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*CORRESPONDENCE Peta Zivec, ⊠ peta.l.zivec@gmail.com

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Natural regeneration of wetlands under climate change

Peta Zivec^{1,2*}, Fran Sheldon¹ and Samantha J. Capon¹

¹Australian Rivers Institute, Griffith University, Nathan, QLD, Australia, ²Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

Wetlands are increasingly valuable under climate change in terms of their ecological functions, ecosystem services, and biodiversity. Simultaneously, wetlands are hotspots for anthropogenic activity due to their high soil fertility and water supply, and have been subject to significant modification, degradation, and staggering losses. With climate change having increasing impacts on ecosystems globally, the need for wetland restoration is rapidly growing. Natural regeneration, whereby vegetation is allowed to regrow via propagules already present within the landscape, provides a cost-effective and large-scale approach to restoration for many, but not, all wetlands. This paper emphasises the importance of natural regeneration of wetland ecosystems as an effective restoration approach under climate change. We discuss drivers and barriers of natural regeneration of wetlands under climate change along with implications for management approaches. Drivers of wetland natural regeneration are depicted along with their interactions, displaying a range of abiotic and biotic factors that influence ecosystem change. Key adaption approaches to maintain and promote natural regeneration of wetlands under climate change include integrated land and water management, protecting and promoting key relevant biotic and abiotic processes within landscapes, and reconsidering current exotic species management strategies. Most importantly, however, natural regeneration should be recognised as an important and viable restoration approach under climate change in order to meet restoration demand and promote landscape resilience to changing conditions.

KEYWORDS

restoration, revegetation, passive restoration, rehabilitation, global warming, spontaneous succession

1 Introduction

Few wetland ecosystems in the world remain untouched by human activity (Foley et al., 2005). Anthropogenic impacts on wetlands are being further exacerbated by climate change (Fluet-Chouinard et al., 2023). Restoration and revegetation of wetlands is increasingly vital for creating resilient landscapes better able to respond to a changing climate without dramatic loss of biodiversity or ecosystem function (Erwin et al., 2009; Bastin et al., 2019). Wetland vegetation, both woody and non-woody, has disproportionately high value, supporting high levels of biodiversity, providing critical ecosystem functions to both terrestrial and aquatic organisms, and delivering a range of ecosystems services vital for human livelihoods (Capon et al., 2016). Key ecosystem services provided by wetlands include carbon sequestration, maintenance and creation of clean water and soil fertility, and regulation of water and climate (Dybala et a., 2019). Consequently, there is an urgent need to better understand and implement effective restoration management approaches for wetlands under climate change (Benayas et al., 2009; Tomscha et al., 2021).

Restoring wetlands can be achieved through a range of approaches spanning active, assisted and passive methods (Di Sacco et al., 2021). In any situation, the best restoration practice, however, will be unique to the set of circumstances at a local and landscape scale (Yang et al., 2020). Consequently, it is critical that we better understand the efficacy and drivers of a range of restoration approaches to ensure efficient use of limited resources at this critical time (Prach & Hobbs, 2008). We define wetlands in line with The Ramsar Convention as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed 6 m". Although, within this paper we are also including floodplain and riparian areas but excluding marine wetlands. Overall, this paper seeks to emphasise the importance of natural regeneration of wetland ecosystems as an efficient and effective restoration approach under climate change. In this paper, we contrast different restoration approaches for wetland vegetation and highlighting situation where natural regeneration is most appropriate under climate change. We identify the key drivers and barriers of wetland regeneration, presenting a conceptual model to provide a better understand of ways to best promote natural regeneration. Finally, we explore why natural regeneration of wetlands is critical under climate change and how it can be best supported.

2 Wetland restoration approaches

Ecological restoration, revegetation, re-wilding, and regeneration are terms used to describe the recovery of an ecosystem following anthropogenic or natural disturbance. Traditionally, two broadly contrasting forms of restoration approaches are recognised: active and passive, the latter also often referred to as natural regeneration (Holl & Aide, 2011). Active restoration involves significant human intervention such as planting tube stock of seedlings or seeds to facilitate regeneration (Perrow & Davy, 2002). In contrast, natural regeneration requires minimal intervention with vegetation permitted to regrow via available plant propagules once a disturbance has ceased (Chazdon and Guariguata, 2016). Intermediate to active and passive regeneration, assisted natural regeneration requires the manipulation of some abiotic and biotic factors to encourage natural regeneration (Mälson et al., 2008). To determine which restoration approach is likely to be possible and effective in each situation depends at least partially on the level of wetland degradation experienced (Jackson & Hobbs, 2009). Natural regeneration, for instance, relies on the availability of suitable plant propagules and establishment sites existing within the landscape, as well as adequate regeneration conditions, including sufficient time (Prach et al., 2014). Where landscapes have been subjected to long-term intense agricultural pressure, significant erosion or are otherwise propagule limited, active restoration may be necessary due to a loss of suitable conditions (Holl & Aide, 2011).

Depending on the level of intervention required for active restoration, it can be associated with high initial costs and ongoing maintenance (Moreno-Mateos et al., 2015). The high costs are due to the acquisition of native seeds and tube stock and the intensive labour required to plant and maintain them, often restricting active restoration efforts to relatively small scales (Summers et al., 2015). Active restoration may be implemented to speed up regeneration, which otherwise would take long timeframes, although this has not always been found to be successful (Chimner et al., 2017; Jones et al., 2018). Active restoration attempts can also have a high risk of failure where abiotic conditions are unsuitable for the successful establishment of vegetation, these pressures are likely to increase under climate change (Clark et al., 2007). With more extreme weather events, higher temperatures and changed rainfall patterns, "climateadjusted" provenancing strategies will be required for sourcing seed for restoration projects (Prober et al., 2015). Extra consideration should also be made when selecting species for restoration, as species historically native to the area, may not be adapted to the conditions which have arisen due to climate change (Harris et al., 2006). The increase investment required needed to maintain planted tube stock via active restoration and species selection may contribute to increase in failure of restoration attempts from active restoration.

In contrast to active restoration, passive restoration or natural regeneration requires minimal human intervention and is therefore typically associated with lower costs and can be applied over a larger scale (Chazdon and Guariguata, 2016). However, disturbances such as livestock grazing, fire, and cropping must often be controlled or stopped before natural regeneration can occur successfully (Prach & Hobbs, 2008), adding to the costs and potentially reducing the efficacy of natural regeneration approaches (Zahawi et al., 2014). In wetlands, such disturbances may also include alterations to hydrological regimes for water resources management and/or flood mitigation, as well as extreme flood events driven by climate change (Devkota et al., 2015; Parra et al., 2021). Natural regeneration is occurring within wetlands globally, although due to wetlands being poorly mapped due to inconsistences in wetland definition and limitation in modelling systems (Tootchi et al., 2019; Glanville et al., 2023), the extant and success of it is unknown in many areas.

In multiple meta-analyses in forest systems, natural regeneration has been found to have better restoration outcomes compared with active restoration (e.g., Crouzeilles et al., 2017; Huang et al., 2019; Shimamoto et al., 2018). Crouzeilles et al., 2017, found in their metaanalysis of 133 studies that natural regeneration surpassed active restoration attempts in tropical forests for all three biodiversity groups (plants, birds, and invertebrates) and five measures of vegetation structure. Another study done by Huang et al., 2019 conducted a meta-analysis on ecological restoration of terrestrial ecosystem collated data from 103 published studies and found that passive restoration performed better than active approaches for the recovery of biodiversity. Shimamoto et al., 2018 completed a metaanalysis from data obtained in 69 studies on the restoration of ecosystem services on tropical forests, found that natural regeneration was the most effective strategy. While none of these meta-analyses' focused specifically on wetlands, they did demonstrate natural regeneration's ability to restore vegetation successfully and, in some circumstances, better then active approaches. Meli et al., 2014, found in their meta-analysis on how restoration enhanced wetland biodiversity and ecosystems servicers, that only 3 out of 70 papers assessed used natural regeneration as their restoration approach. This highlights how underrepresented natural regeneration is for wetland restoration, despite its effectiveness clearly shown in forested ecosystems.



3 Drivers and barriers of wetland natural regeneration

In order to promote natural regeneration within wetlands under climate change, it is vital we understand barriers and drivers of vegetation regeneration (Figure 1) (Piana et al., 2020). Understanding key patterns and drivers of natural regeneration can help better prioritise wetlands which would most benefit from natural regeneration (Widis et al., 2015; Zivec et al., 2021). Key mechanisms driving natural regeneration can be classified into two broad categories: biotic and abiotic factors. Overall, for natural regeneration to occur, both adequate propagules, e.g., seeds (biotic) and suitable conditions for their successful germination and establishment (abiotic) must be present (Prach & Walker, 2011).

In wetland ecosystems, hydrology is a key driver of vegetation regeneration (Todd et al., 2010). By definition wetlands are habitats "that are inundated or saturated by water at a frequency and for a duration sufficient to support a prevalence of vegetation typically adapted for life in saturated soil conditions" (Mitsch and Gosselink, 2015). Therefore, wetland vegetation is more likely to have traits that are triggered by different hydrological cues (Rosbakh et al., 2020). The duration, frequency and timing of different hydrological events

shape vegetation characteristics within wetlands, particularly in floodplain and riparian ecosystems (Capon, 2005). Landscape topography underpins hydrological processes and will also drive patterns of natural regeneration within wetlands (Branton & Robinson, 2020). Wetlands within areas which are more likely to have overbank flow, water pooling or tidal influence will impact what vegetation species are able to regenerate (Grieger et al., 2019). Meso-climatic variation drive natural regeneration due to factors such as soil moisture availability and hydrology, which are strongly link to wetland vegetation. Regeneration of areas that are more benign (e.g., with balanced rainfall and potential evapotranspiration, fertile soils, etc.) is less restricted by abiotic factors and, therefore, natural regeneration often occurs in such places at faster rates (Cramer et al., 2008).

Propagule supply is a fundamental mechanism underpinning the successful occurrence of natural regeneration (Walker & Del Maral, 2003). Propagules, including seeds, tubers, plant fragments, etc., can be stored within existing vegetation, seed banks and transported throughout the landscape (Zivec et al., 2023). Hydrochory is a key process linked to propagule transportation and is responsible for large-scale patterns of species distribution within wetlands (Nilsson et al., 2010). Wetlands, particularly riparian zones, are often a hotspot for exotic species invasion due to the increase in disturbance from flooding and the transportation of seeds via hydrochory (Catford & Jansson, 2014). This risk is even more elevated in wetlands which have altered flow regimes (Catford et al., 2011). This interspecies competition, particularly exotic species, can affect the likelihood of regeneration occurring due to competition for light, nutrients, and resources, which can reduce wetland regeneration (Rehel & Olden, 2008). The presence of adequate existing vegetation as a seed source, however, is vital for regeneration (Houlahan et al., 2006). Existing trees, shrubs, and deadwood within disturbed areas are particularly important for abiotic facilitation for germination and establishment, providing microsites for regeneration (Blood & Titus, 2010).

In wetlands subjected to agricultural activity, natural regeneration may be impacted by legacies from previous land use. Wetlands are disproportionately impacted by grazing and cropping due to the close proximity to water and increased nutrients (Wiegman et al., 2022). Land-use history, including the

type, frequency, duration, and intensity of previous agriculture, influences the vegetation assemblage that regrows via natural regeneration (Cramer et al., 2008). Changes in soil properties through the depletion or addition of nutrients and alteration of soil pH or salinity resulting from agricultural practices, for instance, can have a significant effect on the abiotic conditions needed for regeneration (Arbelo et al., 2006; Breen et al., 2015). Additionally, wetlands throughout the world have been drained of water by ditches to increase arable land, this has resulted in widespread wetland loss (Fluet-Chouinard et al., 2023) and the creation of new human-made wetlands (Kuglerova et al., 2017).

Climate change will influence natural regeneration through the alteration of abiotic and biotic conditions that drives vegetation to regrow (Pugnaire et al., 2019). First, climatic factors are strongly linked to abiotic factors that are vital for breaking seed dormancy and germination (Klupczynka & Pawlowski, 2021). Under climate change, fire regimes, rainfall patterns and temperature are all likely to shift, therefore altering which species may be able to successfully emerge from seed banks (Ooi, 2012; Kiss et al., 2018). Changes to soil temperature and rainfall patterns may impact seedbanks persistence and therefore a depletion of biotic components needed for vegetation regeneration (Ooi et al., 2012). Weedy, exotic and generalist species, that are adapted to altered or a wide range of conditions may then have the regenerative advantage under climate change (Hellmann et al., 2008). Therefore, there may be an increased risk of exotic plant invasions or dominance of generalist species in the future, with these species being "ecological winners" under climate change (Van der Putten et al., 2010). Such eventualities may cause shifts in species compositions and structure, leading to changes in wetlands character and condition, especially in naturally regenerated areas (Capon et al., 2021). Consequently, it's likely we will increasingly see vegetation communities occurring in novel states, and trajectories, with altered species composition and structure (Capon & Pettit, 2018).

4 Discussion

Naturally regenerated wetlands can provide complimentary habitat to remnant wetlands for a low cost and with minimal intervention, offering the potential for much larger areas of wetlands to be rehabilitated then via active methods (De Steven et al., 2010; Holl & Aide, 2011). With respect to climate change adaptation, increasing the amount of wetland vegetation is vital for improving and creating new thermal refuges for biodiversity as the climate and weather events become more extreme (Nelson et al., 2009; Mandelik et al., 2012). Wetlands provide habitat connectivity throughout the landscape and between terrestrial and aquatic areas (Desta et al., 2012). Species will need to disperse in response to changing conditions and increased landscape vegetation achieved from natural regeneration will allow for safer and easier movements (Doerr et al., 2011).

Natural regeneration is of increasing importance under climate change due to demand for restoration, its resilience to altered climatic conditions and capacity to support ecosystem services (Jones et al., 2018). As vegetation regrows via the seed already within the landscape, those species will have local genetic adaptions and high functional diversity when compared to active restoration (Chazdon and Guariguatat, 2016). As nature selects which species will regenerate under natural regeneration, vegetation is likely to be more heterogeneous (Zhang et al., 2021). This combination of genetic and landscape heterogeneity can be expected to increase landscape resilience to future conditions under climate change (Moore & Schindler, 2022). Naturally regenerated vegetation may also alter local climatic conditions by increasing shade, or altering soil moisture and hydrology (McLaughlin et al., 2017). Newly regenerating vegetation areas may act as climate refuges for biodiversity and, in turn, support more vegetation regeneration by providing a seed source and favourable abiotic conditions for further plant establishment (Selwood and Zimmer, 2020; Pradhan et al., 2023).

There is a range of adaption approaches that can be implemented to promote natural regeneration of wetlands under climate change (Simenstad et al., 2006; Capon & Pettit., 2018). First, it is important to minimise landscape stresses such as altered flow regimes (McIver and Starr, 2001). The reintroduction of ecosystem engineers such as beavers, can be an important strategy in restoring natural flow regimes needed for successful establishment of some vegetation species (Orr et al., 2020). Coupling revegetation projects with environmental flows is a promising avenue for research that may lead to improved restoration outcomes in wetlands under climate change (Schlatter et al., 2017). Environmental flows are the quantity, timing, and quality of water flows that sustain freshwater ecosystems (Bunn and Arthington, 2002). Environmental flows may be implemented within systems with altered flow regimes to improve vegetation resilience and promote natural regeneration (Sims and Colloff, 2012). At the same time, a better understanding of how to implement environmental flows and grazing management may assist in reducing woody thickening within naturally regenerated wetlands (Good et al., 2012; Saintilan and Rogers, 2015).

It is vital to promote key abiotic and biotic processes needed for natural regeneration within wetlands on a landscape and local scale (Kentula, 2000). Within wetlands, hydrology is a major driver of biotic processes (i.e., hydrochory) and abiotic conditions (i.e., germination and establishment) (Bejarano et al., 2018). Restoring natural flow regimes can assist in promoting large scale natural regeneration (Chazdon et al., 2021). On a smaller scale, microsites from existing structural features provide shading, lower wind exposure, and reduce grass or ground cover competition, facilitating natural regeneration (Kikvidze & Callaway, 2009). Minimising woody weed removal in some circumstances may be beneficial in creating these microsites and thermal refuges under climate change (Pollen-Bankhead et al., 2009; Schlaepfer et al., 2011). The presence of existing vegetation throughout the landscape are important seed sources for wetlands, particularly higher up in the catchment to enable dispersal via hydrochory downstream (Houlahan et al., 2006; Kuglerová et al., 2019). Therefore, under climate change, it should be the highest management priority to protect any existing vegetation and restore hydrological regimes to promote local and landscape scale natural regeneration.

In conclusion, natural regeneration is critical for rehabilitating wetlands under climate change, due to its low-cost, large-scale application and resilience to changed conditions (Chazdon, 2017). Natural regeneration is spatially and temporally variable, due to it

being shaped by abiotic and biotic drivers and constrains (Zivec et al., 2021; Zivec et al., 2023). This creates heterogeneous vegetation within the landscape which adds to catchment resilience due to its patch diversity, distribution, and climate adapted species (Prach & del Moral., 2015). Although, when regeneration barriers become too high, for example, from intensive agriculture or repeat disturbances, assisted or active restoration may need to occur (Zahawi et al., 2014). Natural regeneration of poses a huge opportunity to rehabilitate large areas of wetlands and should be a key restoration strategy under climate change (Whisenant, 1999; Capon et al., 2013; Chazdon and Guariguatat, 2016; Capon et al., 2021).

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

PZ was involved in the writing, conceptualising, and structuring of the paper. While FS and SC were involved with the conceptualisation, editing, and theoretical application. All authors contributed to the article and approved the submitted version.

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

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