mudflats during 1984–1992. However, being an invasive plant, *Spartina* replaced *Suaeda* after 1992, when it expanded rapidly along the Yancheng coast. It inhibited the growth of *Suaeda*, and the conversion rate from mudflats to *Spartinaalterniflora* fields continues to increase after 1992, when it expanded rapidly along the Yancheng coast (Shen et al., 2002). Due to the expansion of *Spartinaalterniflora*, the injection of seawater was blocked and coupled with the introduction of fresh water by irrigation, the salinity of the tidal-flat area was reduced, and has created a large expanse of reed fields, which are adapted to low-salinity wetland conditions.

The anthropogenic driving forces mainly include resource development, public policies, construction of large projects, increasing population pressure, natural landscape reclamation, and the internal transfer of artificial landscapes. It is reflected mainly in the reed fields converted to farmland (first and second phases), *Suaeda* fields to aquaculture ponds (first, second, and third phases), the reed fields to aquaculture ponds (first and second phases), aquaculture ponds to farmland (the second and third phases), and mudflats to aquaculture ponds (the second and third phases).

To make a quantitative evaluation of the impact of natural and anthropogenic driving forces according to the landscape classification in this study, the landscape configuration change can be divided into four different circumstances. These four categories include the internal transformation of natural landscapes, natural landscapes converted to artificial landscapes, artificial landscapes to natural landscapes, and internal transformation of artificial landscapes.

The natural landscape changed the most: 78.24%, 76.24%, and 59.19% of the total transfer area in the three phases, respectively, which consists of the internal transformation of natural landscapes and natural landscapes converted to artificial landscapes. There was a large-scale transformation from natural landscape to artificial landscape, accounting for 43.94%, 57.57%, and 42.23% of the transfer area in the three phases (**Table 4**). In the artificial landscape, a large area of aquaculture ponds was converted to farmland, and salt ponds into aquaculture ponds. Only a minimal area of artificial landscapes converted to natural landscape. The main reason for this latter conversion was sea erosion, which caused some salt ponds and aquaculture ponds to be destroyed.

TABLE 4 | The transition rate of landscape in study region.

Transfer rate (%)	1984-1992	1992-2000	2000-2008
1	43.94	57.57	42.23
2	34.30	18.67	16.96
3	18.82	20.93	38.61
4	2.95	2.83	2.19

1. The proportion of transfer area from natural landscape to artificial landscape in whole transfer area; 2, The proportion of transfer area among natural landscapes in whole transfer area; 3, The proportion of transfer area from artificial landscapes in whole transfer landscape; 4, The proportion of transfer area from artificial landscape to natural landscape in whole transfer area.

An analysis of the forces driving the entire landscape change in the study area showed that both the internal transformation of natural landscape and artificial landscape transformed to natural landscape could be classified as the effect of natural driving forces. Natural landscapes are converted to artificial landscapes, and the internal transformation of artificial landscapes can be classified as the result of anthropogenic driving forces. Therefore, the transferred area resulting from anthropogenic driving forces was 62.76%, 78.50%, 80.84% of the total transfer area in three phases, respectively (**Table 4**). In summary, the changes in the Yancheng coastal landscape pattern were driven primarily by human forces. The impact of anthropogenic driving forces was significantly greater than natural driving forces, and it gradually increased during 1984–2008.

CONCLUSION

Coastal Landscape Pattern

We analyzed the evolution trends and driving forces in the three phases of the Yancheng coast transformation during 1984–2008. The major landscape has been farmland from 1984 to 2008, not wetland. The Yancheng coastal landscape pattern has changed significantly. The landscape matrix has changed from a situation in which the natural landscape was equal to the artificial landscape in 1984, and the latter was dominant during 1990–2008. The proportion of natural landscape in the study area is declining, while the proportion of artificial landscape is increasing, and the area of natural landscape has been substantially reduced. The area of artificial landscape has increased significantly, comprising farmland and aquaculture ponds. The total area of the natural landscape gradually decreased from 281,700 hm^2 in 1984 to 159,000 hm^2 in 2008, and the proportion of natural landscape in the study area decreased from 51.07% to 28.82%. To obtain more profit, a large amount of unused land, such as mudflats and *Suaeda* fields, has been developed.

Although there is a national nature reserve in Yancheng coast, anthropogenic activities on the reserve continue apace, and the trend of natural landscape loss did not change during 1984–2008. Disorderly reclamation for economic development is the main reason for the loss of natural habitat in the coast, and the lack of supervision and law enforcement encouraged it.

Landscape Succession

The changes in these landscapes of Yancheng coast showed a fixed succession route, from natural landscapes to artificial landscapes. The succession is closely related to the physical and chemical properties of the soil and water in the region. Salinity is the decisive factor of the fixed route for landscape successions of the coast. Mudflats converted to salt ponds and aquaculture ponds (seawater) are based on seawater use on land. *Spartinaalterniflora* fields and salt ponds converted to aquaculture ponds (freshwater), and *Suaeda* fields transformed into aquaculture ponds and reed fields reflect land-use changes after the highly saline soils have been flushed with fresh water, causing soil and water salinity to be reduced. The changes from reed fields to aquaculture ponds (freshwater) and farmland, from aquaculture ponds and rivers to farmland, further indicate that newly developed land has been used for higher value-added industries after soil improvement.

Driving Force

Anthropogenic activity is the primary reason for the reduction of the natural element in the Yancheng coastal landscape. Many natural landscapes were transferred to artificial landscapes between 1984 and 2008. The impact of the anthropogenic driving forces is significantly greater than that of the natural driving force. In future, we need to make full use of high-resolution remote sensing data to identify landscape changes, combined with the field survey to refined the driving force of landscape change, so as to better understand its landscape succession.

In the light of these results, we make the following conservation recommendations. On the one hand, we suggest strengthening the protection of existing natural landscapes. First, enhance law enforcement. The existing natural landscape should be effectively protected by law. Second, all construction projects should be subject to the most rigorous environmental impact assessments prior to inception. Third, we emphasize the importance of protecting and rebuilding the natural habitats of the red-crowned cranes and other birds. Fourth, engineering measures for *Spartinaalterniflora* control should be taken.

On the other hand, we suggest strengthening the management of artificial landscapes. We recommend that the government used the policies of subsidies, leases, land purchase, which encourage community residents to change wheat fields to reed ponds or aquaculture ponds, and prohibit the use of chemical fertilizers, pesticides, insecticides, herbicides, and other toxic substances. Second, aquaculture ponds should be planted with more emergent plants. Third, reed harvesting should be completed before the red-crowned cranes and other migratory birds arrive, and part of the reed fields should be retained. Fourth, farmland should be kept unplowed (Lee et al., 2007) or kept unplowed until the red-crowned cranes leave in early March. Fifth, we should strictly limit the expansion of human activities (Wang et al., 2011), especially residential areas and industrial sites, and punish the surrounding businesses that have contaminated the Yancheng wetland nature reserve and its wildlife to discourage them from doing further damage.

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

ZW and JZ designed the study and methodology. WX, JZ, and XX extracted and compiled the data. JZ analyzed the data with the help of HY and YL. ZW wrote the manuscript with substantial input from WX, JZ, XX, and HY. All authors contributed to the article and approved the submitted version.

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Explaining the Geographic Pattern of Plant Invasion in 67 Nature Reserves in China

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Biological invasion is a serious threat to biodiversity and ecosystem function in nature reserves. However, the knowledge of the spatial patterns and underlying mechanisms of plant invasions in nature reserves is still limited. Based on a recent dataset on both invasive and native plants in 67 nature reserves of China, we used correlation, regression, and variation partitioning methods to statistically assess the relative roles of the "human activity," "biotic acceptance," and "environmental heterogeneity" hypotheses in explaining the geographic pattern of plant invasion. A total of 235 invasive plant species were compiled from 67 nature reserves. The high explanatory power of the human activity variables supported the human activity hypothesis. The biotic acceptance hypothesis was weakly supported since no significant correlations between climatic variables and invasion levels were found when the effects of the other factors were controlled. The environmental heterogeneity hypothesis was partially supported, since the number of native plants, representing environmental heterogeneity at fine-scale explained remarkable proportion of spatial variance of invasive plants but not that of the proportion of invasive plants. We predict that nature reserves with high plant diversity affected by rapid economic development and increasing temperature will face a serious threat of exotic plant invasion. In conclusion, our results provide crucial clues for understanding geographic variance of plant invasion in China's nature reserves and spatial risk assessment.

Keywords: alien species, protected areas, human activity, biotic acceptance, habitat heterogeneity, climate change

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INTRODUCTION

As an important component of global change, plant invasion has intensified with the rapid development of globalization (Roura-Pascual et al., 2021). Plant invasion can severely affect not only the fate of individual species and community structures (Pyšek et al., 2012; Foxcroft et al., 2017), but also some critical ecosystem functions (Parker et al., 1999; Pyšek et al., 2012), and finally lead to economic losses (Vilà et al., 2010; Pyšek et al., 2020). Understanding the mechanisms of plant invasion is crucial to prevent its negative ecological and economic losses.

Previous studies have reported that invasion level (the number or proportion of invasive species) is highly correlated with social-economic conditions, environmental variables, and native species diversity at regional scales (Lonsdale, 1999; Taylor and Irwin, 2004; Allen et al., 2009; Pyšek et al., 2010). Therefore, there are correspondingly three main hypotheses proposed to explain the geographical pattern of invasion: "human activity" (Taylor and Irwin, 2004; Blanchet et al., 2009; Catford et al., 2009, 2011), "biotic acceptance" (Fridley et al., 2007; Blanchet et al., 2009), and "environmental heterogeneity" (Melbourne et al., 2007; Enders et al., 2020). They, respectively, highlight the roles of anthropogenic pressure, environmental constraints, and local habitat heterogeneity. According to the recent consensus network on 39 common hypotheses in invasion biology, five main clusters (propagule, Darwin, resource availability, biotic interaction, and trait) were revealed by a link-clustering algorithm (Enders et al., 2020). These three hypotheses, human activity, biotic acceptance, and environmental heterogeneity, belong to the clusters of propagule, Darwin, and resource availability, respectively. This indicates the weak similarity and overlap among them (Enders et al., 2020; Pyšek et al., 2020). We don't consider the biotic resistance hypothesis because it generally works at local/community scales and has been frequently rejected at regional scales (Lonsdale, 1999; Beaury et al., 2020).

The human activity hypothesis predicts that human activities can augment the establishment possibility of non-native species by disturbing the local habitat and increasing propagule pressure (quantity, quality, composition, and supply rate of alien species) (Taylor and Irwin, 2004; Catford et al., 2009). Positive relationships can be expected between invasion level and the anthropogenic surrogates of propagule pressure and habitat disturbance (Taylor and Irwin, 2004). The biotic acceptance hypothesis focuses on environmental conditions and states that, at large spatial scales, the abiotic conditions that promote high native species diversity also support diverse alien species (Davies et al., 2005; Fridley et al., 2007). Everything else being equal, there should be a positive relationship between the number of native and invasive species because they co-vary with the same environmental variables (Davies et al., 2005; Stohlgren et al., 2006). The environmental heterogeneity hypothesis predicts that regions with higher heterogeneity in the local environment would harbor higher invasive levels because heterogeneous habitat provides more opportunities for the establishment of invasive species (Melbourne et al., 2007). Accordingly, there should be positive relationships between invasion level and various quantifications of environmental heterogeneity (Melbourne et al., 2007; Stein et al., 2014). These hypotheses are not necessarily mutually exclusive, and their relative roles may vary during the successive stages of biological invasion (initial dispersal, establishment, and spread) (Catford et al., 2009), across biogeographic realms (Blanchet et al., 2009; Catford et al., 2009), and among different invading taxa (Stohlgren et al., 2006; Pyšek et al., 2010; Spear et al., 2013). According to the consensus network on invasion hypotheses (Enders et al., 2018, 2020), human activity in this study mostly represents colonization pressure and propagule pressure other than local disturbance, since nature reserves are strictly managed to have a hard boundary from invasion (Foxcroft et al., 2017).

When testing these hypotheses, it's important to use different indices of invasion level, while paying attention to the interactions among different hypotheses. The invasion level is regarded as the extent or severity of observed biological invasion in an ecosystem (Chytrι et al., 2008). At geographic scales, absolute invasive/alien species richness (number of invasive/alien species) has been frequently used to quantify invasion levels. However, its ability to reflect the impacts of invasion depends on the recipient ecosystem (Catford et al., 2012). Relative invasive/alien species richness, the proportion of all invasive/alien species, accounts for variation in native richness. Relative richness is better than absolute richness for comparing invasion levels among regions, in terms of ecological impact, scale dependence, and data availability (Catford et al., 2012; Bai et al., 2013). However, most previous tests were based on absolute richness, especially at regional scales. In addition, variables representing different hypotheses may interact with each other. For example, human activities are affected by environmental variables (Luck, 2007). Therefore, specific predictions should be formulated regarding absolute or relative richness, and the strength and magnitude of each hypothesis should be statistically explicitly evaluated.

Plant invasions have been observed in protected areas located in different ecoregions (e.g., Foxcroft et al., 2017). The mechanisms leading to spatial variation of invasion levels among protected areas are mostly attributed to human disturbance, regional climate, and native biota. Some studies found anthropogenic variables were significant predictors of invasive species richness in nature reserves, climactic variables were usually not (e.g., Spear et al., 2013), while others reported contrasting results (e.g., Gantchoff et al., 2018). This implies the necessity of research in ecoregions with different climate conditions, social-economic situations, and native biota.

In this study, the data on native and invasive plants from 67 nature reserves in China were compiled and used, focusing on the relative importance of human activity, biotic acceptance, and environmental heterogeneity hypotheses. The selected nature reserves cover a wide latitude from 18.6 to 51.4° N, and a wide longitude from 83.0 to 128.9°E. The dominant ecosystem in these nature reserves is forest ranging from tropical to temperate climates. The wide geographic coverage of the data makes it valuable for understanding geographic pattern of plant invasion in nature reserves and effective management.

MATERIALS AND METHODS

Data Sources

We compiled species lists of all seed plants (hereafter referred to plants) from the inventory reports of 67 nature reserves in China (**Supplementary Material**). The species names were standardized by The Plant List.[1] Data on the area, coordinates (latitude and longitude), and topography (minimum and maximum elevation) of each nature reserve were also obtained from original publications. The status of each plant species was then

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[1] http://www.theplantlist.org

determined according to the most recent compilation of invasive plants in China (Bai et al., 2013). The numbers of native plants (NNP) and invasive plants (NIP) were counted according to the species list for each nature reserve. The relative invasive plant richness (RPR) in each nature reserve was calculated by dividing the number of invasive plants by the number of all plants (Catford et al., 2012).

Putative Predictors

We selected 11 variables to test our three hypotheses. For the human activity hypothesis, we used human population density (HPD), gross domestic product (GDP), GDP per unit area (GUA), and GDP per capita (GPC) in the counties/districts where the nature reserves were located (data in the year 2010 obtained from the yearbook of each county/district). For the biotic acceptance hypothesis, we emphasized climatic conditions and used mean annual temperature (TEM), mean annual precipitation (PRE), mean temperature of the coldest quarter (TCQ), and mean precipitation of the driest quarter (PDQ). For the environmental heterogeneity hypothesis, we used altitudinal range (ALR, maximum elevation – minimum elevation), area (ARE), and the numbers of native plants (NNP).

HPD, GDP, GUA, and GPC have been frequently considered as surrogates of anthropogenic pressure for plant invasions at regional scales (e.g., Liu et al., 2005; Allen et al., 2009; Pyšek et al., 2010; Wu et al., 2010). The climatic variables represent the factors controlling the physiological processes limiting the spatial distribution of invasive plants (Liu et al., 2005; Allen et al., 2009; Pyšek et al., 2010; Wu et al., 2010). ALR and ARE represent habitat heterogeneity at the local scale, which is frequently used in macroecological studies (e.g., Chen et al., 2011). NNP well represents heterogeneity at the fine-scale, since it's highly correlated with vegetation structure (Stein et al., 2014). Data for TEM, PRE, TCQ, and PDQ were obtained from WorldClim (Hijmans et al., 2005) according to the coordinates of the midpoint of each nature reserve.

Data Analysis

NNP, NIP, and all the environmental and human variables (except TEM, PRE, TCQ, and PDQ) were ln-transformed to compensate for their highly skewed distributions. RPR was arcsine transformed as arcsin $\sqrt{x}$, which is suggested as an appropriate method to transform proportion data (Sokal and Rohlf, 1995).

We analyzed the form and the significance of the relationships between each variable related to one hypothesis and NIP or RPR, after controlling for the effect of the confounding variables. We did so because the putative predictors were highly correlated (the absolute value of Pearson's correlation coefficient ranging from 0.10 to 0.89). When testing the human activity hypothesis, we related HPD, GDP, GUA, and GPC with the residual of the models of NIP or RPR against TEM, PRE, TCQ, PDQ, NNP, ALR, and ARE. This allowed us to control for the effects of environmental variables, which are related to biotic acceptance and environmental heterogeneity hypotheses. When testing the biotic acceptance hypothesis, we analyzed the form and the significance of the relationship between TEM, PRE, TCQ, PDQ and the residuals from a model explaining NIP or RPR by HPD, GDP, GUA, GPC, NNP, ALR, and ARE. The effects of human activities and regional climate could be controlled in this way. Finally, when testing the environmental heterogeneity hypothesis, we analyzed the form and the significance of the relationships between the NNP, ALR, ARE and the residuals from a model explaining the NIP or RPR by HPD, GDP, GUA, GPC, TEM, PRE, TCQ, and PDQ. We used Spearman rank correlation to assess the relationships between independent variables and model residuals because the model residuals were not normally distributed.

We used hierarchical partitioning to assess the joint and independent effects of each variable on NIP and RPR. Hierarchical partitioning is an exploratory regression technique in which all possible linear models are jointly considered to identify the most likely explanatory factors while minimizing the influence of collinearity. This method allows the identification of the independent contribution of each variable and separates it from the joint contribution due to correlation among variables (Quinn and Keough, 2002). The package hier.part was used for hierarchical partitioning and associated randomization tests of significance.

Since there was significant spatial autocorrelation in the residuals of the OLS models, we used Dutilleul's modified t-test to determine the significance of the correlations based on corrected degrees of freedom (Rangel et al., 2010). Statistical analyses were mainly carried out using "Spatial Analysis in Macroecology" (Rangel et al., 2010).

RESULTS

A total of 235 invasive plant species were recorded in the 67 nature reserves. The number of invasive plants (NIP) in the 67 nature reserves varied from 1 to 129, with a mean value of 30. The proportion of invasive plants (RPR) varied from 0.4 to 6.8%, with a mean of 2.4%. Nature reserves in South and Southeast China were higher in NIP than those in the other regions, while RPR shows a less pronounced spatial pattern although nature reserves in Southeast China generally have higher RPR (**Figure 1**).

After controlling for the effect of environmental conditions, the variables to test the human activity hypothesis were found to be positively related to NIP (gross domestic product, GDP) and RPR (GDP and GDP per capita, GPC). After controlling for the effects of human activity and environmental heterogeneity, no positive correlations between NIP or RPR and biotic acceptance variables were found. After the effects of climatic conditions and human activity were controlled, the only significant correlation was found between NIP and the number of native plant species (NNP) (**Table 1**).

Hierarchical partitioning revealed significant independent effects of HPD, GUA, TEM, PRE, and NNP for NIP, with NNP having the strongest independent effect. While RPR, GUA, ARE, and TEM had significant independent effects (**Figure 2**). The environmental factors (TEM, PRE) and NNP had the greatest independent effect on NIP (83.8%), while for RPR, the total independent effects of human activity variables (32.3%) and

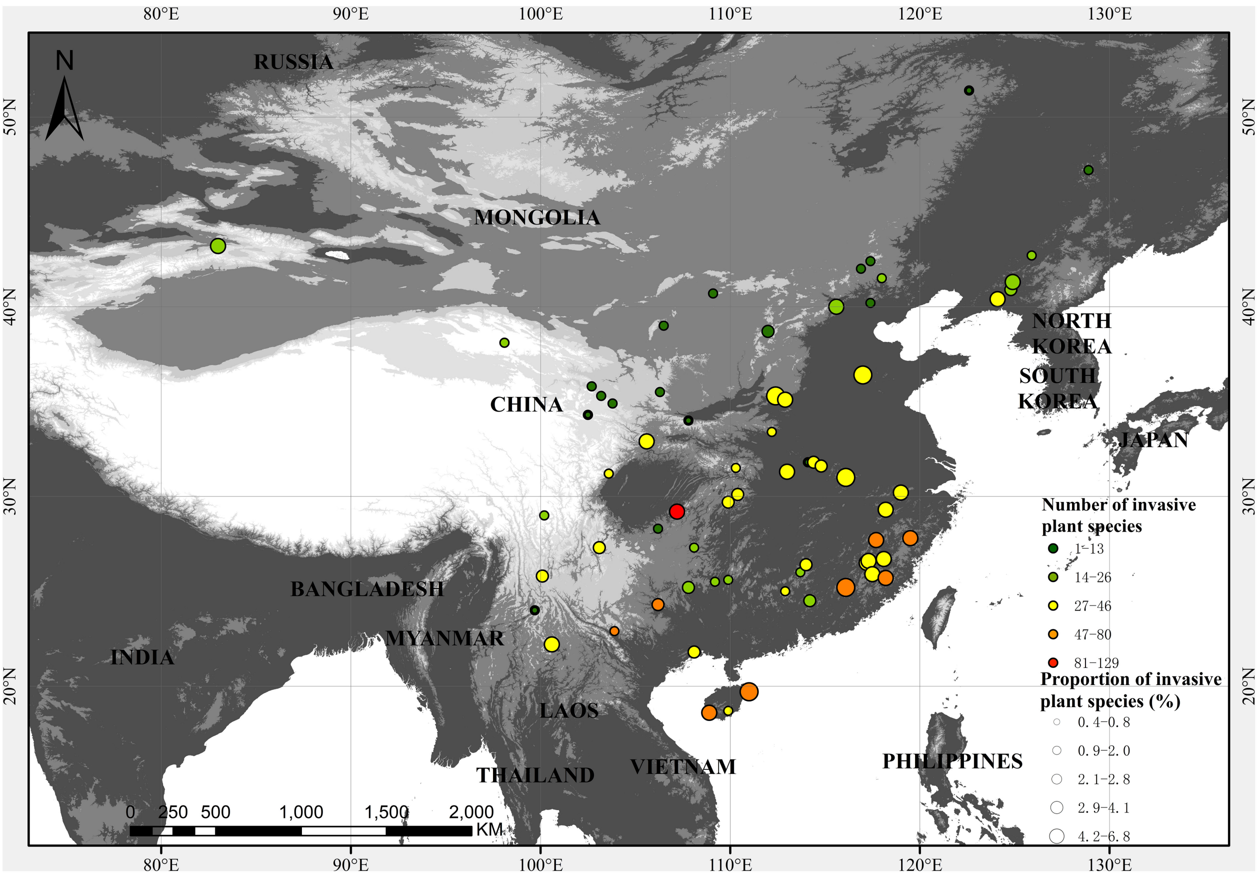

FIGURE 1 | Spatial distribution of the number (color) and proportion (size) of invasive plants in 67 nature reserves.

biotic reacceptance variables (37.7%) were comparable. GUA and TEM had significant independent explanatory power for both NIP and RPR (**Figure 2**).

DISCUSSION

By correlation, regression, and variation partitioning analyses, we determined the relative roles of human activity, biotic acceptance, and environmental heterogeneity hypotheses in explaining geographic patterns of plant invasion levels in 67 China's nature reserves. The results showed that plant invasion level, represented by either the number or the proportion of invasive plant species, was positively related to human activity indicators. They accounted for a significant part of the geographic variation of invasion level, supporting the human activity hypothesis. The biotic acceptance hypothesis was weekly supported because climatic variables explained little of the variation of invasion level when the other effects were controlled. The evidence of the environmental heterogeneity hypothesis was ambiguous since the analytical results based on the number or the proportion of invasive plants were not identical.

The economic aspect of human activities can be well reflected by gross domestic product (GDP), GDP per unit area (GUA, and per capita GDP (GPC). All three factors had significantly positive effects on plant invasion levels in the nature reserves. This agrees with the results of recent analyses which highlight the potential of socioeconomic developments in shaping biological invasion (e.g., Pyšek et al., 2010; Dawson et al., 2017; Roura-Pascual et al., 2021). Pyšek et al. (2010) found national wealth and human population density were statistically significant predictors for biological invasions across Europe. This was reinforced by similar results from a global analysis, which concluded that regions with higher GPC harbor more alien species (Dawson et al., 2017). Furthermore, Essl et al. (2011) proposed that the effect of current socioeconomic activity on biological invasion will emerge in the future. This means that socioeconomic legacy yields an invasion debt. Recognizing the rapid socioeconomic development in China, our finding highlights the high risk of plant invasion in nature reserves.

When using the proportion of invasive plants as the indicator of invasion level in nature reserves, the importance of human activity was more pronounced than taking the number of invasive plants as invasion level. Because previous studies showed that relative invasive richness is more reasonable than absolute invasive richness (Bai et al., 2013), the studies based on absolute richness might underestimate the role of human activity in explaining spatial invasion patterns at regional scales. The

TABLE 1 | Spearman rank correlation (r_S) between the number and proportion of invasive plants and each predictive variable related to the human activity, biotic acceptance, and biotic resistance hypotheses (n = 67).

Hypothesis	Variable	NIP		RPR	
		r_s	p	r_s	p
Human activity hypothesis	HPD	0.145	0.184	0.147	0.280
	GDP	**0.317**	0.045	**0.293**	0.035
	GUA	0.295	0.058	0.317	0.060
	GPC	0.293	0.051	**0.345**	0.018
Biotic acceptance hypothesis	TEM	0.073	0.801	0.224	0.153
	PRE	0.029	0.833	0.202	0.184
	TCQ	0.034	0.915	0.193	0.158
	PDQ	0.036	0.657	0.194	0.212
Environmental heterogeneity hypothesis	NNP	**0.376**	<0.001	−0.031	0.981
	ALR	0.233	0.207	0.036	0.986
	ARE	−0.097	0.478	−0.180	0.267

For each hypothesis, the relationship between the number and proportion of invasive plants and predictive variables considered was quantified by controlling for the effects of the predictive variables relevant to the other hypotheses (see section "Materials and Methods" for more details).

The p-values were calculated after accounting for spatial autocorrelation using Dutilleul's method. NIP, number of invasive plants; RPR, relative invasive plant richness; HPD, human population density; GDP, gross domestic product; GUA, GDP per unit area; GPC, Per capita GDP; NNP, number of native plants; ALR, altitudinal range; TEM, mean annual temperature; PRE, annual precipitation; ARE, area of nature reserve. Bold values are significant according to the p-values < 0.05.

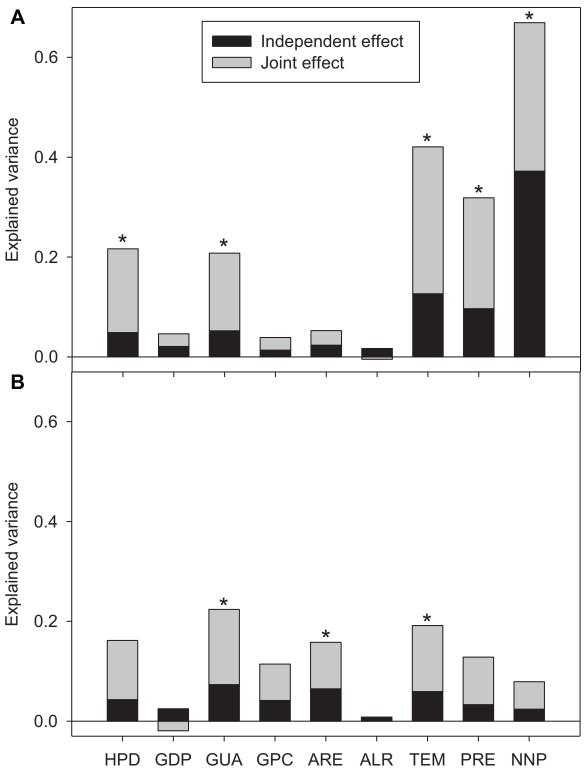

FIGURE 2 | Results from hierarchical partitioning analysis illustrating the independent and joint effects of the predictive variables in explaining the variation in the numbers of native plants (NIP; **A**) and the proportion of invasive plants (RPR; **B**) (n = 67). The predictive variables with significant independent effects were marked with stars.

possibility and magnitude of changes in economic activities and human population are likely to be higher than climate change in the future. Therefore, much attention should be paid to human activity around protected areas to control plant invasion.

Our results explicitly show that the climatic factors in nature reserves are the main drivers of spatial variation in the number of invasive plants, supporting the biotic acceptance hypothesis (Stohlgren et al., 2006). However, when taking the proportion of invasive plants as an invasion level indicator, the ability of biotic acceptance hypothesis decreased remarkably. After the effects of human activity and environmental heterogeneity were controlled, no climatic variables were found to be significantly correlated with either the number or the proportion of invasive plant species. Therefore, the promotion effect of future global warming will be pronounced for the number of invasive plant species, and weak for the proportion of invasive plant species.

Other than large-scale climatic variables, native plants richness represents habitat heterogeneity at the fine-scale (which cannot be described by climatic variables). Variation partitioning analysis showed that native plant richness alone had a significant effect on the number of invasive plant species, but not for the proportion of invasive plant species. Therefore, the support for environmental heterogeneity hypothesis was not consistent.

Plant invasion has been recognized as a potential threat to the conservation of biodiversity in protected areas worldwide (Lonsdale, 1999; Spear et al., 2013; Foxcroft et al., 2017). It may erode the conservation capacity of nature reserves due to its detrimental effects on the native species and ecosystem processes (Vilà et al., 2010; Pyšek et al., 2012; Foxcroft et al., 2017; Beaury et al., 2020). Our analyses provide useful clues about the efficient management of plant invasions in China's nature reserves. First, nature reserves in regions with rapid economic development and population increase should adopt robust and cost-efficient methods to prevent the introduction of invasive plant species. In recent decades, the human population and GPC in Eastern China have increased more rapidly than in the other regions (Zhang and Gao, 2019). Economic development may be associated with increased transportation between regions and enhanced disturbance of the local flora, which in turn translates to an increased number of propagules of invasive plants and a higher chance of establishment of invasive plant species (e.g., Guo et al., 2021). Second, nature reserves in regions characterized by a rapid temperature increase should be carefully evaluated and monitored as warming are critical for the establishment of invasive plants (Dawson et al., 2017; Roura-Pascual et al., 2021). A case study on subtropical nature reserves indicated that climate change mitigation and adaptation from policy and technology should be strengthened (Feng et al., 2020). Third, nature reserves with higher plant diversity should be paid more attention, since these localities may provide significantly high habitat heterogeneity, and provide more chance for invasive plants to colonize.

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

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it 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/fevo.2021.655313/full#supplementary-material

Supplementary Data Resource | References from which species lists of native and invasive seed plants of the 67 nature reserves were compiled.

Supplementary Table 1 | The coordinates, the number and the proportion of invasive plants in each of the 67 nature reserves.

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