Spatial Restoration Ecology: Placing Restoration in a Landscape Context

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Researchers on conservation planning and practice have increasingly recognized and adopted the pivotal role of landscape attributes in shaping the effectiveness of protected areas. However, the degree to which these concepts have been integrated into habitat restoration projects has not been quantified. We reviewed the global literature and found that landscape context was considered in fewer than one in eight restoration projects in the selection of restoration sites (11% of 472 projects). This figure was remarkably similar across terrestrial (10% of 243 projects), marine (13% of 89), and freshwater (13% of 164) ecosystems. Of the 54 restoration projects in which landscape context was considered in site selection, in just over half (56%), animal populations were reported to be larger or more diverse than in control areas. Tighter integration of concepts from spatial ecology and systematic conservation planning into restoration practice could improve the design, optimize placement, and enhance the ecological effectiveness of restoration projects in all ecosystems.

Keywords: connectivity, design, effectiveness, habitat restoration, landscape ecology

Establishing nature reserves and restoring ecosystems are complementary approaches in conservation (Soule 1985, Holl et al. 2003, Pressey et al. 2007, Palmer et al. 2016) that require significant financial investment (Wilson et al. 2006, De Groot et al. 2013). Maximizing the net returns of these investments, in terms of both biodiversity and ecosystem protection, is therefore sensible (Halpern et al. 2013, Possingham et al. 2015). Common strategies for enhancing conservation returns are to place reserves in areas that are threatened, support high biodiversity, or incur lower social and economic costs (Halpern et al. 2013) or to protect or restore sites that might have synergistic benefits for conservation (Thomson et al. 2009, Moilanen et al. 2011).

Conservation and restoration areas, by their very nature, are positioned within heterogeneous landscapes, which comprise multiple ecosystems of different sizes and shapes and with varying degrees of interconnectedness (Forman 1995, Olds et al. 2018). The landscape context can strongly influence several key biotic attributes of a site (Holl et al. 2003). Many of these attributes are of direct conservation and restoration concern (e.g., population dynamics, biodiversity, productivity; Ward et al. 1999, Bunn and Arthington 2002), across terrestrial (Hanski and Saccheri 2006), marine (Micheli and Peterson 1999) and freshwater (Wiens 2002) realms. Animals respond strongly to landscape configuration because most move throughout landscapes, and some use different habitats throughout their lifecycles. Some sites are, therefore, of higher ecological value for animals than others because they differ in terms of their food resources, refuge value from weather or predators, accessibility to dispersal pathways, and numerous other ecological properties that help to shape the fitness of individuals, demographics of populations, and the composition of assemblages (Pittman et al. 2011).

Globally, across multiple ecosystems and realms, it has been established that placing conservation areas strategically within landscapes can have synergistic benefits for their ecological effects on both ecosystems and the animals that inhabit them (Rudnick et al. 2012, Olds et al. 2016). For example, many marine fish move among coral reefs, seagrass meadows, and mangrove forests throughout their lives, and both fish abundance and diversity are often greatest inside marine reserves that conserve these ecosystems and the pathways that link them across landscapes (Mumby 2006, Edwards et al. 2009, Olds et al. 2016). Because some of these fish perform important ecological functions (e.g., herbivory), protecting connections among coral reefs, seagrasses, and mangroves can also help improve the spatial of these ecosystems to disturbance (e.g., Magris et al. 2014, Olds et al. 2014). Furthermore, the benefits of placing reserves into networks to maximize the exchange of individuals, matter, and energy among them are widely recognized (e.g., Arturo Sánchez-Azofeifa et al. 2003, Harrison et al. 2012, Hermoso et al. 2016). Reserves that are placed in areas with greater connectivity among populations,

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among ecosystems, or with other reserves therefore often perform better than reserves with impoverished landscape connections (Stoms et al. 2005, Ribeiro et al. 2009, Olds et al. 2016).

Landscape context can have similarly positive ecological effects on the performance of restoration projects (Metzger and Brancalion 2016). Restored ecosystems with strong connections to other habitat patches, of either the same or different ecosystem types, are more likely to be settled by animals and to receive larger subsidies of matter and energy from adjacent ecosystems. This landscape context modifies the distribution, abundance, and diversity of animals and plants across landscapes (Fahrig 2001, Lees and Peres 2008, Pottier et al. 2009, Hodgson et al. 2011) and potentially improves the ecological function of restored habitats (da Silva et al. 2015, Jones and Davidson 2016).

Modern algorithms for reserve selection explicitly incorporate the importance of positioning within the broader landscape (Hilty et al. 2006, Rudnick et al. 2012, Magris et al. 2016, Weeks 2017). These algorithms have been developed, now, to the point that system- and species-specific data are being used in association with commonly used modeling techniques (e.g., MARXAN, Zonation, and network models), broadly across regions, and within individual systems (Kool et al. 2013, Engelhard et al. 2017, Weeks 2017). Whereas the selection of locations for reserves is often guided by spatial concepts from landscape ecology, including connectivity and landscape context (Margules and Pressey 2000, Sarkar et al. 2006, Almany et al. 2009), site selection for restoration appears to adopt these principles less frequently (Hodgson et al. 2011). However, spatial prioritization is not widely used in restoration (e.g., Adame et al. 2015, Ikin et al. 2016), so, there have been recent calls for tighter integration of the spatial principles from landscape ecology and conservation biology (Wiens and Hobbs 2015, Audino et al. 2017) to both inform the design of restoration projects, and guide the selection of restoration sites (Jones and Davidson 2016, McAlpine et al. 2016). This is surprising because there have long been calls for the more strategic placement of restoration across landscapes, including in some important global restoration guidelines and policies (SER 2008, Keenleyside et al. 2012).

The landscape context of restoration sites is likely to be one of the most important factors influencing the outcomes of restoration investments, particularly for projects that are intended to enhance animal populations (figure 1; Miller and Hobbs 2007, Moreno-Mateos et al. 2012). Because restoration sites usually require colonization by animal populations from other habitat patches, the degree of connectivity between restoration sites and other patches of existing habitat is crucial (Scott et al. 2001, Hodgson et al. 2009, Hodgson et al. 2011). Restoration sites might be placed in areas that are considered appropriate for the establishment and growth of habitat-forming species but that are so isolated or poorly connected that animal populations respond to a lesser degree, thereby reducing the overall values of the habitat restoration for the whole ecosystem or landscape (Howe and Martinez-Garza 2014, Jones and Davidson 2016). For example, restoring to enhance connectivity between habitat fragments can help with restoring metapopulation dynamics (Montalvo et al. 1997, Fischer and Lindenmayer 2007). Increased consideration of metapopulation structure and connectivity can serve to enhance the available genetic pool of animal populations, thereby potentially increasing their fitness (Baguette et al. 2013), reducing population extinction risk (Reed 2004), and increasing resilience to exogenous disturbances (Etienne 2004). Such considerations are now often considered in the placement of marine reserves, especially in cases in which fisheries enhancement is a goal (Gerber et al. 2003, Puckett and Eggleston 2016). However, the regularity with which landscape context more broadly is considered in restoration site selection and how this affects inhabiting animal populations have, however, not been established (Metzger and Brancalion 2016). Consequently, the lines of evidence required for practitioners to properly justify the integration of principles from landscape ecology into the design of individual restoration projects have not been established.

In this study, we identified restoration projects from the global primary literature and assessed the degree to which landscape context was used as a criterion to help guide the selection of sites for restoration when the restoration of associated animal populations is also a principle goal and under which scenarios this is most likely to occur. We chose habitat restoration for animal populations as the focus because animals move throughout a landscape, and so spatial metrics are likely to be investigated first for these over other aims for restoration. We conducted literature searches using a structured literature classification framework. We reviewed the literature using multiple terms used for ecological restoration and a suite of ecosystem- and animal-specific phrases. We then categorized projects into those in which landscape context was considered in site selection and those in which it was not and further categorized projects into environmental realms, ecosystems, and the animal communities they were designed to enhance. We conclude by outlining how greater uptake of fundamental principles gleaned from landscape ecology can improve restoration success.

Methods

Restoration projects were identified using targeted literature searches and a structured literature classification framework (figure 2). All literature searches were conducted using the Web of Knowledge database in July 2017. The initial search was for the term—*((“habitat restoration” or “ecological restoration” or “ecosystem restoration”) and (fauna or inhabit* or animal* or biodivers* or wildlife or fish))*, resulting in 2183 articles returned and 333 articles downloaded for potential inclusion. On the basis of the composition of this initial shortlist, follow up searches included components of the initial search, as well as *wetland**, *seagrass*, *oyster**, *fish**, *mangrove**, *forest**, *grass**, *insect**, *invert**,

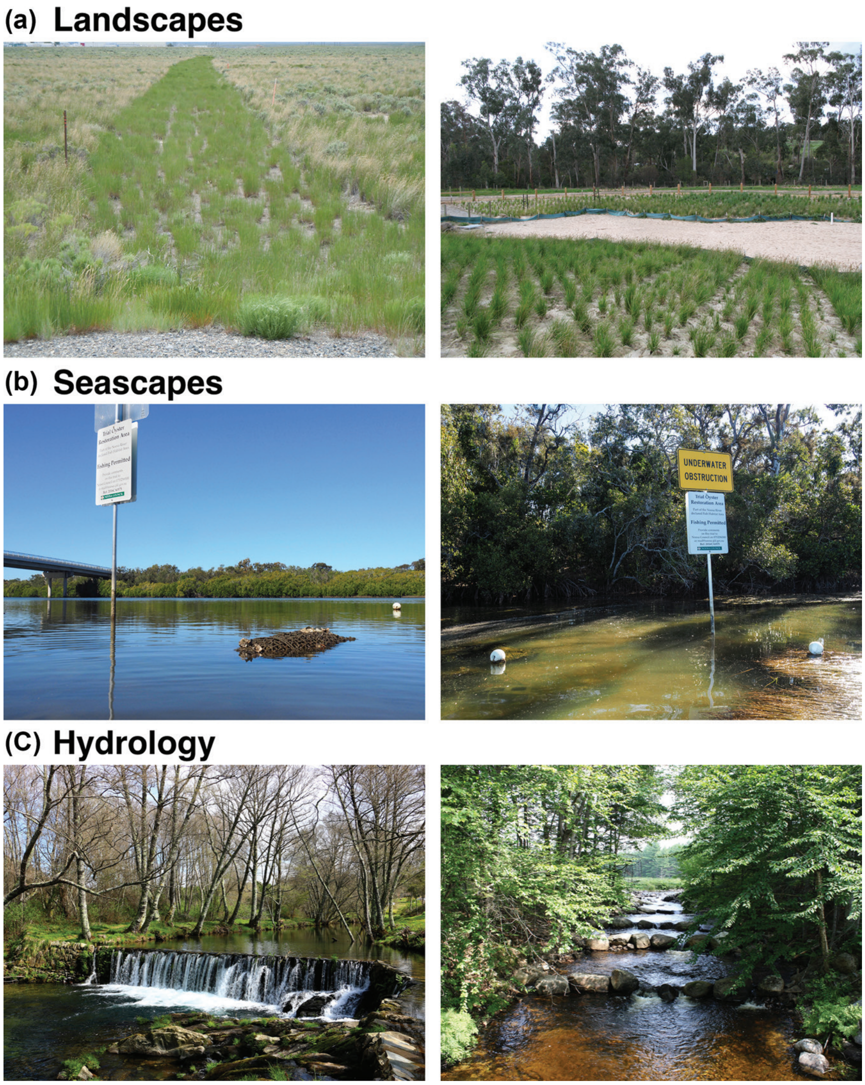

Figure 1. The landscape context of restoration sites has significant consequences for the number and types of animals that inhabit restored ecosystems on land (a), in the sea (b), and where hydrologic connectivity (c) is vital, especially in freshwater ecosystems, and wetlands. For example, isolated patches of restored grassland (a, left) might perform less effectively for animals than restored grasslands close to nearby alternate habitats (right). In the sea (b), connectivity between multiple habitats is often an important consideration because fauna use multiple habitats throughout their lifecycle. In the present study, restored oyster reefs in the Noosa River, Australia, in two seascape contexts: at a distance from nearby mangroves (left) and very close to nearby mangroves and seagrasses (right). Hydrologic connectivity (c) is limited where weirs or dams can restrict flow of propagules and animals (left). These challenges can be overcome by considering connectivity between water bodies and movement of fauna and implementing restoration interventions such as waterway remeandering and fish ways (right). Images courtesy of Cassandra Duncan, Matt Lavin (CC BY SA2.0), Nick Carson.

*bird***, *mammal***, *reptil***, *stream***, *river***, *lake***, and *coral***. All review articles and meta-analyses identified by literature searches were downloaded and scanned by the first author for additional articles that could be included. This method of literature searching was not designed to be exhaustive (i.e., systematic, comprehensive) in identifying all restoration projects in the literature that also sought to enhance animals. It was, however, designed to give the best possible representation of restoration projects across multiple environmental realms and ecosystems, and within the constraints of our search terms.

Inclusion criteria and data extracted. We followed a set classification framework for all studies identified by literature searches (figure 2). Restoration projects were classified as also targeting the restoration of animals to restored habitats if the study tested for effects of the restoration effort for animals or if the article states explicitly that a goal of the restoration effort was also to increase the abundance or diversity of animals.

We concluded that the landscape context of restoration sites was considered in a restoration project if the project specifically chose sites or systems over other areas because of their position within the landscape, especially if the restoration project was intended to reconnect habitat fragments; included the position of sites relative to patches of either similar or different habitat types; or incorporated an aspect or understanding of animal movement, dispersal capacity, or connectivity into site selection. We did not consider a study to have included landscape context if its sites were chosen simply on the basis of existing impacts (e.g., restoration of oil spill sites, erosion mitigation); to revegetate mined land; using "habitat suitability" models for growth of habitat forming species when the position of sites relative to other habitat patches was not also considered; or randomly using a number generator, GIS, or similar method.

Restoration projects were grouped according to country, region and habitat restored, and we pooled studies that reported on the same restoration project to avoid overlap in counting projects. We also identified the types of animals (in broad groups; e.g., birds, mammals, fish, insects, or any combination of these) that each restoration project was intended to enhance on the basis of their stated outcomes. For projects

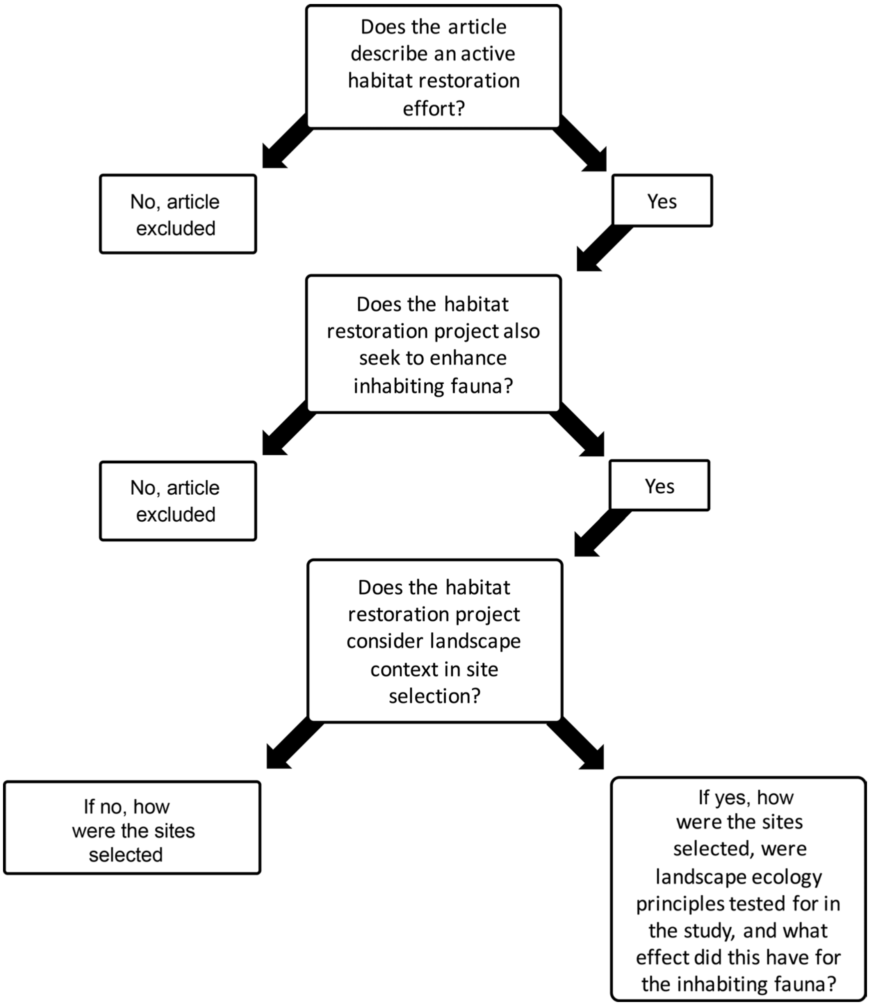

Figure 2. Literature classification framework and decision flow chart. Used to identify restoration projects from the global primary literature.

that did incorporate landscape context into their site selection, we identified whether the restoration effort resulted in the stated aims being achieved for that species (i.e., "positive" effects on fauna).

Studies were classified into environmental realms (terrestrial, marine, or freshwater) according to their location and the animal species being restored. For example, wetlands can be freshwater, marine, or terrestrial; a restored wetland in saltwater intended to restore habitat for fish is classified as marine, whereas a wetland in saltwater enhancing birds or insects is classified as terrestrial.

Results

The final database included 472 restoration projects described in English language journals that sought to enhance animal populations from restoration efforts (for the full list of included articles, see supplemental table S1). We identified restoration projects in 34 countries; most projects were from the United States (*n* = 212, 45%), followed by Australia (*n* = 44, 9%), Finland (*n* = 20, 4%), Sweden (*n* = 14, 3%), and the United Kingdom (*n* = 14, 3%). The most common ecosystems restored were forests (*n* = 134; 28%), followed by streams (*n* = 87; 18%) and grasslands (*n* = 67; 14%). Overall, in 37% of the studies, it was stated explicitly that the landscape context of restoration sites was important in determining the effectiveness of restoration for animals, irrespective of whether they actually implemented landscape concepts into site selection.

Just over half of our data set comprised terrestrial projects (*n* = 243, 52%; figure 3). Forests (*n* = 36, 15% of terrestrial projects) and grasslands (*n* = 34, 14%) in the United States, and forests in Australia (*n* = 30, 12%) were the ecosystems most often targeted for restoration (figure 4). Terrestrial restoration projects most often sought to enhance populations of birds (*n* = 107, 44%), insects (*n* = 53, 22%), and mammals (*n* = 23; 9%). Freshwater projects represented roughly one-third of our data set (*n* = 151, 32%; figure 3). Streams and rivers in the United States (*n* = 47, 31% of freshwater projects) and Finland (*n* = 11, 7%) were the ecosystems most often targeted for restoration (figure 5). Freshwater restoration projects most often sought to enhance populations of fish (*n* = 89, 59%) and macroinvertebrates (*n* = 60, 40%). Marine projects represented roughly one-sixth of our data set (*n* = 78, 17%; figure 3). Oyster reefs (*n* = 30, 44% of marine projects) and saltmarshes (*n* = 10, 13%) in the United States were the ecosystems most often targeted for restoration (figure 6). Marine restoration projects most often sought to enhance populations of fish (*n* = 63, 81%), nektonic crustaceans (*n* = 21, 27%) or macroinvertebrate infauna (*n* = 20, 26%).

Effects of landscape context in restoration. Across all realms, 11% of projects (54 of 472) included landscape context as a criterion in the selection of restoration sites (table 1, figure 3). The integration of landscape context in restoration projects was remarkably similar across realms: terrestrial (10% of 243 projects), marine (13% of 89), and freshwater (13% of 164). In terrestrial ecosystems, the projects in which landscape context was used most often were those in peatlands (100% of peatland projects, but only one project was identified), wetlands (14% of wetland projects), and forests (10%; figure 4b) and those that targeted amphibians (29%) and mammals (13%). Freshwater projects that considered landscape context most often were those in rivers (40%)

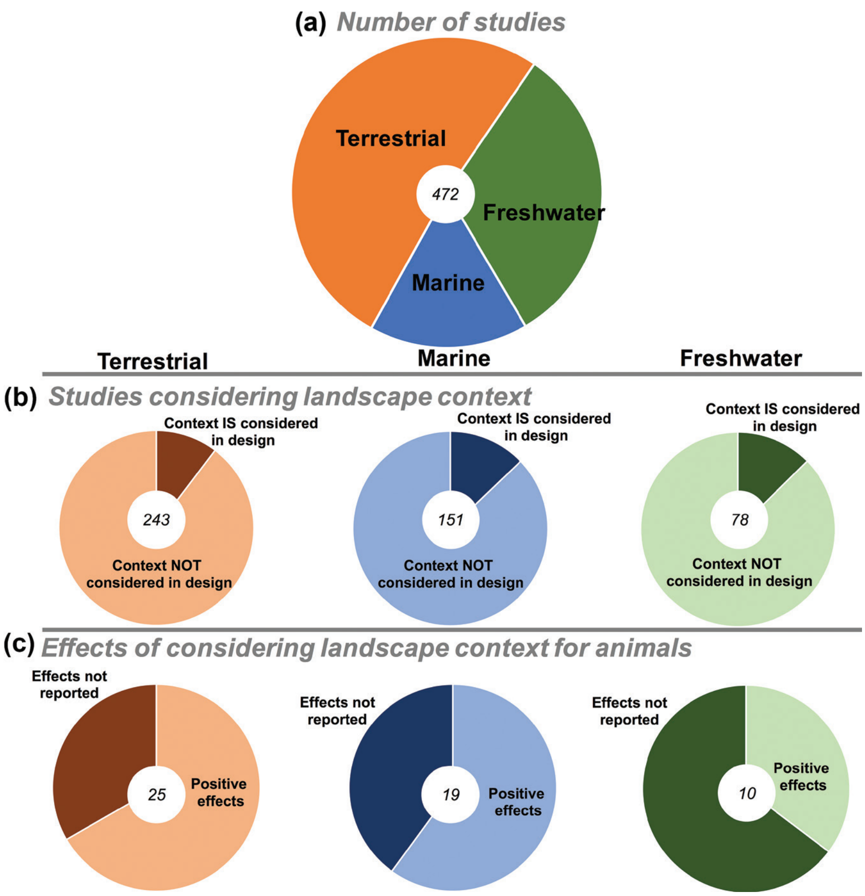

Figure 3. Summary of included studies. Numbers in white circles in the center of each chart denote the number of studies in each category. (a) The total number of studies included in the database, divided by environmental realm. (b) The proportion of studies in which the spatial context of restoration sites was considered during ecosystem restoration projects. (c) The proportion of studies in which landscape context was considered during the restoration design process in which the direction of outcomes was reported for animals.

and streams (7%; figure 5b) and those targeting amphibians (40%) and macroinvertebrate infauna (13%). In marine systems, the consideration of landscape context was most prevalent in marine wetlands (30%) and in seagrass (29%; figure 6b) and when restoration targeted birds (33%) or macroinvertebrate infauna (15%).

There was good evidence to suggest that incorporating landscape context into the selection of restoration sites resulted in positive outcomes for animals, with 56% of the projects (30 of 54 projects) in which landscape context was considered showing positive outcomes for animals (table 2, figure 3). In the remaining 44% (24 of 54) of the projects, whether landscape context affected animals directly was not explicitly tested. The projects in which positive effects of landscape context on animals were reported were more common on land (72% of 25 projects) and in the sea (60% of 10) than in freshwater (32% of 19).

Most included studies focused on the ecological effects of connectivity (74% of 54 projects), either between patches of the same habitat. or with other habitats. The projects in which positive effects of connectivity were reported on animals were common across terrestrial (84% of 25 projects), marine (60% of 10), and freshwater (68% of 19) landscapes. In the majority of these (69% of 54 projects), connectivity was considered between patches of similar habitats, and in fewer studies were the effects of connectivity considered with adjacent alternate habitats (3% of 54 projects, and one in each environmental realm; table 2). The potential ecological effects of other landscape concepts have, however, rarely been tested with empirical data (26% of 54 projects), with most research limited to the effects of hydrology in aquatic ecosystems (table 2).

In most projects (89% of 472 projects), landscape context was not listed as a criterion in the selection of restoration sites (table 3, figure 3). When the spatial attributes of landscapes were not considered in restoration studies, the projects were most often at mine sites (15 projects, 6% of terrestrial projects), located to minimize the effects of erosion on freshwater ecosystems (4 projects, 3% of freshwater projects), or placed randomly in landscapes (12 projects, 4% of terrestrial projects and 1% of freshwater projects). For most studies, however, we were not able to identify how restoration sites were selected from the descriptions provided (74% of 472 projects). This was a common trend across terrestrial (177, 73% of all terrestrial projects), marine (58, 75% of all marine projects), and freshwater (113, 75% of all freshwater projects) realms.

The first restoration studies in which landscape context was explicitly considered when selecting restoration sites were published in 1996 for freshwater ecosystems, 2001 for terrestrial ecosystems, and 2004 for marine ecosystems (figure 7a). The proportion of studies in which landscape context was considered has remained highly variable, with no clear trend between years over the past three decades (figure 7a). By contrast, there has been a sharp increase in the integration of spatial concepts from landscape ecology into the wider fields of biology and ecology during this period (figure 7b).

Discussion

The ecological outcomes of restoration projects can, in many cases, be improved by placing sites at locations in landscapes

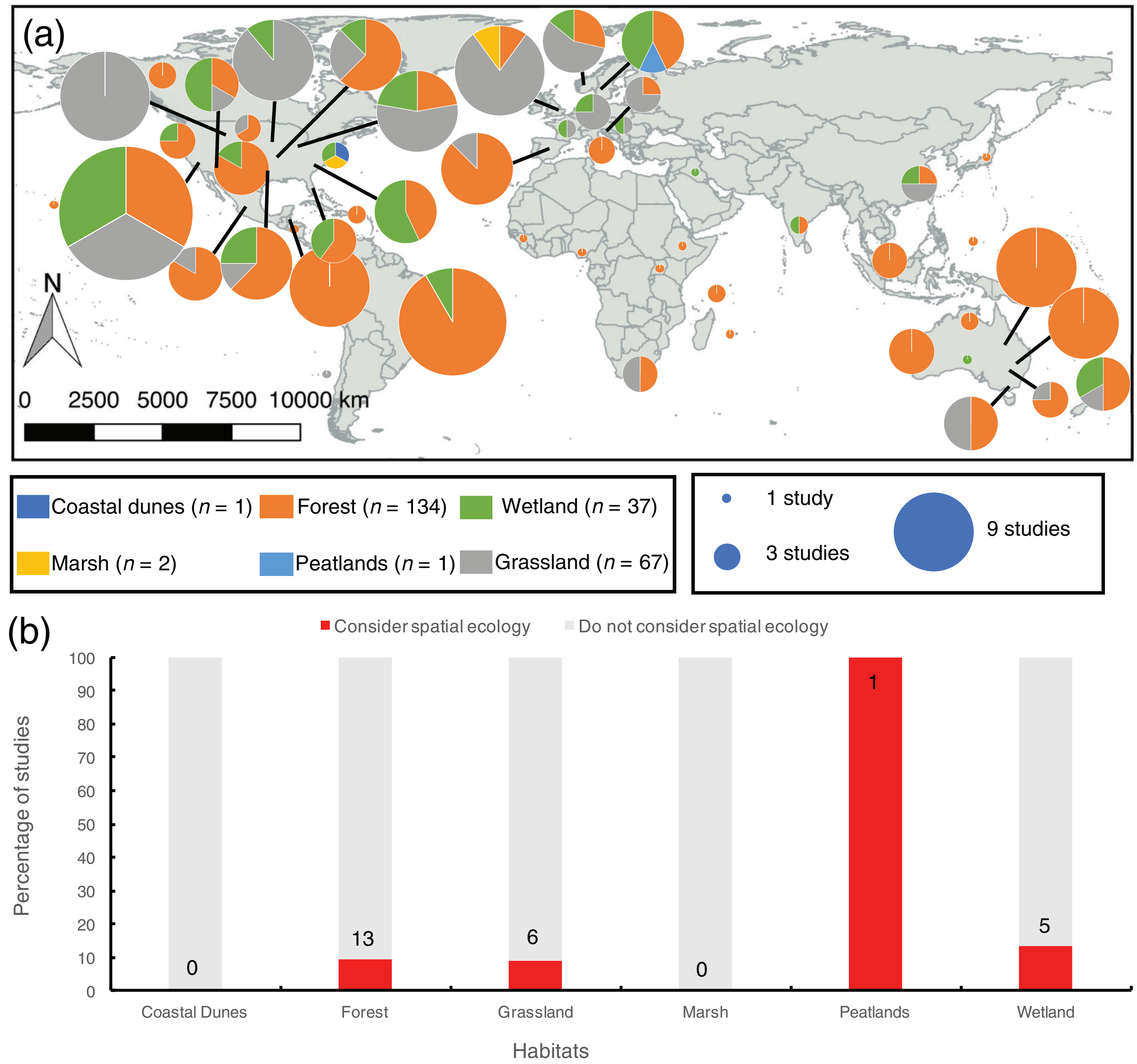

Figure 4. (a) Global distribution of terrestrial restoration projects that aimed to restore animal populations, assemblages, or diversity. (b) Of the 243 terrestrial restoration projects, only 25 (10%) considered landscape context in their design phase (table 2). The integration of landscape attributes did, however, differ among terrestrial ecosystems. Numbers above bars indicate the number of projects that considered landscape context in site selection.

to maximize the recruitment of individuals to newly created habitats (Jones and Davidson 2016). Whereas it is widely appreciated that the landscape context of restored habitats can shape the success of restoration projects, the principles of landscape ecology remain rarely considered in restoration decisions. In this study, we show that a marked discrepancy exists between the stated importance of landscape context for restoration (37% of the studies reviewed) and the extent to which the spatial properties of landscapes are considered in restoration projects (12% of studies reviewed). Furthermore, we found no evidence that the consideration of landscape context in restoration has increased over the past three decades. This is surprising, because spatial concepts have been more widely adopted in conservation during the same period, and there are important global restoration policy documents that advocate for its inclusion (SER 2008, Keenleyside et al. 2012). This result could eventuate because of underreporting in the description of restoration sites.

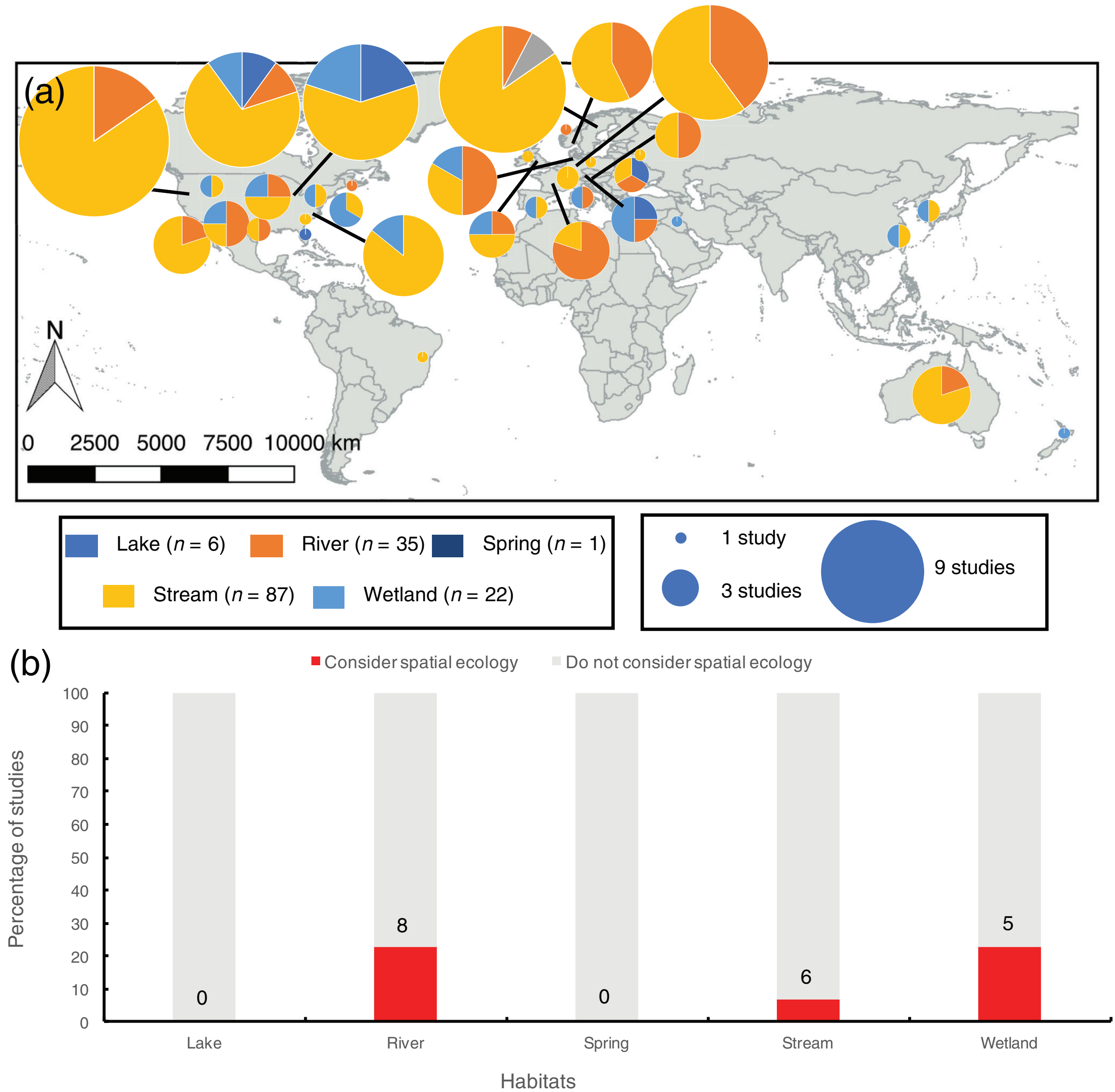

Figure 5. (a) Global distribution of freshwater restoration projects that aimed to restore animal populations, assemblages, or diversity. (b) Of the 151 freshwater restoration projects, only 19 (13%) considered landscape context in their design phase (table 2). The integration of landscape attributes did, however, differ among freshwater ecosystems. Numbers above bars indicate the number of projects that considered landscape context in site selection.

However, restricting our use of only the primary literature offers some safeguard against substantial under-reporting of the design process.

We found no clear reason the uptake of spatial ecological principles varied across different habitats, likely because the uptake was consistently low across all habitats. The exceptions were habitats in which few restoration projects were identified but had very high uptake of landscape context principles (e.g., peatlands); however, little can be gleaned from these few examples from habitats with fewer restoration projects. There were also no clear trends in habitats that have been studied extensively in terms of landscape context. For example, the study of landscape context on coral reefs is highly advanced (Pittman and Olds 2015), but no coral restoration project has yet included it in restoration site selection.

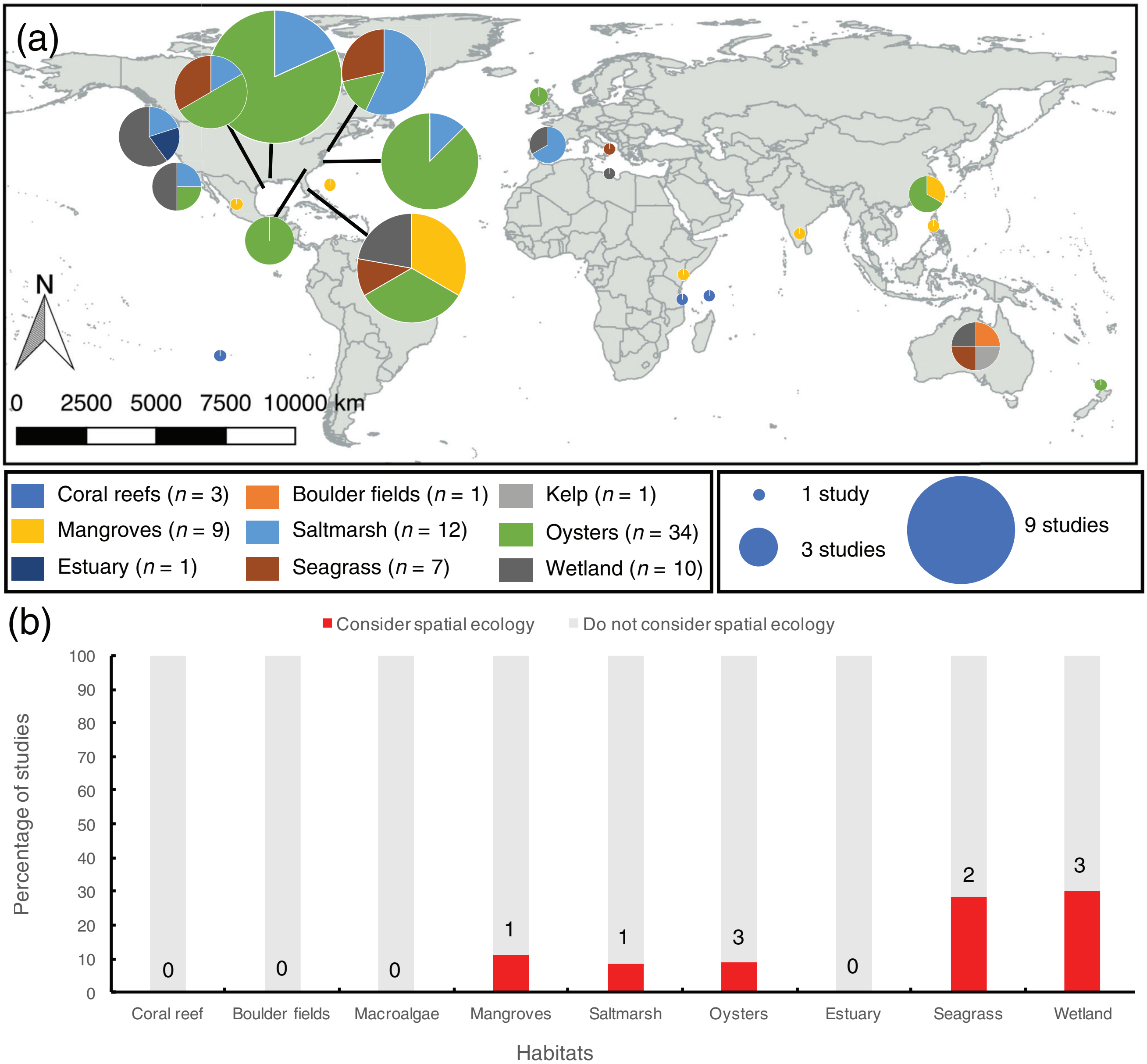

Figure 6. (a) Global distribution of marine restoration projects that aimed to restore animal populations, assemblages, or diversity. (b) Of the 78 marine restoration projects, only 10 (13%) considered landscape context in their design phase (table 2). The integration of landscape attributes did, however, differ among marine ecosystems. Numbers above bars indicate the number of projects that considered landscape context in site selection.

We identified several key types of spatial metrics that are considered in the selection of restoration sites. Predominantly, researchers assessed connectivity with similar patches of habitats (e.g., Angelieri et al. 2016, Derhe et al. 2016), which is unsurprising, given that the role of restoration is often to enhance or reconnect threatened habitats, so considering nearby patches of this habitat is usually important. Concepts such as hydrologic connectivity and connectivity with alternative habitats (i.e., those other than the habitat being restored) were, however, considered an order of magnitude less than connectivity with similar habitat patches. This relatively low number of studies focused on hydrologic connectivity is surprising because reconnecting water bodies hydrologically is an important focus in wetlands and aquatic ecosystems (Kondolf et al. 2006, Jackson and Pringle 2010). Similarly, concepts regarding the spread of propagules by wind or other mechanisms received little attention in the studies we identified. This means that there are several key concepts and metrics within spatial ecology that have yet to be properly studied in restoration but

Table 1. Summary of restoration projects in terrestrial, freshwater and marine realms for all restoration studies.

Terrestrial		Freshwater		Marine		All realms	
Percentage of projects	Number of projects	Percentage of projects	Number of projects	Percentage of projects	Number of projects	Percentage of projects	Number of projects
51	243	32	151	17	78	100	472

Table 2. Summary of restoration projects in terrestrial, freshwater and marine realms for restoration studies in which landscape context was considered in the design phase.

	Terrestrial		Freshwater		Marine		All realms	
Landscape context considered in design	Percentage of projects	Number of projects	Percentage of projects	Number of projects	Percentage of projects	Number of projects	Percentage of projects	Number of projects
	10	**25**	**13**	**19**	**13**	**10**	**11**	**54**
Positive effects	7	18	4	6	8	6	6	30
No effects reported	4	9	7	11	5	4	5	24
Connectivity with patches of similar habitat	8	20	8	12	6	5	8	37
Connectivity with other habitats	1	1	1	1	1	1	1	3
Hydrology	1	2	2	3	4	3	2	8
Other	1	2	2	3	1	1	1	6

Note: Values in bold indicate total number, and proportion of the percentage of the total number of studies that fall into each category.

Table 3. Summary of restoration projects in terrestrial, freshwater and marine realms for restoration studies in which landscape context was not considered in the design phase.

Landscape context NOT considered in design	Terrestrial		Freshwater		Marine		All realms	
	Percentage of projects	Number of projects	Percentage of projects	Number of projects	Percentage of projects	Number of projects	Percentage of projects	Number of projects
	46	**218**	**28**	**132**	**14**	**68**	**88**	**417**
Located on a mine site	7	15	0	0	0	0	4	15
Minimize erosion effects	0	0	3	4	0	0	1	4
Random placement	5	10	2	2	0	0	3	12
Indiscernible	81	177	86	113	85	58	83	348
Other	7	16	10	13	15	10	9	39

Note: Values in bold indicate total number, and proportion of the percentage of the total number of studies that fall into each category.

that are likely to be helpful in placing restoration efforts. Broadening the scope of the types of considerations and metrics used to place restoration should be a key focus of restoration researchers and practitioners alike.

Most projects that incorporated concepts from landscape ecology into their design and site selection showed positive outcomes for animals, albeit with some variation among terrestrial (72% positive outcomes), marine (60%), and freshwater (31%) realms. For example, in freshwater ecosystems, wetland restorations for amphibians reported marked increases in adult breeding populations within 3 years of restoration of ponds that were highly connected to each other (Petranka et al. 2003), an effect that was inconsistent for other similar freshwater restoration projects in which context was not considered (Shulse et al. 2012). These sorts of considerations of adult breeding metapopulations were rare but are likely instructive for the enhancement of animal populations across landscapes (Montalvo et al. 1997, McAlpine et al. 2016). Some counterintuitive results were uncovered for oyster reefs. Higher connectivity (in this case, simply proximity) with adjacent habitats is usually viewed as beneficial for coastal marine organisms (Olds et al. 2018). However, restored reefs in North America contained higher fish abundance when further from existing marshes because they provided new complex habitats on previously low-complexity muddy areas (Grabowski et al. 2005). Conversely, higher connectivity between extant reefs and restored reefs was viewed as a positive influence on inhabiting fauna in other studies (Gregalis et al. 2009). Although the performance of projects or sites that did incorporate spatial context into their design and those that did not (e.g., randomly or for some other ecological reasoning) has not been assessed, these findings

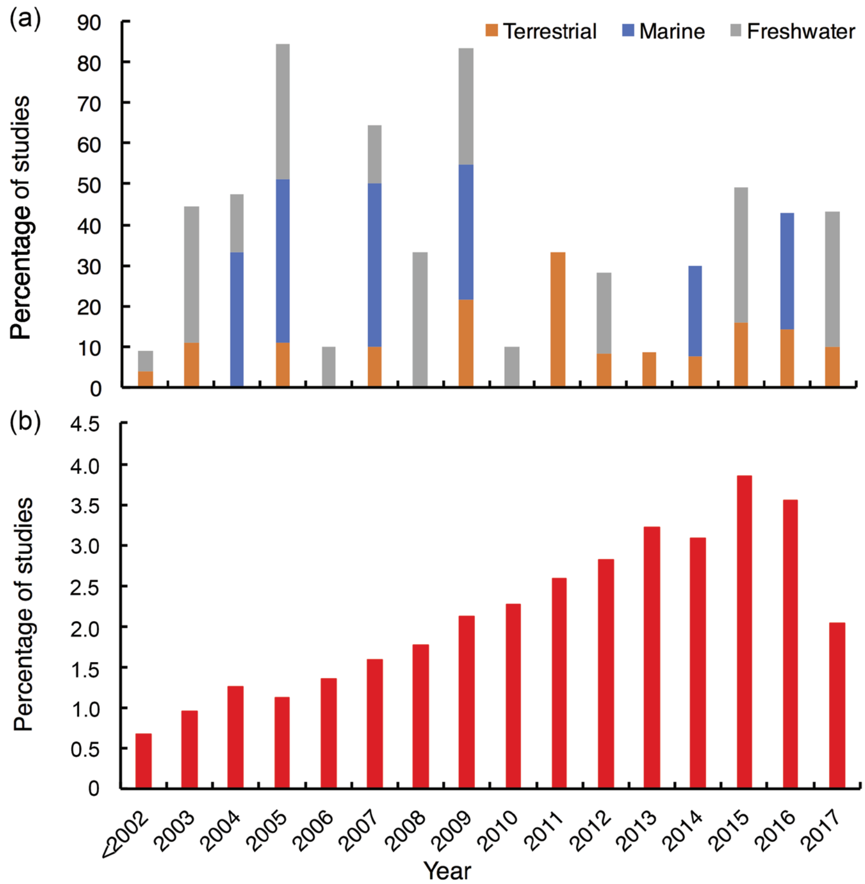

Figure 7. Summary of published studies that have considered landscape context in (a) restoration (separated for terrestrial, marine and freshwater realms) and (b) across the fields of biology and ecology. Data extracted from the Web of Knowledge the key words* restoration *(*"habitat restoration" or "ecological restoration" or "ecosystem restoration"*),* "biology" or "ecology," *and* "landscape ecology" or "spatial ecology." *2017 is part year only.

in a landscape context. Alternatively, restoration sites might be placed in areas to limit the potential for conflict with other human uses (e.g., fishing, farming, recreational use, transport) or legislation (e.g., mooring areas, other forms of conservation; Pressey and Bottrill 2008), and these might not be optimal for the restoration of ecosystems or their inhabiting animals (Fahrig 2001, Pottier et al. 2009). Both approaches might result in restoration sites being unintentionally restricted to locations that provide poor habitat values for animals (cf. "residual" conservation areas; Pressey et al. 2000, Pressey and Bottrill 2008) and that therefore have the potential to yield suboptimal restoration returns for animals.

There are several key research areas that should be promoted to assist in better prioritizing restoration across landscapes. We raise in this review a paucity of restoration projects incorporating systematic conservation planning regimens in the selection of restoration sites. Studies should be conducted to determine the validity of using systematic conservation practices (Margules and Pressey 2000) for restoration across environmental realms (research question 1 in box 1). Despite this review uncovering a diversity of ecosystems and animals that have been the focus of restoration, there are several ecosystems (research question 2 in box 1) and animal groups (research question 3 in

suggest that the spatial properties of landscapes might have broad and largely unrecognized effects on the success of ecological restoration projects.

Ecological restoration is conducted for many purposes, and not all types of restoration are designed to benefit animals. For example, many restoration projects are intended to restore whole ecosystems (e.g., whole of lake restoration), to reverse a particular type of impact (e.g., mine site rehabilitation, oil spill remediation; e.g., Brady and Noske 2010), or to limit the ecological effects of ongoing disturbances, such as erosion, sedimentation, nutrient enrichment, or pollution (e.g., restoring oyster reefs to reduce shoreline retreat or forests to reduce gully erosion; e.g., Piazza et al. 2005). Under these circumstances, restoration sites might be placed in areas that are considered appropriate for the establishment of habitat-forming species but that might be isolated from other remnant patches of the same habitat that serve as sources for the recruitment of animals. Because the locations of these types of projects are often fixed, it might not always be possible for restoration decisions to be placed

box 1) that remain underrepresented within the literature. For example, very few studies have assessed the capacity for coastal dunes to be restored for animals, especially birds, despite beach ecosystems being regularly restored for these purposes (Maslo et al. 2011, Maslo et al. 2012). To date, most work on the effects of landscape context on the outcomes of restoration has been focused specifically on how the metric of connectivity (especially proximity and isolation) between patches of similar habitat affects the abundance of animals. Restoration sites are always positioned within heterogeneous landscapes of multiple habitat types, so further research should be conducted on how connectivity with nearby patches of different habitat types affects the success of restoration more broadly (research question 4 in box 1), as well as the condition of animal populations themselves, where this is a key restoration goal (research question 5 in box 1). Similarly, there are several landscape metrics, beyond simple distance-based connectivity metrics (especially Euclidean distance), that might assist in developing more robust and representative

Box 1. Priority research questions for integrating landscape principles into restoration ecology.

1. Are the principles of systematic conservation planning (Margules and Pressey 2000) directly translatable to all restoration projects and, if not, which principles need to be tailored specifically for restoration?
2. For which habitats does landscape context matter most, and which metrics, and which connections, should be prioritized for individual habitat types?
3. For which animal groups does landscape context matter most, and which metrics, and which connections, should be prioritized for individual animal groups?
4. To what degree does considering connectivity with other habitats (i.e., interhabitat connectivity) affect the outcomes of restoration projects (e.g., Unsworth et al. 2008)? To date, most research and focus in the literature has been on connectivity between patches of the same habitat (i.e., intrahabitat connectivity).
5. To what degree can incorporating metapopulation dynamics and connectivity into restoration planning enhance animal population fitness, persistence, and resilience?
6. Are there more thorough, or better, metrics that can be used to optimize the spatial placement of restoration (e.g., McGarigal et al. 2012)? To date, most work on the spatial metrics that influence restoration has focused on connectivity, especially proximity (Euclidean) between similar habitat patches.
7. Is there consistency in the efficacy of spatial metrics across environmental realms? (e.g., Pittman et al. 2018)

models for incorporating landscapes ecology into restoration. Landscape ecologists have developed several multivariate or multimetric variables that can be used to describe the complexity of landscapes for animals (e.g., McGarigal et al. 2012). The efficacy of these metrics in restoration should be further investigated for different ecosystems and target animals (research question 6 in box 1). Several authors have discussed the validity of landscape metrics and concepts across environmental realms (Pittman et al. 2018). For example, there is some evidence to suggest that the best metrics to describe spatial patterns in animal abundance might differ between the land and the sea because of the movement of water bodies in aquatic ecosystems (Pittman et al. 2018). Establishing the validity of these metrics across environmental realms will assist in generalizing restoration planning regimens across realms (research question 7 in box 1). Collectively, answering these priority research questions will assist in establishing more effective regimens for systematic landscape restoration across all environmental realms, and provide the evidence that managers need to support their decision-making processes.

Systematic conservation planning has made great progress in using diverse landscape characteristics and sophisticated algorithms to guide the design of protected areas and reserve networks (Margules and Pressey 2000, Moilanen et al. 2009). The principles of landscape ecology and the techniques of conservation planning might be useful in the design of restoration areas but have not been widely applied to introduce a crucial spatial element to restoration planning (Hodgson et al. 2011). When selecting sites for a network of reserves, the conservation planning process starts with a broad, landscape-scale perspective. Ecosystems, habitats, and locations are selected for protection to maximize conservation benefits across the entire landscape, and some potential sites are then eliminated because of other considerations (e.g., extractive industries, tourism; Watts et al. 2009). By contrast, restoration projects often start with a narrower perspective focused on the specific ecosystem or habitat to be restored. Sites are then selected on the basis of their suitability to support the particular ecosystem of interest, with little consideration of the attributes of landscapes beyond the restoration site. Incorporating the lessons learned from systematic conservation planning (i.e., goal setting, data-based feedback loops, and improvements) and the principles of landscape ecology (i.e., the placement of sites in heterogeneous land- and seascapes) into restoration should, therefore, lead to significant improvements in the design, placement, and ecological effectiveness of restoration projects. We advocate a landscape-scale approach to restoration and suggest that spatial restoration ecology should start with the identification of ecosystems and habitats that are in the greatest need of restoration (which can be to be determined on the basis of the best historical information available). Sites for restoration should then be selected from all suitable locations within the landscape of interest to maximize their potential ecological benefits for the ecosystems themselves, the animals and food webs they support, and the ecological functions and ecosystem services they provide. This spatial approach to restoration ecology should, therefore, help to broaden both the scope and perceived ecological benefits of many restoration projects and might also improve returns on investment across restored landscapes.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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