

Integrating plant- and animal-based perspectives for more effective restoration of biodiversity

Clive McAlpine^{1*}, Carla P Catterall², Ralph Mac Nally³, David Lindenmayer⁴, J Leighton Reid⁵, Karen D Holl⁶, Andrew F Bennett⁷, Rebecca K Runtting¹, Kerrie Wilson¹, Richard J Hobbs⁸, Leonie Seabrook¹, Shaun Cunningham⁹, Atte Moilanen¹⁰, Martine Maron¹, Luke Shoo¹, Ian Lunt¹¹, Peter Vesk¹², Libby Rumpff¹², Tara G Martin¹³, James Thomson¹⁴, and Hugh Possingham¹

Ecological restoration of modified and degraded landscapes is an important challenge for the 21st century, with potential for major gains in the recovery of biodiversity. However, there is a general lack of agreement between plant- and animal-based approaches to restoration, both in theory and practice. Here, we review these approaches, identify limitations from failing to effectively integrate their different perspectives, and suggest ways to improve outcomes for biodiversity recovery in agricultural landscapes. We highlight the need to strengthen collaboration between plant and animal ecologists, to overcome disciplinary and cultural differences, and to achieve a more unified approach to restoration ecology. Explicit consideration of key ecosystem functions, the need to plan at multiple spatial and temporal scales, and the importance of plant–animal interactions can provide a bridge between plant- and animal-based methods. A systematic approach to restoration planning is critical to achieving effective biodiversity outcomes while meeting long-term social and economic needs.

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Current rates of extinction are 100–1000 times greater than in pre-human times (IUCN 2007). These elevated rates are being driven primarily by the conversion and degradation of native ecosystems by human activities. In response, the 2012 United Nations (UN) Rio+20 Conference on Sustainable Development set the goal of restoring 150 million ha of disturbed and degraded land

by 2020 (Menz *et al.* 2013), with expected benefits for the maintenance or recovery of biodiversity. Given the UN Rio+20 goal, and that many countries are implementing expensive restoration programs, it is timely to review how best to ensure that restoration actions are effective in the recovery of biodiversity.

Ecological restoration is the process of assisting the recovery of entire ecosystems (Hobbs *et al.* 2006). Yet, restoration science and practice are rarely as straightforward as this definition suggests (Palmer *et al.* 2006); one major problem is the lack of accord between the ways in which plant and animal ecologists approach issues in restoration theory and practice. This division is associated with both a dominance of plant-based studies in the scientific literature and a divergence in publication foci. For example, among 1020 papers in the 24 journals that most frequently published relevant articles, 67% focused on plant-only restoration, 9% focused on animal-only restoration, and just 24% were “mixed” – looking at both plants and animals (based on Web of Science 1990–2014; Figure 1).

The number of plant-only papers did not correlate with the number of animal-only papers on a journal-by-journal basis (Pearson $r^2 = 0.02$, $P > 0.05$, $n = 24$), suggesting that the scientific “cultures” of plant- and animal-focused restoration researchers are largely independent of one another. There was a strong correlation between numbers of plant-only and mixed papers ($r^2 = 0.50$, $P < 0.001$, $n = 24$) but little correlation between

In a nutshell:

- Current restoration efforts often focus on either plants or animals, with limited integration between the two approaches
- Stronger collaboration between plant and animal ecologists is vital for restoration of functional ecosystems and effective recovery of declining biodiversity
- Greater emphasis is needed on restoration of key ecosystem functions, plant–animal interactions, and planning at multiple spatial and temporal scales
- Bridging the gap between plant- and animal-based approaches will enhance the success of restoration programs, with long-term benefits for biodiversity

¹The University of Queensland, Brisbane, Australia (*c.mcalpine@uq.edu.au); ²Griffith University, Nathan, Australia; ³University of Canberra, Canberra, Australia; ⁴Fenner School of Environment and Society, Australian National University, Canberra, Australia; continued on last page

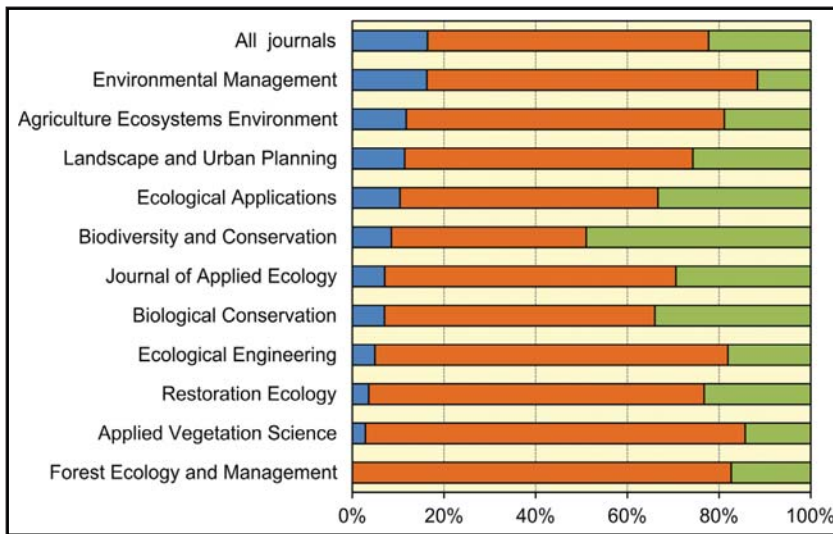


Figure 1. Graphical summary of the main focus of papers in journals publishing papers on restoration ecology and ecosystem restoration. Blue bars are animal-only papers, orange bars are plant-only papers, and green bars are joint plant–animal papers. Journals here represent a high-quality selection from the 28 journals assessed and were limited to those that contained at least 1% of the total papers in at least one category (ie plant-focused or animal-focused).

animal-only and mixed papers ($r^2 = 0.10$, $P > 0.05$, $n = 24$). This lack of plant–animal integration impedes the development of the science needed to underpin the restoration of fully functional ecosystems. Conversely, studies that do explicitly consider both plants and animals, as well as their mutual importance in restoration, can accelerate forest recovery (Panel 1; Figure 2; Holl *et al.* 2012)

Here, we review plant-based and animal-based approaches to restoration, identify the limitations of failing to effectively integrate both perspectives, and suggest ways to improve outcomes for biodiversity recovery. Our focus is on ecological issues (populations, communities, ecosystems) and not the genetic level of biodiversity. The geographic focus is on agricultural landscapes, many of which are economically marginal and ecologically highly modified or degraded, and that represent the largest potential area for restoration globally. Our goal is to initiate discussion as the first step in achieving a more unified – and therefore improved – approach to ecosystem restoration.

■ Review: plant- and animal-based restoration perspectives

We examine five themes relating to plant- and animal-based perspectives on restoration: (1) restoration goal, (2) restoration strategy, (3) temporal scale, (4) spatial scale, and (5) plant–animal interactions. We identify the general characteristics of plant and animal perspectives, respectively, and where they differ (Figure 3).

Restoration goal

Having a clear goal is essential for achieving and evaluating restoration outcomes. For plant-based restoration, an implicit goal is often to restore community composition and key structural elements, such as overstorey tree species (Figure 3). A frequent goal is to return the ecosystem to a historical state or ecological trajectory similar to that which existed before the ecosystem was severely modified by human land use (Suding *et al.* 2003). The goal may be set relative to a benchmark, such as the vegetation community of a neighboring remnant, or may be to compile information on the prior state of the ecosystem, if available (Gibbons *et al.* 2010). The degree of vegetation modification in a given area may make such goals unattainable, especially if there are irreversible abiotic changes to nutrient levels and soil conditions, or if invasive exotic species have become established (Hobbs *et al.* 2006). Plant-restoration goals increasingly are described in terms of measurable ecological objectives, such as percentage of native plant species, structural and compositional diversity, and plant functional diversity (Thorpe and Stanley 2011).

For animals, restoration goals generally emphasize individual species and their habitat needs rather than community structure and composition (Albrecht *et al.* 2010; Manning *et al.* 2013). For example, successful restoration of the Mauritius kestrel (*Falco punctatus*) started with the objective of augmenting its last known population, which was composed of only four individuals in 1974. The work involved captive breeding and provision of habitat resources (ie nest boxes), and success was measured in terms of population growth (Jones *et al.* 1995). The goals of animal-based restoration are also often based on landscape patterns, such as enhancing functional connectivity in a landscape to facilitate an organism's movements (Thomson *et al.* 2009) or optimizing the spatial configuration of restored sites to maximize the number of species occurrences within the landscape (Westphal *et al.* 2007).

Differences in restoration goals can stem from a variety of causes. Policy mechanisms can favor one type of goal over another; for instance, the US Endangered Species Act of 1973 (US Code: Title 16, Chapter 35, Sections 1531–1544) promotes population-level objectives and favors animals over plants, whereas the Brazilian Atlantic Forest Code mandates minimum numbers of tree species to be planted, with no requirements for animal reintroduction or population monitoring (Aronson *et al.* 2011).

Panel 1. Applied nucleation: testing a landscape restoration strategy in southern Costa Rica

A landscape restoration experiment in the moist pre-montane forest zone in southern Costa Rica has shed light on how plant–animal interactions can be manipulated to accelerate tropical forest recovery (Zahawi *et al.* 2013). This experiment compares conventional tree plantations with applied nucleation, a strategy in which “tree islands” are planted to expand and eventually to coalesce. Applied nucleation assumes that succession proceeds patchily (Figure 2). As compared with plantations, tree islands have the potential to accelerate the development of more complex forests and create more heterogeneous habitat conditions at a lower cost.

Local restoration strategies can greatly influence plant–animal interactions and the pace of regeneration. Tree islands received similar abundances of animal-dispersed tree seeds from plantations, and islands and plantations had twice as many animal-dispersed seedlings as naturally regenerating control areas in the first few years. These patterns primarily reflect the habitat preferences of seed-dispersing birds. There seems to be a minimum island size (~100 m²) to increase animal-mediated seed deposition and recruitment during the initial years of recovery. The species identity of the planted trees was important: fruit-eating birds were more likely to visit *Inga edulis* (guaba) than other tree species. *I. edulis* has a complex branching architecture and extra-floral nectaries, which attract insects and their omnivorous, seed-dispersing avian predators. Applied nucleation appears to be a cost-effective strategy, the success of which depends on facilitating multi-trophic plant–animal interactions.

Restoration outcomes in the experiment depended on tree cover at the landscape scale (tens of hectares). Bird communities increasingly resembled communities in mature forests when plantings were located in landscapes with high surrounding tree cover, but this did not occur in tree islands or in natural regeneration. Landscape tree cover was important within 170–750 m of plantings. Although landscape-scale effects have yet to be observed for seed or seedling communities, these patterns are expected to emerge over time as later-successional, large-seeded trees colonize. If so, this would suggest that animals are not only key benefactors and beneficiaries of tropical forest regeneration, but also that their landscape and habitat preferences may help determine future patterns of plant recolonization.

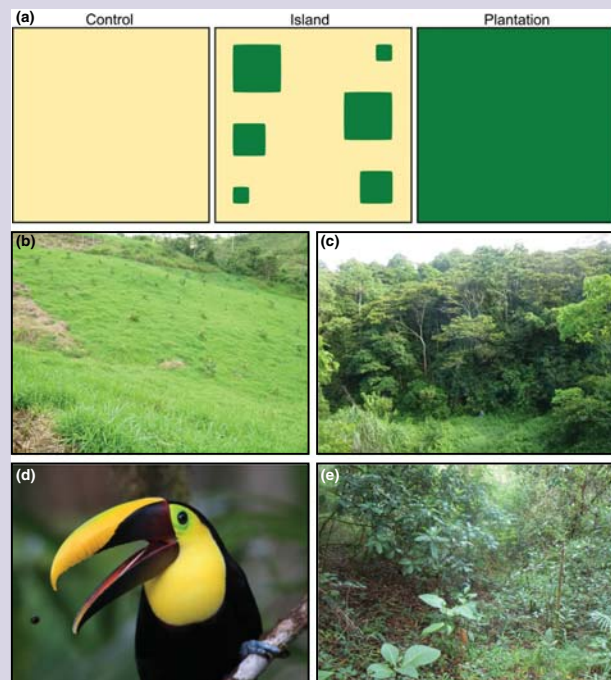


Figure 2. A field experiment investigating the effects of restoration strategies on plant–animal interactions and forest regeneration. (a) Restoration treatments applied to 50-m × 50-m areas of former agricultural land in southern Costa Rica. Green areas are planted with seedlings. (b) Tree plantation (hilltop) and naturally regenerating control after planting in 2004. (c) The same hilltop planting in 2013. (d, e) Bird visitation and seedling recruitment are monitored annually to evaluate restoration outcomes. (d) Black-mandibled toucan (*Ramphastos ambiguus*) regurgitating a palm seed. (e) Seedling recruitment along the edge of a tree island (left).

The divergent goals for plant- and animal-based restoration also arise as a result of different disciplinary histories and “silos” of expertise among zoological and botanical conservationists.

Restoration strategy

For plants, restoration strategies generally focus on actions at the site scale. This involves deciding which species to plant or favor, manipulating resource availability to enhance recovery of vegetation structure and composition, and controlling undesirable species (Figure 3; Blumenthal *et al.* 2003). Attention is concentrated largely on site-scale processes, such as nutrient

and water availability, and is greatly informed by community assembly theory (Temperton *et al.* 2004). A frequent aim is to restore the physical structure and species composition of the prior vegetation community, which may be achieved by initially planting/sowing propagules of many species, by establishing plants in a planned sequence, and by planting diverse overstory and midstory species, all accompanied by weed control. Promoting dominant overstory species provides cover for understory species and may aid in the control of undesirable species. Over the short term, trees and shrubs are relatively less challenging to restore and maintain as compared with species-rich understory/ground-layer herbaceous vegetation and native grasslands (Munro

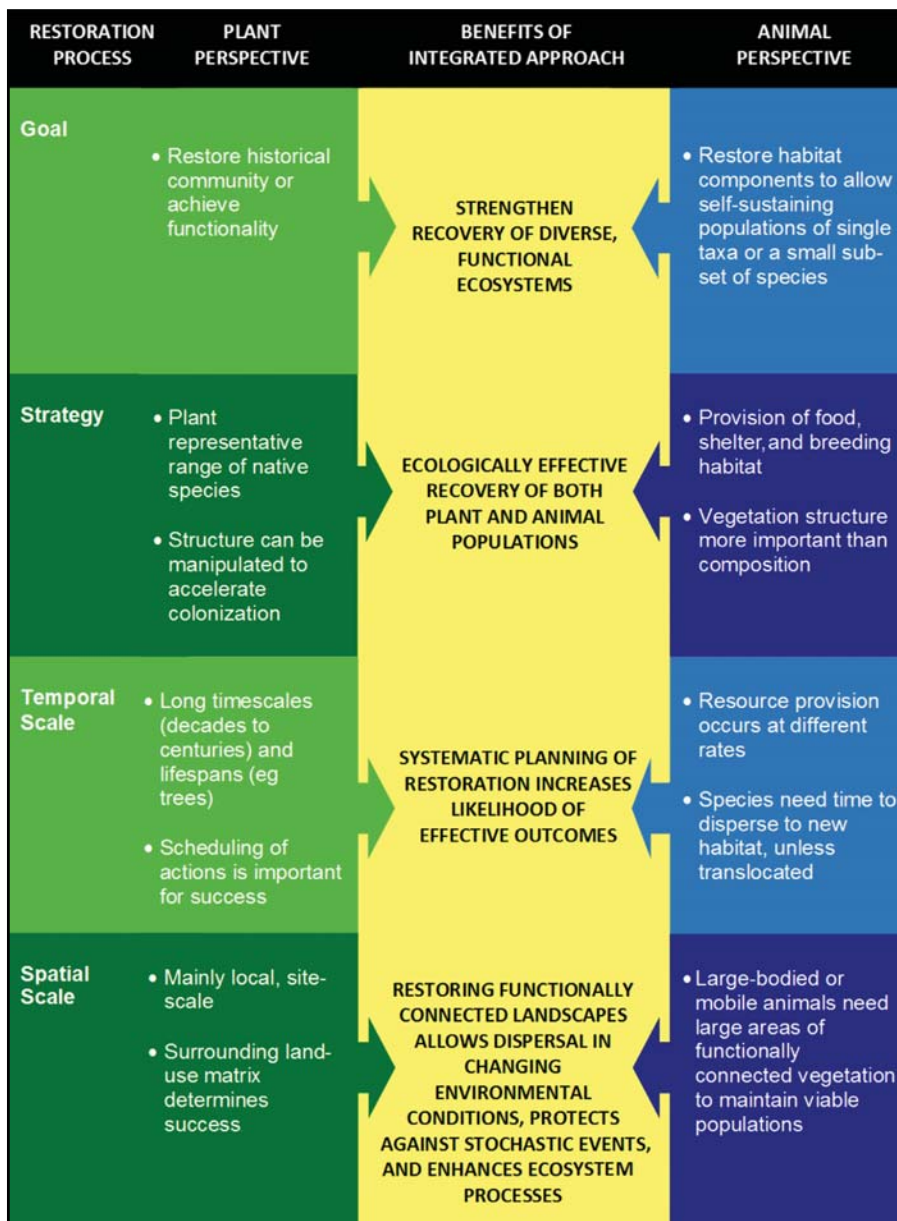


Figure 3. Summary of commonalities and differences among four core restoration themes that could result in disparities in restoration outcomes between plant- and animal-focused perspectives.

et al. 2009). The plant species used in restoration are typically native to the area, especially where the goal is benchmarked against the pre-degradation vegetation composition. Many approaches are based on a “field of dreams” strategy, which emphasizes the re-creation of structural attributes with little attention paid to biotic responses and assumes that degraded areas will progress toward the intended state (Hilderbrand *et al.* 2005). However, colonization of all sites does not necessarily occur as expected (eg Munro *et al.* 2009).

For animals, restoration strategies commonly address the need to enhance breeding populations of target species (Selwood *et al.* 2009), typically through the provi-

sion of habitat resources and the manipulation of landscape patterns to enhance population viability. The re-establishment of critical habitat resources (eg food, feeding substrates, shelter, and breeding sites) across the landscape, and the maintenance of longer-term landscape-scale processes (eg dispersal, migration) that influence population viability, are key elements of these strategies (Sudduth *et al.* 2011). Recognition that resource requirements may change during species’ life cycles is essential (Vesk *et al.* 2008). In the early stages of restoration, it may be desirable to manipulate floristic composition to minimize resource shortages and periods of resource scarcity for animal species (eg Peters *et al.* 2013). Increasing compositional and structural complexity of the restored vegetation generally leads to greater faunal species richness (MacGregor-Fors *et al.* 2010). The restoration of tree species and other plants with complementary seasonal flowering and fruiting patterns attracts a broader diversity of fauna, supporting a complex array of plant–animal interactions (Garcia *et al.* 2014).

Conflicts can occur between plant-based and animal-based restoration strategies. For instance, increased browsing following the recovery of native mammalian herbivore species

may severely damage restored vegetation, whereas the rapid removal of non-native vegetation, which is often prominent in plant-focused restoration efforts, may negatively affect animal species. As an example, the removal of invasive cordgrass (*Spartina* spp) may have caused the rapid decline of the endangered California clapper rail (*Rallus longirostris obsoletus*) (Lampert *et al.* 2014).

Temporal scale

Time is an important factor from both plant-based and animal-based restoration perspectives (Vesk *et al.* 2008). The growth and development of restored

vegetation are important for ongoing community and population dynamics, with different resources becoming available to plants and animals as vegetation matures. However, over time, the colonization of the restored site by both plant and animal species may be limited by the dispersal ability of species and by landscape connectivity (Grimbacher and Catterall 2007).

For plants, changes in environmental conditions (eg above-average rainfall) and disturbance regimes in the early stages of restoration may improve opportunities for regeneration of desired species, but plantings may degrade if the initial cohort of plants dies without replacement (Rodrigues *et al.* 2009). Longer-term outcomes for restored vegetation depend not only on the growth of planted individuals, but also on the *in situ* germination of seedlings from plants re-established at the site as well as colonization from surrounding areas. Identifying the trajectories of species' recovery and barriers to plant succession, such as altered nutrient dynamics and low propagule availability, govern the design and scheduling of restoration actions (Vesk and Dorrough 2006). Rates of establishment and growth of plants depend on the intensity, extent, and duration of current and past land uses, which affect propagule availability and recovery rates (Holl *et al.* 2012). Management interventions can overcome time lags in plant colonization; for example, direct seeding of later-successional species when conditions are appropriate can hasten vegetation growth and ecosystem development (Bonilla-Moheno and Holl 2010). The longevity of many tree species necessitates a focus on longer-term population dynamics.

For animals, the availability of resources over time in restored habitats varies among species. Some species depend on resources or habitat structures that are most available during early- or mid-stages of succession (Catterall *et al.* 2012), whereas late-successional resources, such as tree hollows, may take many decades to develop (Vesk *et al.* 2008). The method of restoration may influence such temporal patterns: for example, restoration plantings at high densities can greatly reduce tree growth rates and delay development of tree hollows by decades (Dorrough and Moxham 2005). Colonization of restored areas by animals is usually unassisted, and the timing depends on species' mobility and the functional connectivity of the landscape. Suitable resources may be available, but limited dispersal ability of less-mobile species and poor landscape connectivity may delay colonization (Grimbacher and Catterall 2007). Whereas plant-based restoration often takes a long-term perspective on community development, especially for forests, animal-focused restoration frequently deals with shorter time frames.

Spatial scale

Spatial scale influences both the spatial extent and configuration of restoration actions, as well as spatial

processes, such as the flows of organisms, material, and energy through the landscape (Metzger and Brancalion 2013). Dispersal of propagules/individuals is crucial for both plants and animals. Although plant-based restoration generally occurs at the site scale (<5 ha), the surrounding landscape context can affect propagule dispersal. The distance over which seeds disperse depends on a plant's life-history traits in addition to vectors and soil conditions, which can differ greatly over time and space. Restoration outcomes for plants are also governed by the land-use and ecological condition(s) of adjacent areas (Dorrough and Moxham 2005). Restoration activities adjacent to undegraded and degraded areas will promote propagule donations by native species and limit invasion of exotic species, respectively (Vesk and Mac Nally 2006; Lindenmayer *et al.* 2010). Restoration practitioners must also consider landscape-scale disturbances, such as fire, which can influence plant recruitment and establishment.

The spatial scale and context of restoration are critical for many animal species, especially large or mobile vertebrates that need large expanses of functionally connected vegetation to maintain viable populations. Landscape context is generally considered at scales much larger than the restored area(s) (eg at 1000s or 10 000s of hectares) and highlights the importance of restoring the whole landscape mosaic for animal populations (eg Westphal *et al.* 2007; Thomson *et al.* 2009; Sudduth *et al.* 2011). Proximity of restoration to large patches of intact vegetation of suitable habitat quality can enhance outcomes for animals (Grimbacher and Catterall 2007; Lindenmayer *et al.* 2010), and restoration of vegetation cover in the landscape can positively influence animal species occurrence and richness at the site scale (Cunningham *et al.* 2014). Complementary restoration actions at the site and landscape scales will therefore improve the chances of recovery for many animal populations.

Plant–animal interactions

Explicit consideration of plant–animal interactions can enhance the success of restoration and is a key element in unifying plant- and animal-based perspectives (McConkey *et al.* 2012). Plants provide resources needed by animals, and interactions between plants and animals influence both plant and animal communities. Animals pollinate and disperse seeds but also prey on seeds and seedlings. Forest regeneration on former agricultural lands depends on plant–animal interactions (Panel 1; Holl *et al.* 2012): for example, fruit-eating birds and bats can initiate succession by dispersing the seeds of pioneer plant species (Neilan *et al.* 2006).

Larger vertebrates often affect seed dispersal and the predation of seeds and seedlings in landscapes (Panel 2).

Panel 2. Plant–animal interactions: crucial restoration roles in agricultural landscapes

Successful long-term restoration of vegetation depends on re-establishing seedling recruitment and survival. Interactions between plants and animals influence these processes through mutualisms (pollination and seed dispersal) and “top-down” predation (Table 1). These interactions typically involve functionally similar groups of species rather than specific species pairs. Seeds of most fleshy-fruited plant species are generally consumed and dispersed by many fruit-eating species, whereas plants with large seeds interact in this way with a few large-bodied frugivores (McConkey *et al.* 2012). The removal of large carnivores from native ecosystems has been associated worldwide with the loss of woody vegetation, mediated by increases in mammalian herbivores (Ripple *et al.* 2014), but this process can be reversed by the return of large carnivores. Such ecosystem-level effects of food-chain

interactions are widespread, although knowledge of their role in agricultural landscapes remains scarce. There are two important implications for post-agricultural restoration. First, without functions provided by large vertebrates as herbivores, predators, or seed dispersers, the plant-based approach of reinstating a mix of native flora may not achieve the restoration goals. Second, animal-based restoration actions that return functionally important fauna may be effective for reinstating native vegetation. This idea has been explored in several recent experimental restoration projects, including introducing giant tortoise species that are functionally similar to recently extinct species on oceanic islands, either as frugivores to disperse the seeds of indigenous plants or as herbivores to suppress competitively aggressive, non-native ground plants (Griffiths *et al.* 2013).

Table 1. Pathways by which plant–animal interactions can mediate the recruitment and growth of seedlings and the extent of current research into these pathways

Interaction type	Main animal groups	Amount of research	Large vertebrates involved?	Example reference
Pollination	Nectar- and pollen-feeding insects and vertebrates	Little	Rare	–
Seed dispersal	Frugivorous birds and mammals	Considerable	Common	McConkey <i>et al.</i> (2012)
Seed predation	Seed-eating mammals (rodents) and insects (beetles)	Moderate	Uncommon	Howe and Brown (2001)
Seedling defoliation	Herbivorous mammals and insects	Moderate	Uncommon	Côté <i>et al.</i> (2004)
Trophic cascades	Carnivorous mammals and their prey	Moderate	Predominant	Ripple <i>et al.</i> (2014)

They typically operate over broader spatial scales than invertebrates, such as seed-dispersing ants, which move over shorter distances and provide within-site rather than among-site functions. In many settings, however, larger vertebrates may be absent due to land conversion and hunting mortality (McConkey *et al.* 2012). Invertebrates in soil and leaf litter play important roles in nutrient dynamics and in soil structure (Hättenschwiler *et al.* 2005; Majer *et al.* 2007), which may assist plant colonization and establishment. Managing pollination is mutually advantageous to pollinators and plants, and so also underpins the long-term sustainability of restoration (Dixon 2009).

Interactions between plants and animals may have complex consequences that create dilemmas for restoration managers (Buckley 2008). For example, dispersal by frugivores can spread non-native plants – which may be regarded either as detrimental invaders or, conversely, as useful pioneers – to restoration sites (Neilan *et al.* 2006). Conflict can arise when restored animal populations detrimentally affect newly established plantings, such as leaf-cutter ants (*Atta* spp and *Acromyrmex* spp) in the neotropics (Meyer *et al.* 2011) and mammalian herbivores in temperate forests (Parsons *et al.* 2006). Such animal species can limit seedling establishment and alter restoration trajec-

ries. Restoring populations of large, functionally important vertebrates may also induce wildlife–human conflict if, for example, large carnivores are involved, or if non-native fauna are the only extant functional substitutes for extinct vertebrates (McConkey *et al.* 2012; Ripple *et al.* 2014).

■ Synthesis – potential conflicts and failures

Many of the underlying ecological foundations of the plant-based and animal-based approaches to restoration overlap. Achieving effective ecological outcomes for both plants and animals depends on the restoration of self-sustaining ecosystems, although the importance of various ecosystem components may differ between (and among) plant and animal species. Temporal aspects of restoration are important for both plants and animals, and a long-term (decades or even centuries) perspective is required for achieving effective outcomes. The spatial scale at which restoration actions are planned and implemented often differs between plants and animals, with a notable issue being the extensive areal requirements for the recovery of viable populations of mobile, large-bodied animal species. There is a need for greater consideration of spatial ecological processes

in restoration, including population dynamics, plant–animal interactions, and the roles of species in wider ecosystem function (Sekercioglu *et al.* 2004; Chadès *et al.* 2012).

Many of the apparent differences between plant- and animal-based restoration may be artifacts of the scientific background of the individuals involved, as well as of the lack of disciplinary cross-fertilization and collaboration (Figure 1). In agricultural landscapes, investing resources to restore highly modified and degraded ecosystems may not result in ecologically and economically effective outcomes, due in part to inadequate integration between plant- and animal-based approaches; fostering such integration has the potential to improve biodiversity in these landscapes. If this integration is successful, the goal becomes the long-term, cost-effective restoration of functional ecosystems and landscapes for all components of biodiversity, rather than taxon-specific restoration.

■ The way forward

We propose four strategies to achieve a more unified approach to the recovery of biodiversity in fragmented agricultural landscapes.

Strengthen collaboration between plant and animal ecologists

Close dialogue between plant and animal ecologists in the planning stage of restoration is vital in fostering interdisciplinary collaboration and harnessing complementary skills for making decisions about the most efficient design of projects to achieve restoration goals. It is also necessary to explicitly recognize the interdependence of plants and animals at multiple temporal and spatial scales (Panel 1). Integrated restoration approaches are likely to have the highest potential for achieving effective, long-term outcomes for biodiversity. The “gold standard” of ecological restoration should be the restoration of functional, self-sustaining ecosystems.

Give priority to restoration projects that will benefit both plants and animals

Restoration approaches that focus on a single taxonomic group may have few benefits, or may even be detrimental, to other components of the ecosystem (Panel 2). For example, planting a few fast-growing pioneer tree species that shade out pasture grasses in tropical forest restoration will have poorer biodiversity outcomes than a strategy designed to provide resources for a range of animals. An integrated plant–animal-based approach is more challenging in terms of information

requirements, policy mechanisms, design, and scheduling, but provides greater overall biodiversity benefits through the restoration of a more compositionally diverse, structurally complex ecosystem.

Pay greater attention to restoring plant–animal interactions

The explicit consideration of key plant–animal interactions, such as pollination, seed dispersal, and seed predation (Panel 1; Sekercioglu *et al.* 2004), will enhance restoration success and provide a bridge between plant- and animal-based approaches. Important questions to consider include: which animals might be attracted to particular plant species, which other animals will be attracted to those animals, and what effects might both groups of animals have on plant community development? Knowledge of plant–disperser relationships is critical to improving plant selection in restoration projects (Panel 2).

Adopt a systematic restoration planning approach

Systematic planning is critical in order to combine ecosystem restoration with the long-term social and economic needs of human communities. This requires the integration of site-scale restoration actions within a landscape ecological framework to achieve synergies among restored areas (see WebPanel 1). Using a decision-making framework that defines the restoration goals, includes a realistic assessment of the ecological and socioeconomic opportunities for restoration, and identifies the constraints on achieving landscape-scale restoration (Menz *et al.* 2013) will help to resolve potentially competing demands for resources. Increasing levels of detail can be added to account for the costs and benefits of different types of restoration activities, the likelihood of restoration success, the possible effects of stochastic events, and spatial connectivity (McBride *et al.* 2010; Wilson *et al.* 2011).

■ Conclusions

Ecological restoration has the potential to achieve substantive gains for the recovery of biodiversity; the challenges are great but the conservation outcomes are potentially substantial. A unified approach to ecosystem restoration is necessary to integrate the currently divergent plant- and animal-focused approaches. This requires pushing the frontiers of restoration ecology by challenging restoration ecologists and practitioners to develop complementary and integrated approaches to restoring degraded landscapes, rather than working from narrow, taxonomic perspectives. The strategies proposed here will help

lay the foundations for a more unified research agenda for ecosystem restoration for the next decade.

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■ Supporting Information

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⁵Center for Conservation and Sustainable Development, Missouri Botanical Garden, St Louis, MO;

⁶Department of Environmental Studies, University of California, Santa Cruz, Santa Cruz, CA; ⁷La Trobe University, Bundoora, Australia; ⁸The University of Western Australia, Perth, Australia; ⁹Deakin University, Burwood, Australia; ¹⁰University of Helsinki, Helsinki, Finland; ¹¹Charles Sturt University, Albury, Australia; ¹²The University of Melbourne, Carlton, Australia; ¹³CSIRO Land & Water, EcoScience Precinct, Brisbane, Australia; ¹⁴Arthur Rylah Institute for Environmental Research, Heidelberg, Australia