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# How understanding aboveground–belowground linkages can assist restoration ecology

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The topic of aboveground–belowground linkages has seen much recent activity, resulting in several conceptual advances regarding plant–soil feedbacks, multitrophic interactions, and how organisms drive ecosystem processes. Although restoration ecology has been rapidly evolving as a scientific discipline, the principles that have developed regarding aboveground–belowground linkages have yet to be thoroughly integrated into it. In this review, we conceptually integrate the role of aboveground–belowground linkages with the principles of restoration ecology through a framework that transcends multiple levels of ecological organization, and illustrate its application through three examples: restoration of abandoned land, reversal of biological invasions, and restoration of natural disturbances. We conclude that this integration can greatly assist restoration ecology, through aiding identification of effective invention practices and prediction of ecosystem recovery.

## The linking of two emerging fields of research

Terrestrial ecosystems are comprised of two distinct components or compartments, one aboveground and the other belowground. The role of interactions between these two components in driving community and ecosystem properties is an emerging area of research which has seen several conceptual advances over the past decade [1–5]. As a result, there is increasing recognition that aboveground and belowground components of ecosystems are strongly linked through a variety of both direct and indirect interactions that operate across levels of ecological organization [1,2,6] (Figure 1). For example, recent studies have shown how alteration of trophic interactions in aboveground food webs can greatly influence soil food webs and *vice versa* [7,8], leading to reciprocal shifts in community composition between plant and soil communities [9,10]. In addition, mutualistic interactions and networks that span the aboveground–belowground interface, such as those between plants and mycorrhizal fungi, are increasingly recognized as critical for plant performance, plant associations with their consumers, and composition of aboveground and belowground communities [11,12]. Other recent studies have provided compelling evidence that aboveground–belowground linkages at the community level in turn drive the structure and functioning of ecosystems, including fluxes of carbon and nutrients [13,14].

Aboveground–belowground linkages have important implications for restoration ecology, here defined as the science associated with the 'intentional human intervention in enhancing ecosystem recovery after disturbance' [15]. Since its emergence in the 1980 s, the science of restoration ecology has increasingly sought to improve its conceptual basis [15–17], for example through drawing on basic ecological concepts such as succession theory, threshold dynamics and state transitions, community assembly rules, and niche differentiation [15–21]. However, studies of restoration ecology that have explicitly considered aboveground–belowground linkages are currently scarce [22]. Approaches founded on aboveground–belowground linkages suggest that restoration of one of these components would be improved by inclusion or consideration of the other, e.g. process rates in one subsystem may be regulated by the composition or interactions in the other subsystem. As such, considerable potential exists for the effectiveness of restoration efforts to be enhanced through the explicit consideration of aboveground–belowground linkages. Figure 1 illustrates examples of multiple intervention points where increased knowledge of aboveground–belowground linkages can facilitate ecological restoration. Some of these have been applied already (e.g. interactions of plants with aboveground herbivores and the abiotic soil environment [23]), while others show considerable potential but have been largely neglected in restoration ecology.

Some comprehensive recent reviews [19,22] have explicitly recognized the importance of interactions between plants and soils for underpinning ecosystem restoration. Here, we build on earlier efforts through explicitly considering restoration ecology within a combined aboveground–belowground context. We do this by presenting a synthetic conceptual framework which emphasizes how understanding of aboveground–belowground linkages ranging from low to high levels of ecological organization and involving multiple trophic levels could contribute usefully to the goals of restoration ecology. We then show how our framework might aid restoration efforts through three examples: restoration of degraded and abandoned land; reversal of biological invasions; and restoration of natural disturbance regimes. Through doing this we aim to achieve a fuller incorporation of recent advances in our understanding of aboveground–belowground linkages into the principles of restoration ecology.

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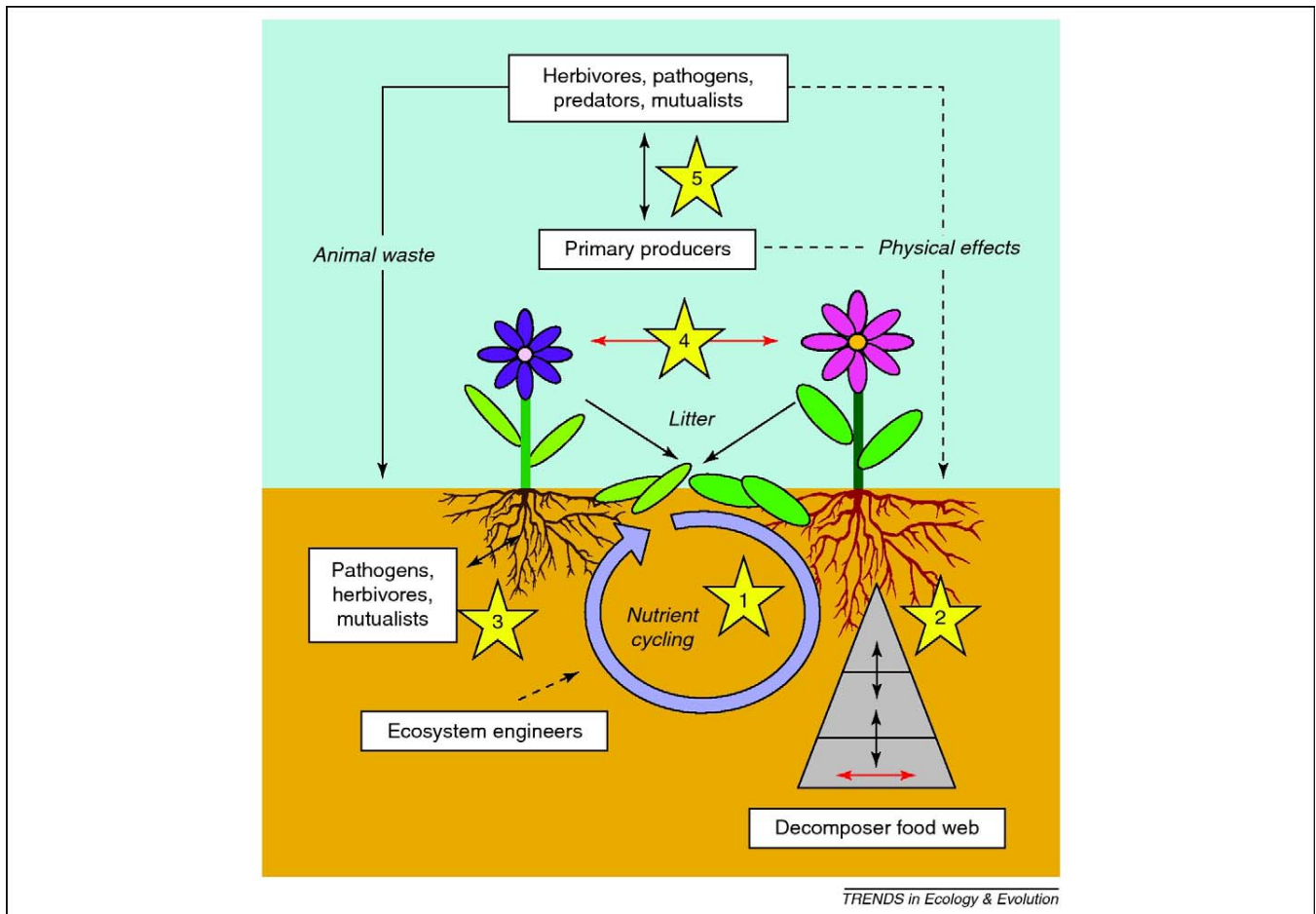
**Figure 1**. Schematic diagram illustrating the role of aboveground–belowground linkages in restoration of key ecosystem components, and how intervention practices can cascade through the ecosystem. Potential intervention points for ecosystem restoration (indicated by numbered star symbols) comprise trophic linkages (solid black arrows), competitive linkages (solid red arrows) and linkages via habitat modification (e.g. physical alteration) (broken black arrows). (1) Direct manipulation of soil biogeochemical cycles by addition of fertilizers [23], (2) indirect manipulation of biogeochemical cycles via soil decomposer communities, i.e. microbial nitrogen-immobilization through addition of organic substrates [61], (3) introduction of soil organisms such as mycorrhizal fungi that promote plant growth [35,65], (4) manipulation of plant-competitive interactions by species removal or introduction [98], and (5) manipulation of herbivores and predators by species introduction or removal, for example of large mammalian grazers [26,56].

## Conceptual framework

Ecological restoration can either follow a holistic approach through focusing on the disturbed ecosystem 'as a whole', or a more targeted approach concentrating on particular ecosystem components or properties. Effective implementation of either approach requires a full understanding of aboveground–belowground linkages across multiple levels of ecological organization. Here, we present a conceptual framework (Box 1) which is based on explicit recognition that (1) interventions during restoration of aboveground ecosystem components affect belowground ecosystem components, and *vice versa*, and (2) interventions at one level of ecological organization cascade to other ecological levels. We identify three such levels along which key restoration attributes can be organized: species, communities and ecosystem processes. Below, we outline the role of aboveground–belowground linkages of restoration attributes at each level, with explicit focus on the interactions between the levels.

### Restoration of (non-competitive) species interactions

Ecological restoration can involve deliberate manipulation of species interactions, where performance of the focal target species depends on the presence or absence of one (or more) other species [24] (Box 1). Re-establishment of trophic interactions has traditionally been focused aboveground, for example through manipulation of plant–herbivore interactions. However, recent studies have shown that species manipulation of aboveground trophic levels, notably through the removal of invasive herbivores and predators, can have strong knock-on effects for the soil food web [25–27], as we explore later. Further, there is increasing evidence of the importance of the composition and food web structure of belowground biota in driving aboveground biota such as invertebrate herbivores and their predators [28]. This means that successful restoration of aboveground organisms and interactions could potentially benefit from explicit consideration of the belowground community and trophic relationships. However, our understanding of the role of aboveground–belowground trophic interactions in ecological restoration remains limited.

The soil food web consists of organisms that interact indirectly with plants through influencing available nutrient supply (i.e. decomposers) and those that interact directly (i.e. pathogens, mutualists and herbivores) (Figure 1). Those organisms that interact most directly

## Box 1. Coupling aboveground–belowground linkages with restoration attributes: a conceptual framework

Aboveground–belowground linkages occur at multiple levels of ecological organization. Here, we distinguish between species interactions, communities and ecosystem functions (Figure I, left). Moreover, linkages at one level of organization can affect aboveground and belowground components, and their linkages, at other levels of organization (Figure I, white arrows). For example, the performance of individual species depends on the community context, while community processes depend on the component species. Similarly, community-level attributes can serve as important drivers of ecosystem-level processes, and some ecosystem processes are major determinants of community attributes. Depending on the type and severity of human disturbance, as well as land management and policy targets, restoration attributes may relate to these same levels of ecological organization both above and below ground (Figure I, right). Aboveground–belowground linkages might be most effectively manipulated during ecological restoration when there is recognition of the range of levels of ecological organization at which they operate. More generally, to restore aboveground ecosystem components, it might be necessary to manipulate belowground ecosystem components (and *vice versa*), and to restore ecosystem components at one level of ecological organization could require manipulation of components at other levels of organization. Taken together, recognition and integration of aboveground–belowground linkages in ecological restoration can help with the development of effective intervention practices and may improve the predictive outcome of intervention practices.
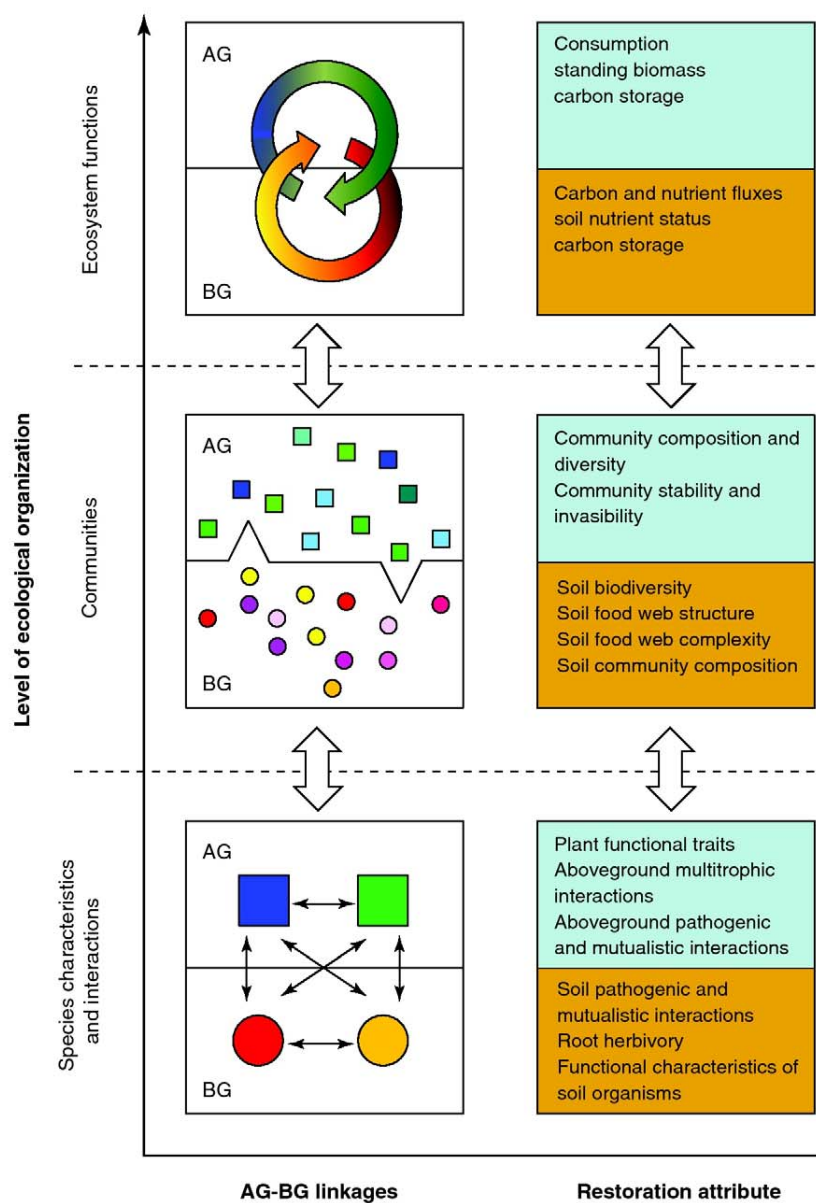


**Figure I**. Conceptual model describing linkages between aboveground and belowground ecosystem components across levels of ecological organization and potential aboveground and belowground restoration attributes at each of these levels. AG = aboveground, BG = belowground.

with plants are generally the most amendable to restoration. Despite increasing recognition of the role of plant pathogens in mediating aboveground–belowground linkages [3,4], plant pathogens have only recently been seriously considered in restoration ecology. For example, Fichtner *et al.* [29] tested soil-mediated strategies for controlling *Phytophthora ramorum*, the invasive fungal root pathogen that causes Sudden Oak Death in North American forests. Further, several studies have suggested that the release of some invasive plant species from native soil pathogens may help explain their success [30,31]. However, control of invasive plants by reuniting them with their native pathogens [32] has yet to be attempted, and may be problematic because of the unknown effects of introduced pathogens in their new environment. Recent work indicates that plant performance can also be affected by control of root herbivores by microbial pathogens [33], but manipulation of pathogenic interactions among soil organisms to facilitate restoration of aboveground communities remains untested.

Re-establishment of disrupted mutualistic species relationships can be a prerequisite for successful restoration of target species [34], as has been shown for mycorrhizal associations [35]. Moreover, increasing evidence that plant–mycorrhizal associations have cascading effects on aboveground invertebrate communities through changes in leaf chemistry [36] suggests a wider importance of mutualistic associations in the restoration of species relationships. Importantly, interactions between plants and mutualists often form complex ecological networks, such as plant–pollinator networks [37] or common mycorrhizal networks [11]. Recent theoretical developments indicate that manipulation of single network connections, such as through the introduction or removal of species, can affect the organization of the whole network [38]. Hence, implementing ecological network theory can improve understanding of species dynamics during restoration, as has been shown for plant–pollinator networks [37]. Mycorrhizal networks have yet to be considered in this context. However, recent studies [12,39] have shown that the relative importance of multiple functional relationships between plants and mycorrhizal fungi is sensitive to changes in environmental conditions, indicating the importance of structural changes in mycorrhizal networks during restoration.

*Restoration of ecological communities*
Alterations of aboveground–belowground species interactions in turn have important consequences for community structure and associated properties such as taxonomic richness, evenness and stability (Box 1). Most work on community-level restoration has focussed on plants and on the role of belowground abiotic factors (e.g. nutrient status) that directly affect plant communities [40]. However, recent work has recognized biotic soil conditions as key determinants of plant community properties [34,41,42], leading to progress in our understanding of how feedbacks between plant and soil communities affect the rate of plant community recovery after disturbance. For example, Kardol *et al.* [42] showed that negative feedback between the plant community and soil pathogens promotes grassland succession in early successional communities, while positive feedback between plants and mycorrhizal fungi retards plant succession and enhances community evenness later in succession. In turn, such biotic plant–soil feedbacks might affect, or be affected by, higher aboveground trophic levels. Further, the effect of soil communities on plant community properties is increasingly being recognized as driven by the functional trait spectrum of the component species [43]. In particular, functional differences among soil mycorrhizal communities have recently been shown to affect the relative performance of co-occurring plant species [44]. Improved understanding of how the functional trait spectrum of the soil community impacts on the plant community, and the interventions causing this spectrum to shift, has the potential to greatly benefit plant community restoration.

Recovery of communities of soil organisms during restoration depends on gradual colonization from external species pools (at least when species have been lost), release from disturbance, and the response of the component species to changes in environmental conditions [45]. Recovery of soil communities further depends on the composition of the developing vegetation, because plant species differ in the soil communities that they support [46]. For example, in an experiment performed on ex-arable land in northern Sweden, Viketoft *et al.* [46] showed how taxonomic and functional composition of soil nematode communities diverged between communities that differed in both plant species diversity and identity. Further, the recovery of soil food web structure after cessation of agricultural disturbance (such as occurs during the shift from bacterial-dominated food webs characteristic of disturbed systems to fungal-dominated food webs characteristic of low disturbance) may be determined by functional characteristics of the plant community and the resources that plants return to the soil [47]. Hence, restoration of soil food web properties may benefit from intervention that involves alteration of the composition of plant functional traits. A growing body of literature also suggests that aboveground trophic interactions can exert major effects on plant communities that in turn affect communities of soil organisms [48,49]. As such, there can be substantial indirect consequences for belowground community properties of changes in densities of aboveground consumers during restoration. So far, few studies have considered this [27].

*Restoration of ecosystem functions*
Restoring functional ecosystem attributes is of critical importance for the provision of ecosystem services. Evaluating restoration success by quantifying ecosystem processes might offer better insight into ecosystem recovery than reliance on data on species and communities alone [50]. While the relevance of taxonomic diversity *per se* for restoration of ecosystem functioning continues to be debated, functional diversity (i.e. the level of functional dissimilarity among species) is undoubtedly of considerable importance [51]. There is an accumulating body of literature showing that ecosystem processes are heavily influenced by the spectrum of functional traits shown by the dominant plant species in the community [13,52]. There is also emerging evidence of an important functional role for

traits of dominant belowground organisms [43]. Moreover, there is recent recognition [43] that an understanding of associations between organism traits and ecosystem processes can help with identification of predictable trait–ecosystem service clusters which involve multiple trophic levels, such as clusters of traits of plants and soil organisms that drive the cycling of nutrients.

Changes in plant functional group composition and trait spectra during restoration potentially have important implications for ecosystem processes both aboveground and belowground [20] (Box 1). In particular, the role of plant traits in driving the sequestration of organic carbon has attracted significant recent attention [53]. Shifts in functional group composition after restoration of disturbed plant communities have been shown to greatly influence community-level carbon storage in shoots and roots, and in soil organic matter [54,55], demonstrating the importance of consideration of aboveground–belowground linkages in restoration of ecosystem functions. Restoration of natural densities of large herbivorous mammals also has the potential to greatly influence belowground fluxes of carbon and nutrients through altering the quality and quantity of plant-derived resources entering the soil, both positively and negatively [25,51]. While many restoration efforts have been aimed at either reintroducing mammals following their loss from an ecosystem [56,57] or reducing densities of invasive or hyperabundant mammals [25,58], few studies have explicitly considered how such shifts in herbivorous mammal densities affect belowground processes that drive ecosystem functioning.

Importantly, belowground ecosystem functions are driven by the abundance and activity of soil organisms, their (functional) community composition and their food web structure [47,59]. Changes in soil food webs during ecosystem restoration have been shown to alter carbon and nutrient cycling rates, with important implications for plant growth and ecosystem carbon sequestration [60]. The functioning of soil decomposer communities (bacteria, fungi and soil fauna) is highly responsive to the quality and quantity of organic matter input by plants and animals [53], and this is directly applicable to restoration ecology. For example, some restoration attempts have involved temporarily reducing soil fertility through adding high quality carbon substrates to stimulate nitrogen immobilization by the decomposer community, thereby favouring slow-growing target plants at the expense of fast-growing weeds [61]. Finally, ecosystem properties both aboveground and belowground can be greatly altered by direct addition of soil organisms that are perceived to be beneficial for ecosystem restoration goals, as can be done for mycorrhizal fungi and earthworms as described below.

## Application of the framework
### Restoration of degraded and abandoned lands
Restoration of (semi-)natural ecosystems after cessation of human land use such as mining and agriculture is frequently performed to aid biodiversity conservation [62]. Consideration of aboveground–belowground linkages can inform intervention practices guiding the successional development towards the historical (or desired) ecosystem state, as has been shown for the restoration of species-rich grasslands on ex-arable land (Box 2). Inter-dependent groups of organisms may differ greatly in their rate of recovery during restoration [63], and recovery of some components of the soil biota is particularly slow, potentially resulting in long-term biological soil legacies that may have aboveground consequences. A major challenge is to synchronize such aboveground–belowground species associations when abandoned lands are being restored. At issue here is whether soil-dwelling and soil-associated organisms that directly or indirectly influence plant growth passively follow the vegetation development because of their dependence on plants [64], or whether introduction of soil organisms is necessary for restoring disturbed plant communities [65]. For example, direct inoculation of mycorrhizal fungi to restore severely degraded soils is increasingly recognized as a prerequisite for successful reestablishment of target plant communities [35,66].

During restoration of degraded lands, community-level interventions such as the re-assembly of aboveground and belowground communities can influence other levels of ecological organization and thereby also drive ecosystem functioning [52,54] (Box 1). One aspect of particular importance is the build-up of ecosystem carbon storage, because of the importance of soil organic matter for restoring soil fertility, and the potential of carbon sequestration to offset rising atmospheric $CO_2$ levels. Cultivated systems have often lost a large proportion of their previous soil carbon pool [67], and re-vegetating these systems with trees or perennial grasses (particularly those with high standing biomass or poor quality litter) aids the recovery of this pool through promoting accumulation of biomass and soil organic matter [68]. Further, aboveground and belowground carbon and nutrient fluxes can be manipulated through altering densities of large herbivores, and thus plant biomass removal and the quantity and quality of resources entering the soil [69]. However, the effects of herbivore manipulation on belowground fluxes can be difficult to predict, because of the variety of mechanisms through which grazers can affect these fluxes, both positively and negatively [70]. Besides plant- and herbivore-mediated interventions, manipulation of the soil food web may also contribute to restoration of ecosystem processes [71]. For example, the deliberate introduction of earthworms is sometimes employed during rehabilitation of severely degraded soils with the intention of promoting soil biological activity and fertility, and ultimately the nutrition and growth of the plant community [72,73].

### Reversal of biological invasions
Invasive organisms are recognized as important drivers of aboveground–belowground linkages and community processes [70,74] through displacing or even eliminating native species, and by disrupting multitrophic and mutualistic species interactions [75–77]. Restoration of communities invaded by exotic species requires active eradication of the invader, and in many cases (particularly when some resident species have been lost), subsequent active reestablishment of the native community. For example, the reestablishment of native soil communities may be a limiting factor in the restoration of native plant diversity and composition [75,78]. Further, some aboveground invasive

## Box 2. Aboveground–belowground linkages in restoration of species-rich grasslands on ex-arable land

In industrialized countries, large areas of former agricultural land have become available since the 1980 s for restoration to a (semi-)natural state. Such restoration might help counteract current plant species loss in grasslands and heathlands. Plant community restoration has traditionally been recognized as constrained by high soil fertility and seed limitation of later-successional target species [40], but recent evidence also points to restoration being constrained by degraded and disturbed soil communities [41,42]. These and other examples indicate that more integrated aboveground–belowground interventions might facilitate the transition towards the (semi)-natural state. Figure I illustrates linkages between the aboveground and belowground components that may facilitate conversion of ecosystems from the disturbed human-driven state to the (semi-)natural restored state across levels of organization. Below we highlight two main aspects that have been explored in recent studies.

*Restoration of plant–soil organism interactions through species introductions*

At the community-level, the presence of soil fauna and mycorrhizal fungi in Dutch grasslands has been identified as a factor that shifts plant communities to a later-successional state [41,42]. However, soil organism introduction as a management strategy for restoration of species-rich grasslands has not yet been proven effective [65]. Conversely, manipulating plant community composition through sowing later-successional plant species may affect the

taxonomic composition of soil communities and soil food web structure [61,99]. Probably the best integrated aboveground–belowground community intervention involves transplantation of intact turfs obtained from a target habitat (containing desired plant and soil communities) to ex-arable fields being restored [65]. Species may spread from the turfs and thus enable restoration of plant and soil communities at the field scale. Turf transplantation has proven more successful for plant than for soil communities, probably because of the environmental sensitivity of soil biota and the difficulty in matching environmental conditions between donor and receptor sites [65].

*Interventions are likely to cascade through multiple levels of ecological organization*

This means that restoration of ecosystem attributes at high levels of organization requires intervention at lower levels of organization. For example, a field-based study by Van der Wal *et al.* [100] suggests that re-establishment of *Calluna vulgaris*, which depends on association with ericoid mycorrhizal symbionts, can cause substantial reduction of nitrogen-mineralization through the exudation of polyphenolic-rich compounds. Because of the nature of its mycorrhizal association, *C. vulgaris* may be less nitrogen-limited than co-occurring grass and forb species, giving it a competitive advantage and thus enhancing restoration of heathland plant communities and their associated aboveground faunal communities.
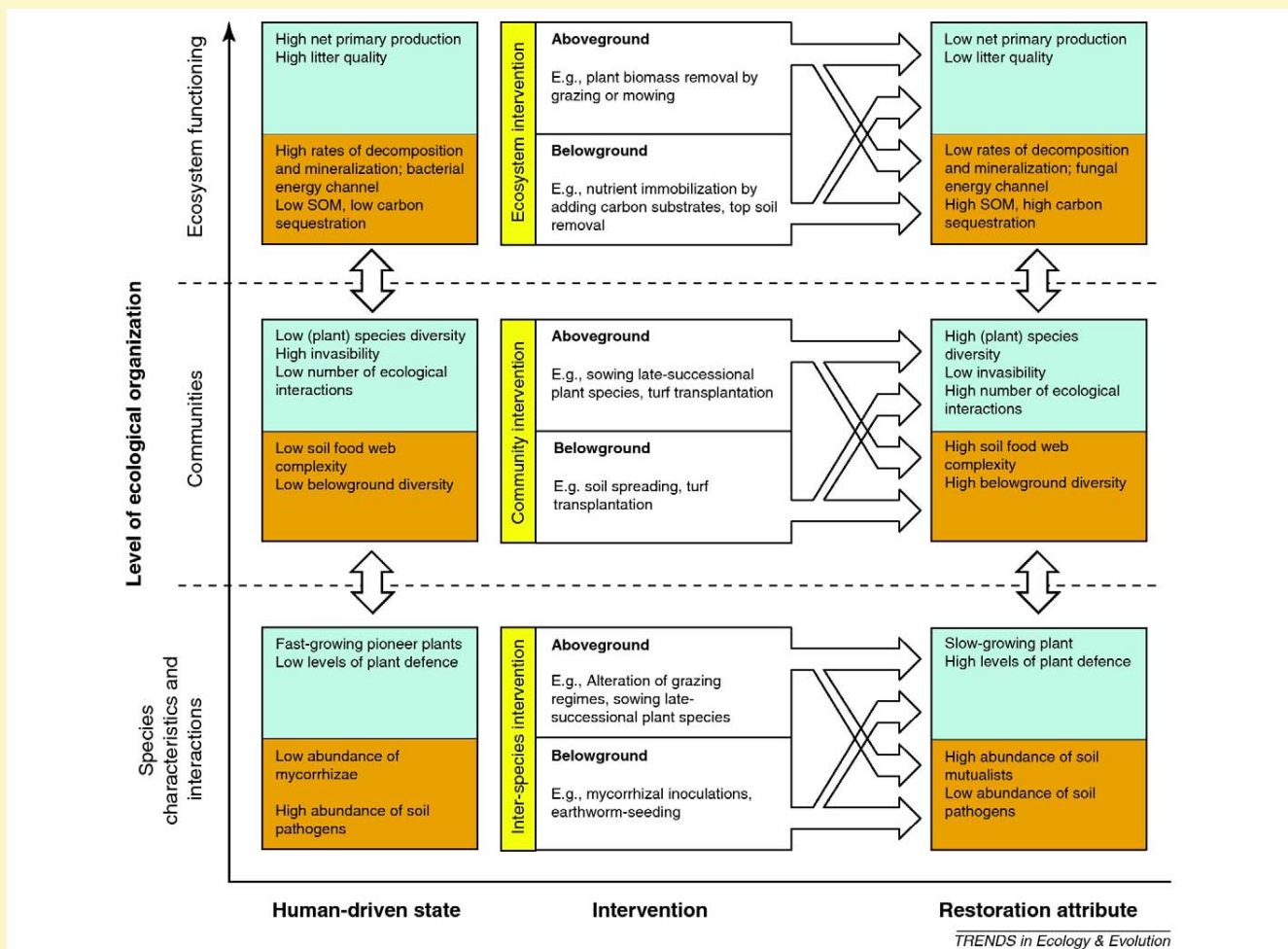


Figure I. Aboveground–belowground linkages relevant to restoration after abandonment of agricultural land. Restoring belowground ecosystem attributes might depend on aboveground interventions, while restoring aboveground ecosystem attributes may benefit from belowground interventions. Restoration goals and opportunities for intervention span ecological levels from species to community to ecosystem. Further, interventions at one level inherently affect the restoration attributes at other levels. SOM = Soil organic matter.

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**Box 3. Belowground ecosystem recovery following removal of aboveground invasive species**

Biological invasions are among the primary agents of global environmental change, and much recent work has explored the effects of invaders on both sides of the aboveground–belowground interface [70]. Restoration of ecosystems transformed by invaders not only requires an understanding of these effects, but also of how reversible they are once the invader is removed. While a combined aboveground–belowground approach has much to contribute to understanding how ecosystems may recover following the removal of invasive organisms, relatively few studies have explicitly explored this.

- Invasion of Portuguese coastal dune systems by the leguminous tree *Acacia longifolia* increases soil biological activity through its capacity to fix atmospheric nitrogen and return nitrogen-rich litter to the soil [86]. Marchante *et al.* [86] showed that 2.5 years after removal of *A. longifolia*, the belowground subsystem showed large responses; basal respiration and microbial biomass decreased by about 30%, while potential nitrification increased by >95%. Although the invasive tree causes relatively rapid build-up of soil biological activity and fertility, reversal of these effects is apparent a few years after the invader is removed.

- Rocky Mountain elk (*Cervus elaphus*) was introduced to northern Arizona about a century ago, where they have reached high population densities and contributed to the decline of several native plant species [85]. Stritar *et al.* [85] found that surface mineral soils rapidly regained soil organic carbon, total nitrogen, and microbial nitrogen pools following elk exclusion, but that this recovery varied with time since fire. This highlights that removal of an invasive aboveground herbivore can reverse its indirect effects on belowground properties, but that the rate of this reversal depends on environmental context, in this case fire history.

- For marine offshore islands in New Zealand, seabirds are a major driver of ecosystem processes both aboveground and belowground through transferring nutrients from the ocean to the land; invasive rats (*Rattus* ssp.) on these islands serve as predators of seabird eggs and chicks and therefore reverse seabird effects [26]. Extermination of rats has failed to fully restore island soil properties and plant community characteristics, because restoration requires not just removal of the invader but also reintroduction of seabirds [58]. Here, the invader has caused the ecosystem to switch to an alternative stable state, which might not be reversible simply through removal of the invader [19].

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predator species can greatly transform community properties both aboveground and belowground through extirpating prey species [26,79]. Here, restoration of native ecosystems (including the belowground component) may require aboveground species interventions, including not only the eradication of the predators but also the deliberate reintroduction of the prey species once the predator has been removed [58]. Removal of invasive plants through restoration efforts has also been shown to restore the food web structure of native aboveground arthropods [80], though the effects of removal of invasive plant species on belowground communities has only occasionally been explored [81].

Invasive species are also known to transform ecosystem-level properties such as fluxes of nutrients and carbon, and biomass pools [82–84]. A small but growing number of studies have explored how altered belowground properties might be restored following the removal of invasive plants and aboveground consumers [85] (Box 3). Soil legacies after the removal of invasive plant species can be persistent [86], and simultaneous aboveground and belowground interventions that explicitly aim to re-construct altered soil communities have potential for restoring belowground ecosystem processes following invasive species removal. However, this option has seldom been explored [34]. Invasive belowground organisms (notably earthworms, ants and some plant-pathogenic fungi) can also greatly alter aboveground and belowground ecosystem properties [70,87]. There are few effective ways to remove these organisms, despite this being the first prerequisite for reversing the ecosystem-level impacts of such invaders. However, interventions aimed at indirectly altering their densities may have some potential. For example, the removal of exotic plant species has been shown to reduce the abundance of invasive earthworms through disrupting positive nutrient feedbacks between the plants and the earthworms [88].

*Restoration of natural disturbance regimes*
Natural disturbance regimes are an integral part of most ecosystems, but human activities have often caused substantial suppression of these regimes, leading to major ecosystem changes [70]. One notable example is wildfire, which is an essential natural element of many ecosystems worldwide, but which humans have historically often sought to suppress. The reintroduction of fire regimes, such as through prescribed burning, is increasingly recognized as important for restoring naturally pyrogenic ecosystems [89,90] (Figure 2). At the community level, reintroduction of fire is well known to select for plant communities with particular suites of functional traits, including those that drive soil communities [91,92]. As such, there is evidence that restoration of fire regimes may alter belowground community attributes through inducing shifts in the functional composition of the plant community [90]. Meanwhile at the ecosystem level, the return of fire following suppression is likely to both enhance and reduce soil nutrient availability depending on environmental context, and to often reduce soil organic matter and carbon storage. These effects occur through various mechanisms, including direct effects of combustion, indirect effects through alteration of spectra of plant functional traits, and the quality of plant-derived resources entering the soil [93–95]. Although these types of effects highlight how wildfire might influence linkages between the aboveground and belowground subsystems, and in particular how plant community composition drives carbon and nutrient cycling, they have seldom been considered in relation to reintroduction of natural fire regimes.

Human activities have also led to the loss of biotic disturbances, such as those caused by large herbivores. Herbivore-driven disturbances have sometimes been regarded as analogous to those of wildfire because both can involve substantial plant biomass removal [96], despite their belowground consequences and aboveground feedbacks often being quite different [25]. Here, restoration involves reintroducing large mammals that have become extinct (or their functional analogues), so that the ecosystem is again subjected to the disturbance regime that they cause (Figure 2). In this light, several studies have explored how the re-introduction of large herbivores affects biogeochemical processes, both through selective biomass removal and through direct physical
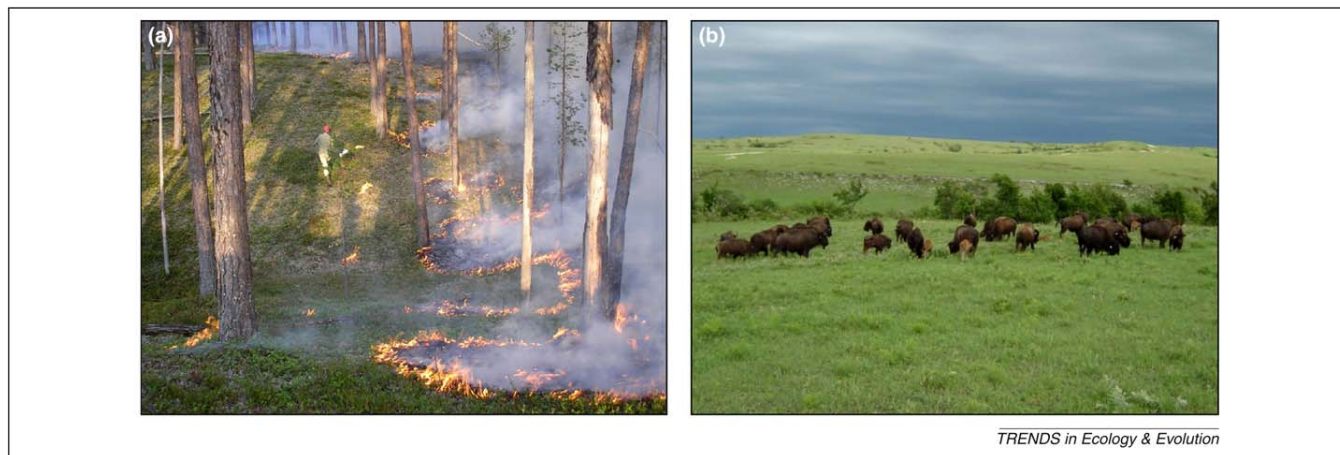
**Figure 2**. Restoration of agents of natural disturbance regimes that involve substantial plant biomass removal. **(a)** In boreal forests of northern Sweden, prescribed fire is a common intervention in counteracting shifts in plant dominance patterns resulting from fire suppression (photo: Anders Granström) [89,91]. **(b)** At Konza prairie, Kansas, USA, bison have been reintroduced to allow forbs to flourish by releasing them from competitive suppression by dominant grasses (photo: James Koelliker) [56]. In both examples, the restoration of these disturbance regimes are well known to have important consequences for the decomposer subsystem through a range of mechanisms, and these in turn determine carbon and nutrient fluxes both aboveground and belowground.

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**Box 4. The way forward**

While there have been significant recent advances in understanding aboveground–belowground linkages, there are several areas in which future research in this field could further assist its integration with the goals and practices of restoration ecology.

- Despite significant recent advances in understanding the cascading influences of multitrophic interactions both aboveground and belowground, little remains known about how restoration of these interactions following their disruption can guide the recovery of key ecosystem functions.
- We have yet to fully recognize how the recovery of aboveground–belowground linkages and ecosystem processes during restoration might be governed by the functional trait spectra of the component organisms, including plants, animals and microbes.
- Although many recent studies have considered invasive organisms in a combined aboveground–belowground context, few have

explicitly considered whether and how the aboveground and belowground subsystems respond over time to restoration efforts that involve their removal.

- The well recognized role of natural disturbances as drivers of linkages between the aboveground and belowground subsystems has seldom been explicitly considered in the context of restoration.
- Much remains to be understood about how aboveground–belowground linkages can drive critical ecosystem transitions between human-driven states and alternate desired restoration states (i.e. 'threshold dynamics').
- Ecological restoration has the potential to greatly contribute to our understanding of the role of aboveground–belowground linkages in the disassembly and reassembly of ecological networks, communities, and whole ecosystems, although this has seldom been recognized.

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soil disturbance [56,97]. As such they provide clear evidence of how aboveground species interventions affect belowground processes and thus ecosystem functioning [70]. A more holistic approach involves the restoration of whole historic ecosystems, including functional aboveground–belowground linkages. Such an approach has been adopted in projects aiming to reconstitute 'Pleistocene ecosystems', which vanished about 10 000 years ago after the extinction of mammoths and other large vertebrate herbivores and predators [57].

## Conclusions

Counteracting human-induced transformation and degradation of natural ecosystems necessitates active ecological restoration and intervention. Although many questions remain unanswered (Box 4), there have been significant recent advances in our understanding of the links and feedbacks between the aboveground and belowground subsystems, and this in turn has great potential to advance the field of restoration ecology. As we illustrate through our conceptual framework (Box 1) and three examples, integration of recent advances in our understanding of aboveground–belowground linkages with the principles of restoration ecology can assist in identifying effective

invention practices, and aid predictions of how ecosystems may recover following ecological restoration. By pointing out how aboveground and belowground restoration attributes are linked across levels of ecological organization, our framework shows what interventions (aboveground, belowground or a combination) may lead to the desired state of the restoration attribute. Restoration of belowground ecosystem functions often requires manipulation of aboveground communities and species interactions, while restoration of aboveground community properties may require manipulation of belowground ecosystem processes as well as those organisms that drive them. Importantly, integrating aboveground–belowground linkages in restoration ecology is not a 'one way fits all' situation; it rather requires a customized approach that can be adapted to any specific situation. As such, we emphasize that the choice of interventions is dependent on which restoration attributes are prioritized, on their deviation from the desired state, and on which aboveground and belowground ecosystem components can be manipulated to restore them.

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