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Influencing Landscape-Scale Revegetation Trajectories through Restoration Interventions

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Abstract

Purpose of Review This review focuses on potential approaches to restoring vegetation across former agricultural land, mainly considering the relatively well-studied case of once-forested landscapes. It presents an ecological framework within which the potential consequences of different practical interventions are described and compared, and then identifies implications for restoration decision-making.

Recent Findings There is a still-growing range of restoration interventions other than high-cost intensive tree-planting. These aim to accelerate vegetation recovery at different stages of forest redevelopment, by removing factors that would otherwise have an inhibitory influence. Potential interventions include adding seed, installing structures to attract seed dispersers, selectively protecting or removing different vegetation elements (trees or ground plants) in the regenerating communities, and managing fire, livestock grazing or wildlife.

Summary Given the potential variety of approaches, at a landscape scale, the best solution is most likely a spatial mosaic that tailors specific restoration interventions to differing contexts and outcomes. However, the current evidence base is insufficient to adequately guide decisions about how to match method to site, landscape and cost. Research has typically been small-scale and often disconnected from restoration practice. Larger-scale investment in collaborative and innovative restoration trials and experiments is needed to enable better decision-making.

Keywords Regeneration · Succession · Forest · Ecosystem · Oldfield

Introduction

The advent of the Anthropocene epoch has seen the emergence of rapid and unprecedented industrial-scale destruction of native vegetation, and its conversion for human use. There has also been a growing realization of the widespread environmental impacts of large-scale land clearing and of the need to rapidly restore quasi-natural ecological communities at landscape and regional scales [1–7]. Large-scale return of forest to formerly cleared and cultivated land has several precedents in human history. For example, a recent review estimated that 56 million hectares of formerly cultivated land in the Americas regenerated to native forest in the 1500s, following decimation of indigenous peoples after European invasion [8]. Similarly, detailed historical reconstruction of changes after European settlement [9] showed that agricultural use in Massachusetts' landscape peaked in the mid-1800s (with about 50% of land converted), but that much of this land had become reforested by the late twentieth century. Meanwhile, agriculture declined to about 7% of the land area due to technological and socioeconomic changes [8, 9]. In such cases, a diverse biotic community with broad similarity to communities present before clearing has typically re-emerged without active restoration.

During the 1900s, scientific observations of how forest ecosystems had progressively redeveloped on areas of abandoned farmland ("oldfields") in North America and Europe underpinned the emergence of the foundational concept of ecological succession [10]. Ecological succession is most simply defined as "processes of vegetation change" [10]. Much

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early literature about the rates and patterns of vegetation change over time in oldfields was focused on the extent to which these successional processes were predictable and deterministic in the absence of much human intervention, albeit with largely unresolved outcomes [10, 11]. More recently, restoration ecologists have turned their attention to how the rate of vegetation recovery can be accelerated by human interventions (e.g. 1, 12–16). Many earlier concepts, even though somewhat unresolved, remain fundamental to ecological restoration [12, 13, 17, 18]. Additionally, contemporary thinking in successional processes and restoration ecology now also recognises the presence of high intrinsic variability, uncertainty and risk [17–19]. Moreover, the past 5 years have seen an upsurge in literature commentaries and reviews grappling with the theoretical and conceptual issues associated with ecological restoration, especially how these can be applied across large spatial scales [1–7, 14–16, 18–24]. The field is no doubt advancing in general terms, but there remains a persistent disconnect between some poorly resolved scientific concepts (such as "resilience", and "degradation") and the kinds of specific interventions that are typically involved in practical restoration [7, 11, 12, 25].

This paper synthesises current knowledge about the ecological processes and restoration practices involved in interventions to accelerate the recovery of forest vegetation on former agricultural land. Forest restoration in this context has been relatively well-studied, yielding approaches from which can be drawn analogues relevant to other ecosystems (e.g. 26, 27). First, I establish a summary framework within which the potential ecological consequences of different practical interventions can be compared, with reference to the speed and direction of vegetation redevelopment. Second, I describe the ecological interactions whereby each of these interventions operates. Finally, I outline some important emerging corollary issues that are faced by decision-makers who seek to achieve landscape-scale restoration.

An Ecological Framework for Post-Agricultural Interventions to Restore Forest

In once-forested landscapes, the plants that initially occupy disused agricultural land are typically pasture grasses, ferns, vines or herbaceous species that form a dense low-growing vegetation (henceforth termed "ruderal" vegetation), with few upright woody plants, and with a greatly depleted supply of soil-stored forest seeds [17, 28]. The subsequent pattern of vegetation development (i.e., the rate and trajectory of succession) then depends on the dispersal, survival, and growth of progressive generations of more diverse species and functional types of plants, and on the animals and microbes with which they interact (e.g. 19). These processes can all vary greatly, depending on many ecological factors, and can also be strongly influenced by human interventions (e.g. 17, 18), as shown in Fig. 1.

In optimal situations (Fig. 1, left-hand side), scattered small trees will rapidly grow from dispersed seeds, or regrow from scattered rootstock, initiating "Early Regeneration" of woody vegetation [17, 19]. Further recruitment and growth of trees results in canopy formation, along with the development of a somewhat forest-like structure, but with greatly different floristic composition ("Progressing Regeneration", Fig. 1). This stage then transitions into several decades of ongoing further recruitment of a wider range of plants and animals, eventually producing a relatively high ecological similarity to never-cleared mature forest ("Advanced Regrowth", Fig. 1) [17], albeit with some differences that slowly diminish over many subsequent decades.

However, this successional process can be greatly slowed, or even stalled [18, 19, 27]. Sometimes, especially where large areas were intensively used for decades, the transition from Early Regeneration to Progressing Regeneration is greatly inhibited by a series of ecological barriers which suppress early recruitment and growth of tree seedlings, creating a state of persistent ruderal vegetation which is often dominated by nonnative pasture grasses (Fig. 1, right-hand side) [29, 30]. These barriers include a lack of seeds of forest trees, physical stressors (such as exposure to sun and wind, fire and a scarcity or imbalance of soil nutrients), competition from ruderal vegetation, and predators or pathogens of seeds and seedlings [29]. In later successional stages (Early Regeneration, Progressing Regeneration), physical stressors are less extreme, but vegetation development may still be retarded by other factors, sometimes including competition from dominant tree species that inhibit the growth of many others [e.g. 31]. In highly modified landscapes, these early dominants can be nonnative trees, which are often assumed to be inhibitory, although this assumption has rarely been rigorously tested [28].

Most of the processes that inhibit the development of Early Regeneration can be bypassed by nursery-rearing trees from seed and then establishing them in plantations at a young sapling stage where they are better able to compete successfully with ruderal plants [30]. Tree planting is usually coupled with actions to suppress any redevelopment of ruderal vegetation. Methods for plantation establishment are derived from well-developed technologies used for timber and orchard production. If a high diversity of appropriate native species is planted at high density (henceforth "complex plantation"), the speed of transition from retired agricultural land to Advanced Regrowth can be greatly accelerated [32, 33]. However, complex plantations are limited to small areas because of their high cost, which can be most clearly justified in cases where ruderal vegetation is known or reliably predicted to be persisting over time [34–36]. At the other end of the cost

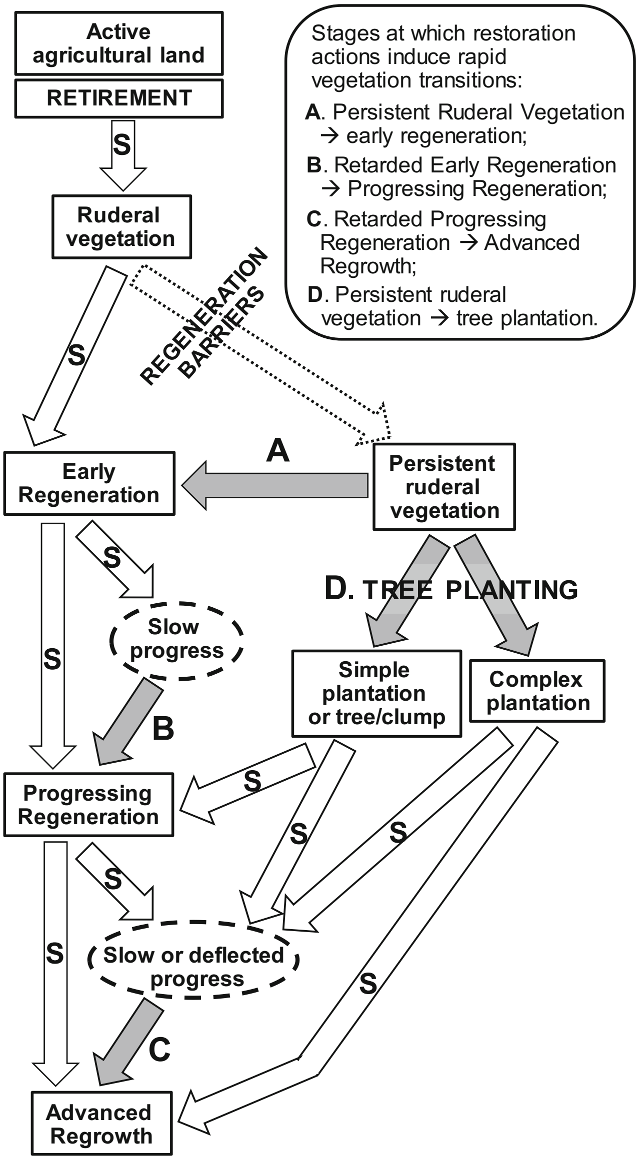

Fig. 1 Alternative pathways of forest redevelopment on former agricultural land, with and without restoration actions. Arrows show transitions over time, but do not represent rates of change. Unshaded arrows labelled S denote successional processes (patterns of vegetation development) in the absence of restoration actions; these vary greatly in speed. The unshaded arrow with dotted outline flags that significant barriers to early regeneration have formed. Shaded arrows labelled A, B, C, and D show stages at which restoration actions may catalyse or accelerate vegetation transitions if succession has been stalled or slowed by ecological barriers to regeneration. Restoration techniques and regeneration barriers are listed in Table 1. Ruderal vegetation is a dense low-growing cover (often of grasses or soft-stemmed plants). In Early Regeneration, trees are small and scattered. Progressing Regeneration has a well-established multi-aged tree layer and canopy (without large-diameter trees), but its species composition differs greatly from uncleared mature forest (MF). Advanced Regrowth is generally similar to MF in structure and species composition, but with under-representation of slow-returning species and life-forms (e.g., large trees, tree-hollows, large woody debris, poorly dispersed biota); it is expected to slowly develop towards MF. Progress at all stages can be reversed by severe disturbances such as flood, wildfire, drought or livestock incursions. Tree planting after removal of Early or Progressing Regeneration is not shown

spectrum lies unassisted successional regeneration over larger areas, although with more time needed to reach recovery goals [33, 37]. Indeed, some overviews of restoration have placed all approaches within such a binary framework of higher-cost "active" restoration (involving human intervention), compared with lower cost ("passive") successional processes that proceed without human assistance (e.g. 2, 21, 23).

However, a dichotomous "passive-active" classification of approaches to landscape-scale restoration is incompatible with the real-world variety of pathways by which vegetation actually returns to disused agricultural land. This "passive-active" classification could also become misleading, because it ignores the following issues. First, even "passive" restoration requires often-unrecognised human interventions, which have direct or indirect costs (e.g., of livestock removal, fence installation and maintenance [37, 38]). Second, all types of approaches rely to varying degrees on the occurrence of "passive" successional processes after the completion of restoration interventions, because these actions are often restricted to the first few years. Third, there is a wide range of possible "active" tree planting designs, varying greatly in intensity (site preparation, tree density, species mix and variety, post-planting interventions), which produce a wide range of potential costs per hectare. Finally, there is also a range of interventional approaches other than conventional plantation technologies. These other forms of intervention also vary in intensity, duration and cost (e.g. 32, 39). The next part of this review is largely focused on the potential ecological roles and practical uses of these often-neglected "middle-ground" interventions, some of which may provide lower cost opportunities for large-scale restoration of forest ecosystems.

Expanding the Menu of Interventions to Accelerate or Redirect Forest Regeneration

An emerging variety of restoration interventions involve actions to accelerate forest succession by targeting one or more of three transitional stages: (A) persistent ruderal vegetation to Early Regeneration, (B) Early Regeneration to Progressing Regeneration and (C) Progressing Regeneration to Advanced Regrowth, as shown in Fig. 1 and Table 1. Here, I identify nine different approaches which act in various ways to potentially remove one or more factors that may otherwise inhibit the rate of vegetation development, describe the ecological logic of why and in what context they could be used, consider their limitations and flag selected examples. Many of the projects which have investigated or applied these approaches have employed a tailored combination of methods, both in small-scale trials by researchers [e.g. 40–46] or large-scale applications by practitioners [e.g. 47, 48]. Different methods may depend on similar ecological processes, and the available evidence suggests that many techniques' effectiveness depends

Table 1 Approaches (techniques) to accelerate or redirect forest regeneration other than conventional tree planting; ecological barriers that are reduced to achieve this outcome; and the stages at which each technique takes effect

Technique	Stage of transition (Fig. 1)	Barrier that is directly removed or reduced						
		Seed source	Seed dispersal	Ruderal competition	Seed predation	Seedling predation	Physical stressors	Tree succession inhibition
Seeding	A	Y	Y	N/P	N/P	N	N/P	na
Seed-disperser attractants	A	N	P	N	N	N	N	na
Ruderal suppression	A	N	N	Y	N	N	N	na
Seedling/sapling protection	B	N	P	Y	N	N	P	na
Nurse tree plantation	A, B	Y, N	Y, P	Y, Y	N, N	Y, N	Y, P	na
Nucleation and tree islands	A[1], B	Y[1], N	Y[1], P	Y, P	N, N	Y, N	Y, P	na
Advanced tree suppression	C	N	N	na	N	N	na	Y
Livestock and fire management	A, B, C	N, N, N	N, N, N	P, na, na	N, N, N	P[2], P[2], P[2]	P[3], P[3], P[3]	na, na, N
Wildlife management	A, B, C	N, N, N	P, P, P	P, na, na	P, P, P	P, P, P	N, N, N	na, na, N

Each technique affects each barrier by either: Y always seeking to remove it; N not aiming to affect it; P potentially removing it, depending on circumstances. na denotes not applicable (only relevant to earlier or later successional stage). Transitional stages are (A) persistent ruderal vegetation to early regeneration, (B) retarded early regeneration to progressing regeneration, and (C) retarded progressing regeneration to advanced regrowth (see Fig. 1). Where a technique affects more than one transition, outcomes for each transition are separated by commas. For the seeding technique, slashes separate alternative outcomes that depend on specific extra component actions. Superscripts flag cases where as follows: [1] outcomes vary depending on details of technique and context; [2] for seedling predation, effects are Y from livestock management but N from fire management; and [3] for physical stressors, effects are Y from fire management but N from livestock management. Physical stressors include moisture or nutrient deficiencies and extreme events such as fire

on their use in specific combinations with others [39]. The use of such combinations is flagged where relevant in the following descriptions.

Seeding

The first potential barrier to regeneration is a lack of tree seeds, due to depletion of soil seed banks, absence of nearby seed sources (mature trees) and a lack of seed-dispersing agents. Often all three are limiting, and actions to add seeds overcome them all. Seeding is mainly relevant to accelerating the transition from ruderal vegetation to Early Regeneration, but also has potential applications for enriching plant diversity in later phases. A range of techniques that were developed initially for agriculture and plantation forestry has been adapted for rapid and efficient delivery of a diverse mix of forest tree seeds over large land areas. Seed delivery mechanisms include sowing by aerial vehicles (plane or drone) and by ground-based agricultural machinery [47–50]. Because successful seedling establishment also requires overcoming further barriers (including competition from ruderal vegetation, seed predators and pathogens, Table 1), mechanised seeding techniques are most successful when they include additional treatments. For example, various projects have also incorporated seed burying or accompanying chemical agents (or pre- and post-seeding treatments) that selectively suppress competitors and repel or kill predators and pathogens [49•]. Other constraints include plant traits such as patterns of seed dormancy and the ability of seedlings to establish in exposed conditions [48, 49].

Seed-Disperser Attractants

A second type of intervention is to accelerate transitions from ruderal vegetation to Early Regeneration by adding devices to attract seed-dispersing fauna, which defecate or regurgitate seeds that were consumed elsewhere. This is most relevant to rainforests, where many trees are fleshy fruited and dispersed by vertebrates (mainly birds, but also bats or other mammals), and to a landscape context in which patches of remnant forest are not too remote. This technique has mainly been used in small-scale ecological trials, often with bird perches of varying construction [41, 51–55]. These trials have been very informative in revealing barriers to regeneration, and in demonstrating significant roles of fauna-mediated seed dispersal. However, their promise as cost-effective large-scale restoration tools seems limited because post-dispersal recruitment barriers may result in negligible tree seedling establishment even when many seeds have been deposited [51, 53, 55]. Studies reporting greatest recruitment of seedling trees have combined disperser-attractant devices with other actions, including suppression of ruderal vegetation and exclusion of seed and seedling predators (terrestrial granivores and herbivores) [52, 54].

Ruderal Suppression

Successful interventions to accelerate transitions from ruderal vegetation to Early Regeneration almost always include action to suppress the persistent ruderal vegetation using a wide range of methods (e.g. 32, 39–44, 46–48, 51, 52, 56). Over large areas, ruderal vegetation has been effectively removed by scalping (mechanical removal of topsoil) or by killing growing plants with herbicide application. Because broad-spectrum herbicides (such as glyphosate) also kill desired tree seedlings [43], grass-selective herbicides may be preferred in some situations [41]. Over smaller areas, ruderal plants have been killed with solarisation (light-absorbing ground sheets that intercept photosynthetic radiation and apply heat) and pulling (weeding). Depending on the situation and size of treated area, ruderal regrowth can be common (from seed, or partially killed plant parts) and requires repeat treatments over time. Additionally, above-ground parts of ruderal plants may be removed by cutting (slashing, mowing), although this does not prevent rapid regrowth from rootstock. Other treatments have included mulching, soil disturbance (ploughing), and addition of sugar to decrease soil N levels through microbial activity. Many of these treatments do not spare desirable emerging tree seedlings if applied repeatedly. Ruderal suppression alone may suffice to accelerate vegetation recovery in some situations (e.g. 41). However, it does not remove barriers of limited seed availability and dispersal (Table 1, see also [39]) and, therefore, often needs to be coupled with other interventions.

Seedling/Sapling Protection

The transition from Early Regeneration to Progressing Regeneration (Fig. 1) can be accelerated by interventions to protect pre-existing tree seedlings (or saplings or shoots from remnant rootstock) from ruderal competition, thereby increasing seedling survival and growth. Foundational applications of the idea were trialed in the Philippines in the 1980s [32], and the method was first described in the scientific literature by Shono and others in 2007 [57] as "assisted natural regeneration" (ANR). In that example, ANR actions suppressed dense tall nonnative grasses around rainforest tree seedlings that were otherwise struggling to persist; these actions resulted in the rapid growth of tree seedlings. More generally, suppression of any type of ruderal vegetation in a functionally relevant radius around the stems of tree seedlings or saplings may potentially be achieved with a range of different methods (including pulling, cutting, herbicide or mulching) as described above. A constraint to this approach is a requirement for pre-established regeneration of enough scattered tree recruits; Shono [57] recommended a minimum pre-existing density of 700 seedlings more than 15 cm tall per hectare. "ANR" has been used by some authors to encompass a very broad range of restoration interventions [1••], including installation of bird perches and selective removal of taller woody elements (e.g. 32, 56). Therefore, for clarity, I have avoided applying this term to define any method described here.

Subsequent vegetation development in the vicinity of these protected trees follows a pattern which has been frequently described in situations where scattered trees grow in persistent ruderal vegetation, with or without active interventions [41, 51, 57–60]. That is, once each tree has grown to form a local canopy that is sufficiently tall and dense to overtop the grasses, the competitive balance tends to reverse because the grasses are shade-intolerant and because the increased shade and leaf litter promote more favourable ground conditions for survival and growth of further tree seedlings. The trees may also attract seed-dispersing fauna, initiating a positive feedback cycle of further recovery. Similar processes have been described following initial tree establishment in large-scale direct seeding [48], and experiments have confirmed that seedlings beneath isolated remnant pasture trees grow faster than those in the open [61, 62]. These processes form the basis of two other types of restoration approach: nurse tree plantations, and nucleation and tree islands, as discussed below. The principle involved can be extended to different situations in which environmental factors substantially constrain the growth of existing seedlings, if their release would establish conditions that stimulate further recruitment of desired plant species. For example, shelters (using small plastic tubes to ameliorate extreme physical conditions) have been experimentally used to accelerate restoration of shrub cover in an arid ecosystem, with some short-term success [26].

Nurse Tree Plantations

The concept of nurse tree plantations [32, 63] involves an intervention that operates across two transitional stages (Fig. 1, Table 1). First, barriers to the transition from ruderal vegetation to Early Regeneration are bypassed by planting a simple tree cover (often of a single fast-growing species). Second, if planted trees establish successfully, they may accelerate the subsequent transition to Progressing Regeneration, through the same ecological feedback cycles described above under "seedling protection" provided that there are seed sources within reasonable distance, together with seed-dispersal processes. The costs of establishing nurse tree plantations include rearing seedlings, planting them, and follow-up protection until they are established. However, these costs could potentially be partly offset at a later time, by marketing timber from the initially planted trees, after sufficient naturally recruited seedlings have become established [64]. Accordingly, simple plantations that were initially established for purposes other than ecological restoration (such as carbon storage or timber production) may also have potential for later being repurposed as nurse plantations.

Nevertheless, in all cases, the longer-term potential for seedling recruitment from ex-situ seeds is likely to be highly variable depending on complex interactions between nurse species selected, local conditions, landscape context and land-use history. Irrespective of the initial goal of the plantation, advanced tree suppression (see below) may become desirable decades later, if planted species also have inhibitory effects on later-stage regeneration.

Nucleation and Tree Islands

The related concepts of nucleation and tree islands also influence the same two transitional stages and harness the same positive ecological feedback cycles as for nurse tree plantations, but in a different manner. First, to bypass the initial barriers to Early Regeneration, interventions comprise either protecting isolated tree seedlings (or saplings or resprouts, as for "seedling protection" above (e.g. 57) or growing trees from seed and outplanting groups of several seedlings [46, 60, 65], with follow-up protection until they are established. Protection has typically involved at least ruderal suppression and livestock exclusion. An alternative variant of this approach is to use well-established larger trees as nuclei, but to mitigate against other regeneration barriers, such as ruderal competition [41] or livestock grazing [59] beneath them. Second, the transition from Early Regeneration to Progressing Regeneration is accelerated, because any resulting small trees or tree-clusters that grow amidst ruderal vegetation (forming a shady canopy a few metres above ground) constitute nuclei beneath and around which deposition of ex-situ tree seeds, and their subsequent germination, survival and growth are catalysed [41, 46, 59–61, 65, 66].

Robust evidence that the positive feedback for ongoing tree recruitment extends to areas beyond the canopy radius of the original trees has been provided by a relatively long-term (8 years to date) replicated restoration experiment using "tree islands" of 16, 64, and 144m2 [46, 66]. This trial has shown that separate tree nuclei tended to expand and ultimately coalesce over time, enabling tree-planting to be used more economically than is the case in conventional restoration plantations [66•]. As for nurse tree plantations, success must also depend on having seed sources within reasonable distance, suitable seed-dispersal processes, and overcoming other early-stage barriers through appropriate actions.

Advanced Tree Suppression

This approach accelerates the transition from Progressing Regeneration to Advanced Regeneration (Fig. 1, Table 1). It requires situations where there is a well-established regenerating forest (i.e., a canopy that shades the ground, reduced numbers of ruderal plants, and either a good supply of regenerating seedlings and saplings or a reinstated seed bank), but where the rate of development may be slower than desired because one or a few early-established tree species numerically dominate the canopy. Actions to remove or reduce the canopy trees (e.g., by cutting or poisoning them) cause a rapid increase in light penetration, which releases the growth of established seedlings and saplings and triggers further germination of soil-stored seed. The ecological changes triggered by this tree removal can ultimately lead to a more rapid increase in similarity to uncleared forest, for both ecosystem processes [56, 67] and composition of flora and fauna [68]. The newly released generation of seedlings and saplings can have a more forest-like diversity than the former low-diversity tree canopy because even this simple canopy provides the conditions for further seeds and seedlings to establish. However, achieving sufficient seedling recruitment is contingent on the previously discussed caveats regarding context-dependence (such as seed sources). Additionally, canopy removal may also stimulate establishment of ruderal plants or of undesired overstorey species [69], requiring additional actions to suppress them [68], and further barriers of seed and seedling predation may potentially limit outcomes.

Building on the opportunity provided by existing regenerating forest areas where an established tree canopy already exists, this approach bypasses the time that would otherwise be needed for early regeneration (Fig. 1). Some multi-use landscapes contain these regenerating forests as unexpected legacies of past land use decisions [28]. For example, understories of naturally recruited native seedlings and saplings may develop within industrial tree plantations that are not intensively managed [64, 70] and within tracts of "weedy" regrowth dominated by nonnative pioneer trees that establish readily in disused agricultural land [56, 68].

Management of Livestock and Fire

Regimes of livestock grazing and fire have the potential to strongly influence all stages of vegetation transition during forest redevelopment. Since both can often kill tree seedlings, their exclusion has frequently been a part of interventions to achieve Early Regeneration by increasing tree recruitment in retired agricultural land, typically accompanied by treatments to suppress ruderal vegetation whose growth would otherwise be released [e.g. 40, 41, 52]. In restoration case studies, exclusion of fire and grazing has often been mentioned within the description of the project, rather than having been manipulated as separate factors. Grazing can directly suppress survival and growth of tree seedlings [43, 71], but light grazing can also indirectly assist tree recruitment by suppressing ruderal vegetation [32, 72]. Indeed, grazing and fire interact in complex ways with each other, and with ruderal suppression, to either inhibit or promote tree regeneration

[42], in a manner that is likely to be very context-dependent [32].

Moreover, the importance of managing regimes of livestock grazing and fire has been most extensively considered in the context of how suboptimal regimes can either degrade or restore remnant native forest (e.g. 45). In drier forest landscapes, naturally occurring forest-grassland mosaics are created and maintained dynamically by complex ecological interactions between fire regimes and grazing by large native herbivores [73, 74]; the latter having broad functional similarity to livestock. Grazing and fire are clearly important potential regulators of forest succession, and the ways in which they could potentially be managed to facilitate large-scale forest regeneration on former agricultural land deserve greater attention.

Wildlife Management

Wild animals, especially mobile vertebrates, can also significantly influence all stages of vegetation transition during forest redevelopment because they are key agents of seed dispersal and seed or seedling predation [75, 76]. These processes endow a strong potential to either enhance or suppress the recruitment, survival and growth of trees. However, the potential for targeting animals, rather than plants, as a primary intervention in forest restoration has rarely been explored. There is increasing discussion of wildlife management as a restoration tool in remnant native vegetation (e.g. 77). However, much less attention has been directed towards understanding how animal wildlife influence vegetation recovery in areas from which indigenous forest cover has been cleared [5, 75–77]. Harnessing wildlife management to accelerate revegetation requires improved knowledge of which animal species (or functionally similar groups of species) inhibit regeneration through their absence or their presence (depending on the interaction). Accordingly, interventions would aim to either exclude/reduce [55] or include/increase [78, 79] local populations of the target animals. These interventions could include approaches that alter the quantity or quality of local or landscape-scale habitat, in order to indirectly modify the animal populations.

Maintaining or reducing local densities of larger-bodied wild animals often involves management at the population level and landscape scale [76], either because the animals use resources in different parts of the landscape at different times or because they need to move across landscapes for other reasons. Consequently, consideration of their roles in vegetation regeneration requires greater attention to landscape-scale decision-making. In comparison, plant-centred approaches have been much more focused on manipulating individuals at the site scale [76], as described for the other approaches to revegetation.

Key Emergent Issues in Decision-Making for Large-Scale Restoration

The array of different potential interventions canvassed above, and the currently expanding state of this field of research and practice, indicates a promising outlook for achieving large-scale return of forest ecosystems across parts of former agricultural landscapes. However, there are also significant challenges and potential difficulties, especially in relation to two over-arching issues: the emergence of novel ecosystems and the landscape-scale decision processes.

Novel Ecosystems

During the past century, human actions have caused large local- and landscape-scale shifts in both abiotic conditions and species combinations, giving rise to novel ecosystems in which coexisting native and nonnative species are entwined within increasingly complex webs of interaction [5, 80, 81]. These changes have stimulated reconsiderations of the goals and methods of vegetation restoration, together with some vigorous and unresolved debate about many aspects of conservation and restoration [81–83]. The diverse ecological interactions during oldfield succession provide opportunities for species to have functional roles that either accelerate or retard regeneration trajectories, irrespective of their origin [28, 84]. For example, among the different interventions described above, the facilitative ecological role of nurse trees and regeneration nuclei in Early Regeneration is independent of whether they are formed from native or nonnative species, while both native and nonnative species can sometimes dominate the earlier stages of Progressing Regeneration, and retard further development [28, 41, 64].

From the perspective of biological conservation, a frequent goal of restoration actions has been to suppress or eradicate nonnative species, aiming to increase compositional purity towards a native-only species mix. However, in practice, efforts to remove nonnative species as a primary management goal have often been unsuccessful [85], or they have failed to produce ecosystem recovery [86]. Furthermore, in cases where nonnative species are nurse trees or nuclei, their successful removal at early stages of vegetation development is likely to inhibit existing regeneration trajectories [e.g. 28, 68]. Embracing some types of novel ecosystem is arguably a useful ecological and socioeconomic option for re-establishing diverse and well-functioning ecosystems in the Anthropocene [15, 80, 87], especially in the transitional stages towards recovery of forested landscapes [83].

Context, Decision Processes and Landscape Mosaics

In a field of research where reviews of empirical studies have tended to yield long laundry-lists of potential factors that influence the outcomes of forest regeneration, one theme has commonly emerged: there is large variation in outcomes among different sites [19, 88], even when they are subjected to the same treatments in the same landscapes [e.g. 34, 66, 89]. Factors underlying this variation include both those at the immediate site scale (such as soil condition, pre-existing vegetation and unpredictable disturbances) and those associated with large scales of space (landscape context) and time (land use history) (e.g. 1, 20, 66, 90). However, the available evidence is insufficiently firm to support conclusions about the relative importance of these factors. Moreover, high outcome variability for any given method means that rules of thumb for deciding which technique to implement may be elusive, and rigorous empirical research may yield outcomes that contradict expectations [66•].

Since the outcomes of any given restoration action potentially vary among different environments, what succeeds in one place or time may fail in another. Additionally, what is costly or difficult in one place or time may be more feasible in another. Unassisted regeneration has recently been advocated as a preferred first-line approach since it could be most cost-effective over large areas [1, 19, 21], but this logic would only apply where the risk of ruderal vegetation persisting is low [34], and the timeframe for recovery is not urgent [37]. Conversely, in situations where either unassisted regeneration or lower-intensity forms of intervention are likely to achieve acceptable outcomes in reasonable timeframes, it would be a waste of money and resources to invest in intensive actions such as complex tree planting. Among the various available and emerging approaches discussed in this paper, no single method can be generally preferred. The best solution for a given landscape is likely to be a spatial mosaic of different approaches, tailoring restoration interventions to differing contexts and likely outcomes.

However, this raises the complex question of how to design and implement a useful combination of interventions. Researchers and decision-makers have begun to consider this question [5], both within landscapes [30, 37, 80] and at regional [90], national [91], and global [20] scales. Landscape-scale prioritisation methods similar to those developed for selecting conservation reserves have been applied to setting restoration priorities using GIS layers of current land conditions [90, 91]. However, an important limitation to these case studies is the absence of an explicit time dimension. Restoration is intrinsically a time-dependent process, and a site's vegetation characteristics at any given time depend on both the past (land use history, e.g. 66•) and the future (expected rates of change and their variability, e.g. 37•). The development of decision tools that can incorporate these variable temporal dynamics is a frontier of future landscape-scale restoration.

Many lines of information are needed if specific restoration interventions are to be effectively matched to sites and landscapes. This information includes the full menu of potential interventions, what outcomes might be expected over time from each type of intervention and with what feasibility and cost, in any given place. However, robust evidence relating to all these issues is generally unavailable. In particular, the evidence base for quantitative cost comparisons among different approaches is insufficient to support comparative analyses. Many of the interventions described previously have been limited to small-scale and short-term (often < 5 years) scientific trials that assessed the establishment of individual plants or early-stage woody vegetation, in case studies that focused on a single method. Their costs (and associated variability) have typically been either unreported or described in general terms only. Application of any technique over larger areas will bring economies of scale, which have been well developed for some methods only (e.g., seeding). Moreover, evaluating the ultimate success of different interventions depends on much longer-term assessments of physical structure, ecological functions and biological characteristics [12, 25]. Establishing comparative trials, coupled with monitoring of costs and outcomes, is an additional challenge for future research and practice.

Finally, in recent decades, both large-scale ecosystem destruction and large-scale revegetation have occurred in different regions globally, as consequences of decisions driven by socioeconomic and cultural factors (such as finances, competing land uses and new technologies) that are unrelated to environmental goals [92]. Conversely, the pressing contemporary environmental goal of restoration is likely to be achieved in some cases through actions that are social or economic rather than ecological in nature [93]. For example, these could include measures that encourage abandonment of agricultural activities in areas that have a high ecological potential for rapid regeneration with minimal intervention, and provision of alternative options for landholder livelihoods. Therefore, actions directed at economics and human behaviour are at least as fundamental to restoration as those involving ecological science and technology [1, 5, 15, 88].

Conclusions

Ecological restoration is needed over large aggregate land areas. Despite a range of strategic policy initiatives towards this end, maximising landscape-scale outcomes from targeted and cost-effective restoration interventions, while also conserving remaining natural ecosystems, is a current and future challenge [e.g. 3, 5, 20, 37, 94]. This review has described a growing array of options for less- or more-intensive interventions, but restoration science remains far from establishing the evidence base that is needed to make effective decisions about how, where, when and why to act.

If the goal of devising and implementing useful and economically feasible interventions for large landscape restoration is to be achieved, the disconnect between practice, evidence and policy will need to be bridged [4]. This means undertaking sound economic and ecological assessments of both the costs and outcomes of different methods, across multi-year sequences, in realistically scaled and well-replicated restoration projects. And that needs to be done multiple times, for a wide range of techniques, across many regions and ecosystems. To achieve this will require an order of magnitude increase in funding [3], establishment of processes and incentives for science-practice collaboration [7, 14] from design through to implementation and monitoring, and a much greater emphasis on innovation and risk-taking [14, 15]. Unpredictability of outcomes could be partially addressed by establishing both small-scale no-intervention plots and low-intervention trials and then monitoring to assess the extent of tree recruitment over a few years, before implementing large-scale or high-cost restoration projects [34, 36]. Within large-scale trials, there would also be considerable benefit from embedded small-scale research-driven experimental manipulations [7] to clarify ecological processes.

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Compliance with Ethical Standards

Conflict of Interest The author states that there is no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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