

REVIEW ARTICLE

Evaluating where and how habitat restoration is undertaken for animals

Robin Hale^{1,2}, Ralph Mac Nally³, Daniel T. Blumstein⁴, Stephen E. Swearer¹

Habitat restoration is vital to ameliorate the effects of anthropogenic disturbances on animal habitats. We reviewed the peer-reviewed literature to examine where and how habitat restoration is undertaken. Our aim was to identify key knowledge gaps as well as research and monitoring needs that can inform future restoration actions. We found: (1) marine and terrestrial actions focus most commonly on restoring vegetation, and freshwater actions focus on restoring the in-channel habitat; (2) arthropods are the most common focal group; (3) there is often no collection of pre-restoration data, so certainty in attributing environmental changes to restoration actions is limited; and (4) population and community measures are most commonly used in monitoring programs, which only show if animals are present at restored sites and not whether they are able to grow, survive, and reproduce. We highlight three important considerations for future restoration actions. First, more integration of knowledge among freshwater, marine, and terrestrial systems will help us to understand how, and why, restoration outcomes might vary in different contexts. Second, where possible, restoration projects should be assessed using before-after-control-impact designs, which will provide the strongest evidence if desired restoration responses occur. Third, if the goal of restoration is to develop self-sustaining breeding populations of target animals, then measures of fitness (i.e. breeding, survival) should be collected. These recommendations will hopefully help guide more effective restoration practices and monitoring in the future.

Key words: biodiversity, ecological restoration, fitness, habitat loss, monitoring

Implications for Practice

- Understanding where and how restoration is undertaken can guide future programs and highlight research needs.
- More communication between freshwater, marine, and terrestrial restoration ecologists will facilitate knowledge exchange, and allow outcomes to be compared in different contexts.
- Before-after-control-impact designs provide the strongest way to evaluate responses to restoration and collecting pre-restoration data is a critical component of a robust design.
- If the target of restoration is self-sustaining populations of target animals, then key aspects of fitness (breeding and survival) should to be monitored to assess if this target is likely to be met.

Introduction

In 2018, the World Wildlife Fund published their biannual Living Planet Report, which reported that wildlife population sizes have decreased by 60% since 1970, principally from habitat loss, fragmentation, and degradation (World Wildlife Fund 2018). Given the unprecedented rates and global scales at which humans are transforming ecosystems (Vorosmarty et al. 2010; Halpern et al. 2015; Venter et al. 2016), restoration is critical for combatting the adverse effects of habitat loss and transformation on animals.

Habitat restoration involves a diverse range of actions. Revegetation at large spatial scales can be used to reconstruct landscapes (Thomson et al. 2009), and environmental flow releases in rivers can restore ecosystem processes (Arthington et al. 2006). For animals, site-scale habitat restoration is likely to be particularly important for rebuilding populations. This involves restoring ecosystems with the explicit goal of providing habitat, either for individual species or for species assemblages, in an area (Miller & Hobbs 2007). Typical examples of habitat restoration include revegetation to provide habitat resources for birds, such as dense canopy in the short term (<10 years) that supplies food (insects) and hollows for breeding or shelter over longer time periods (Vesk et al. 2008b) or stream restoration to provide spawning habitat (boulders and gravel beds) for fish (Palm et al. 2007).

Scientific studies of habitat restoration have historically been species- or system-focused (Hobbs & Norton 1996). As with much of conservation practice, there has not been a strong

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¹School of BioSciences, The University of Melbourne, Parkville, Victoria 3010, Australia ²Address correspondence to R. Hale email robin.hale@unimelb.edu.au

³Institute for Applied Ecology, The University of Canberra, ACT 2617, Australia ⁴Department of Ecology and Evolutionary Biology, Institute of the Environment and Sustainability, University of California Los Angeles, Los Angeles, CA, U.S.A.

focus on systematic appraisals of the evidence to guide decisions about where and how to restore habitats (Sutherland et al. 2004). However, in the past two decades, several works have described general principles for restoration ecology (Hobbs & Norton 1996; Bond & Lake 2003; Palmer et al. 2005; Miller & Hobbs 2007; Perring et al. 2015; Miller et al. 2017). These papers outlined how to set appropriate goals to guide restoration, and to identify and mitigate factors that might impede progress toward these goals. To our knowledge, though, there has not been a quantitative assessment of the peer-reviewed literature to examine where and how habitat restoration is being undertaken.

Restoration ecology is still a relatively young discipline, and often focused heavily on plants, as recent assessments have shown (e.g. nearly 70% of studies focus only on plants; McAlpine et al. 2016). We focus on animals here because programs that involve improving vegetation often are enacted to provide habitats for animals (Vesk et al. 2008a, 2008b). In general, habitat restoration projects for animals typically focus on reinstating self-sustaining breeding populations of a single, or a small subset of, species through the provision of food, shelter, and habitat (McAlpine et al. 2016). Conducting a quantitative assessment of how habitat restoration is done can help identify key knowledge gaps and future research and monitoring needs. With this in mind, we conducted a literature review to ask: (1) what habitat elements are being restored, and for what taxa; (2) how are restoration actions being monitored; and (3) what indicators are used to measure responses to habitat restoration actions. Our article provides information that can help future habitat restoration actions to produce improved outcomes for animals, especially an increased likelihood of population persistence.

Methods

We searched the Web of Science database across all years using the following search term: ([biodiversity OR abundance OR density OR richness OR select* or choice* or prefer* or settle* or coloni* or recruit* or metamorph* or breed* or reprod* or growth* or fitness or surviv* or mortal* or death* or birth* or spawn* or matur* or condition or metamoph* or fidelity or population*] AND habitat* AND restor*). This search term was selected to encapsulate likely responses of animals to restoration at the individual (e.g. births, deaths, body condition), population (e.g. abundance), and community (e.g. assemblage composition) levels. We included key words that describe how animals colonize restored sites (i.e. their habitat selection behavior) to gain a wider representation of restoration studies. Our search found 11,545 publications.

Our review was not designed to follow the systematic review guidelines published by the Collaboration for Environmental Evidence (COEE 2018), which entails pre-review and publication of the protocols alongside an explicit strategy for searching the "gray literature" (unpublished government reports, etc.). Rather, we evaluated peer-reviewed studies systematically and included only those that met the following criteria:

- Focused on the restoration of structural habitat at the site scale; we did not consider process- or landscape-based restoration because these were not our specific interest. This meant the following activities were excluded: environmental flow releases, dam or impoundment removal, landscape reconstruction, and the establishment of reserves and marine protected areas.
- Contained empirical data and evaluated individual restoration projects rather than provided a summary of whole-ofprogram outcomes.
- Examined the responses of animals to restoration (conservation outcomes), not just whether habitats had changed (restoration actions). For example, we excluded studies that examined whether restoration had improved spawning habitat for salmon but that did not measure salmon responses per se.
- Included a comparator against which responses could be assessed. This includes concurrent monitoring of control or reference sites, monitoring sites before and after restoration, or both (i.e. before-after-control-impact [BACI] designs).
- If multiple papers reported on the same restoration project through time, we included only the most recent.

Two hundred and fifty-eight papers met these criteria, from which we extracted the following:

- Descriptive information (e.g. location, focal taxa, types of restoration activity).
- The study monitoring design, classifying studies as those that monitored: (1) restored sites before and after restoration (B/A); (2) monitored control and restored sites following restoration (i.e. a control/impact design; C/I); (3) restored and control sites before and after restoration (BACI); and (4) sites along gradients, either of time since restoration (chronosequence) or spatially (sites in different landscape gradients).

We recorded whether studies measured:

- Responses to restoration at the community (e.g. composition, richness, biomass), population (e.g. abundance/density/biomass of individual species, population size, and growth rate), or individual (e.g. body condition, growth rate, behavior) level. Behavior relates to assessing biotic responses to restoration (e.g. foraging rate being used as an indicator of a response to restoration).
- Measures of fitness (i.e. reproduction, survival).

Most papers were on individual species or assemblages of one taxon (e.g. birds). If a paper focused on ≥ 2 taxonomic groups, we considered the group that was discussed most in the paper.

Results and Discussion

Where and How Is Habitat Being Restored and for What Taxa?

Marine and terrestrial actions most commonly focused on restoring vegetation through replanting native plant species or by removing invasive plant taxa (Fig. 1). Freshwater

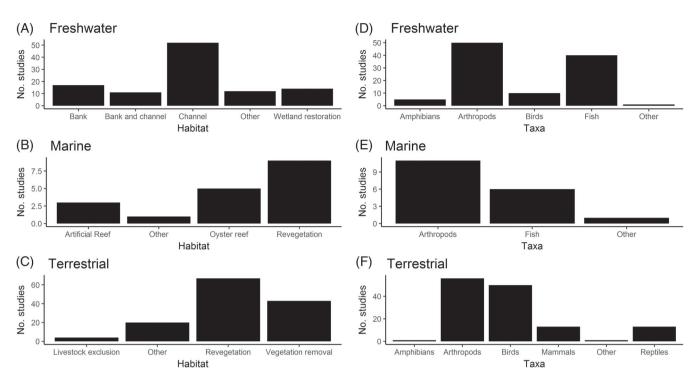


Figure 1. Habitat elements and taxa involved in habitat restoration projects in the 258 studies. Here, we have characterized the habitat elements (panels a,c,e) and taxa (panels b,d,f) that are the focus in freshwater, marine, and terrestrial realms. Note that revegetation here refers to the active planting of vegetation and not just the cessation of disturbances (e.g. livestock removal).

restoration often focuses on the in-channel habitat (e.g. adding large woody debris; Roni et al. 2008), but there is likely to be geographic variability in these activities, with previous assessments highlighting the predominance of works focused on the riparian zone in some regions (e.g. southeastern Australia; Brooks & Lake 2007).

There were substantially fewer studies of habitat restoration in marine systems. While restoration ecology is a young discipline, this is especially the case in marine systems (Abelson et al. 2015), which may explain this result. However, there are specific challenges in marine systems, such as logistical constraints on where restoration can be implemented, or difficulties in observing target animals, such as highly dispersive larval fish. Greater communication between restoration ecologists working in marine, freshwater, and terrestrial systems will help to facilitate knowledge exchange, and to understand how lessons learnt in one system can help to inform actions in another.

Comparisons among different systems can help ecologists to understand broader ecological processes and patterns, including potential generalities and regional or continental idiosyncrasies (Munguia & Ojanguren 2015). The use of such comparisons is an important step in restoration becoming more predictive by understanding how outcomes might differ depending on when, where and how restoration actions are done (Brudvig et al. 2017). Aquatic and terrestrial systems differ in a range of fundamental ways that relate to their ecological and environmental characteristics, especially in terms of the former having a greater extent and rate of dispersal of animals and other

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materials (Carr et al. 2003). However, research in ecosystem types is often being undertaken in disciplinary "silos." That marine and terrestrial projects often involve similar actions suggests that the integration of knowledge among systems, which we highlight above, is likely to help identify transferable approaches and thinking. For instance, in both marine and terrestrial contexts, replanted vegetation is likely to provide different resources along restoration chronosequences. In some terrestrial systems, the timing at which different habitat elements develop following restoration has been well described and has been used to develop hypotheses about when fauna will respond (Vesk et al. 2008a). We found three examples relating to seagrass and mangrove restoration but more studies in the future could help similarly describe temporal trajectories following restoration in different marine restoration systems.

Arthropods were the most commonly studied taxon in all three systems probably because arthropods can be sensitive and rapid (short generation times) indicators of environmental change and are important for many ecosystem processes (Tiede et al. 2017). Fish and birds were second in aquatic and terrestrial systems, respectively. The focus on fish is probably related to many restoration actions being undertaken to provide habitat for species that are fished either recreationally or commercially, such as salmonids in North America. Birds are studied broadly owing to their observability (most species are diurnal, often have bright coloration and loud vocalizations) and there is a long history of work linking individual species to their key resources (Wiens 1989*a*, 1989*b*).

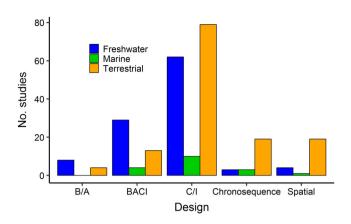


Figure 2. Frequency of use of different monitoring program designs in habitat restoration in the 258 studies: before/after (B/A), before-after-control-impact (BACI), control/impact (C/I), and sampling either chronosequences (i.e. sites of varying age since restoration) or spatial gradients (i.e. sites in different land uses).

How Are Restoration Actions Being Monitored?

It is vital that outcome goals are set in restoration projects, and that monitoring is undertaken to assess progress toward these goals (Palmer et al. 2005). However, monitoring programs differ in their ability to distinguish change due to restoration from background spatial and temporal variability (Downes et al. 2002). Monitoring restored sites before and after restoration allows a change to be detected, but not for this change to be attributed necessarily to restoration actions (Keough & Mapstone 1995). A C/I design, in which restored and control locations are monitored after restoration, has similar limitations. To definitively attribute changes to restoration, a BACI design is required, where restored sites and plausibly comparable reference locations ("controls") are monitored before and after restoration. Replication here is important, with multiple restoration and control sites used to test for the potential generality of restoration trends. However, replication requires compromises between the extents of restored areas and their number because programs typically have limited funding. Moreover, there are compromises between how well individual locations are monitored and numbers of locations monitored because survey effort typically is limited (Mac Nally & Horrocks 2002).

In all three ecosystem types, the most commonly used monitoring-program design was the comparison of restored and control sites after restoration (i.e. C/I—Fig. 2). This raises the potential that in many habitat restoration projects, changes that are detected at restored sites might be due to inherent differences between control and restored sites (e.g. different soil types, disturbance histories). Terrestrial restoration projects are also often assessed using chronosequences (i.e. sites of differing ages since restoration) or along spatial gradients (i.e. sites within different land uses). Space-for-time chronosequences are commonly used in ecology, and assume that space can be a surrogate for time (Pickett 1989). However, incorrect conclusions can be drawn when other factors (e.g. site history) mean that the assumption that sites of different ages are following the same trajectory is not met (Johnson & Miyanishi 2008).

BACI designs should be implemented to monitor responses to restoration wherever possible, with replicated restoration and control sites. We found that this replication commonly occurs; in the 46 studies that used BACI designs, only 11 were conducted at single restoration and control sites. This suggests that when BACI designs are used, they are employed in ways that should allow appropriate evaluation of restoration responses, albeit with the limitations outlined above.

It is important to consider the spatial scale of restoration actions relative to the spatial scales that are most important to animals. Small-scale restoration experiments, even those that use BACI designs, still may not provide strong inferential strength e.g. if the target animals respond to habitat at larger spatial scales (i.e. home or foraging range). Many animals have scale-dependent relationships with habitat, and knowledge of these relationships ideally should guide restoration (Hale et al. 2019). However, spatial scales often are selected for other reasons, such as convenience, prior practices, land ownership, or to meet policy or legal specifications. This is a problem that is not specific to restoration but is a general issue in ecological research, where work often is done at spatial scales that are too small for the ecological processes being studied (Englund & Cooper 2003), or in which there is no biological justification for working at a particular scale (Jackson & Fahrig 2015). Therefore, it is important to consider the appropriate scale at which restoration needs to be undertaken.

Which Indicators Are Used to Measure Responses to Habitat Restoration Actions?

Previous reviews have described the frequency of use of broad indicator types (i.e. diversity, vegetation structure, ecosystem processes, and subgroups within these categories: Ruiz-Jaen & Mitchell Aide 2005) but not in the context of habitat restoration. The selection of ecological indicators is a critical component of any monitoring program, and should result in indicators being chosen that relate to the outcome goals of the project (Cairns et al. 1993; Jackson et al. 2000). In general, restoration to improve habitat for animals will be judged to be successful if target animals develop self-sustaining breeding populations. While some actions might appear not to fit this objective directly (e.g. restoration of stopover habitats for migratory species), such actions will ideally provide fitness benefits in survivorship and recruitment. Typically, while showing that species are moving toward self-sustaining populations is a difficult task, at least measurements relating to fitness (i.e. survival and recruitment) of the target animals provide stronger evidence for the success of a restoration program than do species presence or counts per se (Selwood et al. 2015). Our third aim was to tally whether these fitness-relevant indicators of success commonly are monitored in habitat restoration.

We found that only 11% of studies used indicators that were relatable to fitness (e.g. breeding activities, fledging, or survival directly, Fig. 3). For example, Selwood et al. (2009) and Mac Nally et al. (2010) measured bird breeding along restoration

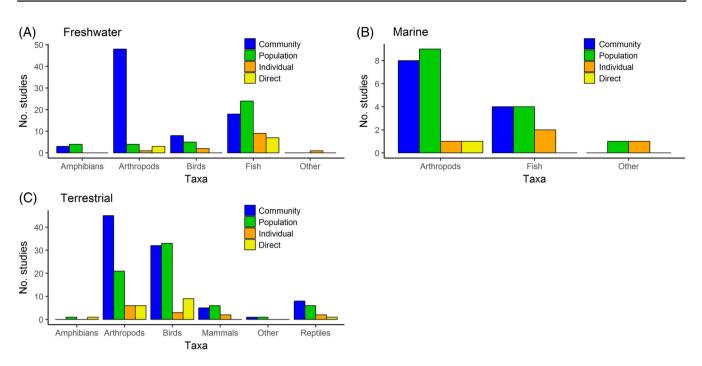


Figure 3. Numbers of studies (of the 258) that assessed biotic response to restoration at the community (e.g. community composition, species richness), population (e.g. abundance), or individual (e.g. body condition, growth rates) level, or that measured fitness directly (e.g. reproduction, survival).

chronosequences in upland and floodplain forests in southern Australia, while Palm et al. (2007) monitored a range of demographic indicators, including egg-to-fry survival rates, to assess responses of brown trout (Salmo trutta) to spawning habitat restoration. Most studies (240 of 258) measured responses using indicators that did not relate to fitness or to population demography, such as information on communities (70% of studies) and populations (45%). While community and population measures can show that animals are more often present at restored than unrestored sites, they do not indicate whether the animals survived, grew, or reproduced. Population increases of target taxa are an important outcome of restoration but without concurrent monitoring of fitness, it is impossible to tell if these increases are due to increased recruitment at restored sites or from individuals being attracted from nearby locations (Stier & Osenberg 2010). This "attraction vs. production" hypothesis has been discussed in detail in relation to the use of artificial reefs to provide habitat in marine systems (Bohnsack et al. 1997) but is directly relevant to all restoration actions.

Developing breeding populations of target species depends on animals both colonizing restored sites and their habitat requirements being met once there. Therefore, how animals behave is an important component of how they respond to restoration (Lindell 2008). In particular, habitat selection behavior is critical. The examples of "undervalued resources" and "ecological traps," whereby animals either avoid appropriate habitats (Gilroy & Sutherland 2007) or mistakenly prefer lower quality habitats (Robertson et al. 2013), demonstrate how restoration can fail when animals exhibit maladaptive habitat selection behavior (Hale & Swearer 2017). Clearly, appropriate

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measurements of fitness are needed but so is recognition of the importance of habitat-selection behavior.

Implications for Future Habitat Restoration

Given the pervasiveness of anthropogenic ecosystem disturbance, habitat restoration is a critical tool to reverse declining animal biodiversity. Our review highlights three important considerations for future restoration actions. First, the integration of restoration work among ecosystems (i.e. freshwater, marine, and terrestrial) is likely to help us to develop a more general understanding of how to best restore habitats. Second, wherever possible, restoration projects should be assessed using monitoring programs that implement BACI designs. This will result in the strongest evidence that changes at restored sites are due to restoration. While not a new recommendation, with seminal publications from the 1990s outlining the advantages of BACI designs (e.g. Underwood 1994; Keough & Mapstone 1995), >90% of the papers we reviewed were published since 2000, indicating that BACI designs are rarely employed despite on-going calls for their use. Third, the target of restoration is to lead to self-sustaining breeding populations of focal animals. This means that it is important to measure fitness attributes, preferably all elements of a full demographic model (i.e. survival, breeding, dispersal, and colonization; Selwood et al. 2015). We acknowledge that this may be aspirational and may be beyond the scope of most monitoring programs, but it is one that should underlie planning because demography determines population dynamics. Nevertheless, an increased focus on fitness attributes is important because changes in community composition or population size provide information that animals are present at restored sites, but not necessarily whether they are able to survive and recruit. Considering these recommendations will help to guide the development and implementation of effective habitat restoration practices in the future. In turn, more effective habitat restoration will help ameliorate the effects of human-driven habitat loss and degradation on biodiversity.

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