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Plant succession as an integrator of contrasting ecological time scales

Lawrence R. Walker[1] and David A. Wardle[2]

[1] School of Life Sciences, Box 454004, University of Nevada Las Vegas, Las Vegas, NV 89154-4004, USA
[2] Department of Forest Ecology and Management, Faculty of Forestry, Swedish University of Agricultural Sciences, SE901-83, Umeå, Sweden

Ecologists have studied plant succession for over a hundred years, yet our understanding of the nature of this process is incomplete, particularly in relation to its response to new human perturbations and the need to manipulate it during ecological restoration. We demonstrate how plant succession can be understood better when it is placed in the broadest possible temporal context. We further show how plant succession can be central to the development of a framework that integrates a spectrum of ecological processes, which occur over time scales ranging from seconds to millions of years. This novel framework helps us understand the impacts of human perturbations on successional trajectories, ecosystem recovery, and global environmental change.

Plant succession as a tool to understand temporal processes

Plant succession, a central yet elusive concept in plant ecology (see Glossary), can be understood better by placing it in the broadest possible temporal framework (Figure 1). We suggest that plant succession (hereafter 'succession'), which can be measured at temporal scales ranging from years to millennia [1] but is most commonly studied at decadal scales, is explained better by using a multi-scalar approach [2,3] that encompasses temporal scales ranging from seconds to millions of years. Our approach incorporates recent insights about processes that can act as both shorter-term drivers of succession (e.g., organic matter decomposition pathways and plant–soil feedbacks) [4,5] and longer-term constraints on succession (e.g., ecosystem retrogression and soil formation) [6]. Such an explicit, multi-scalar, temporal approach to successional studies can also help clarify such ecological topics as facilitation [7], community assembly [8], and phylogenetics [9], which all occur at temporal scales that overlap with succession.

An improved understanding of the broad temporal context of succession has the additional benefit of linking other processes that operate at highly contrasting temporal scales. The principle influences on a given temporal process are those that most closely match it in terms of time, in a manner analogous to the meshing of adjacent gears (Figure 1). Processes that operate over distinctly shorter or longer time scales will be less influential (i.e., analogous to gears that do not mesh). Processes occurring at intermediate temporal scales, such as succession, can provide critical links between otherwise unconnected phenomena operating at vastly contrasting (shorter and longer) time scales. Such insights have the potential to enhance the effectiveness of restoration and land management [10,11]. They can also assist our understanding of the impacts of global change phenomena that are altering disturbance regimes [12] and ecosystem processes [13,14] both above and below ground [15], and that are leading to novel successional trajectories [16,17]. To our knowledge, no framework comparable to that depicted in Figure 1 exists, perhaps because of the difficulties in studying particularly fast or slow processes, and because of the dearth of theory explicitly addressing integration across temporal scales.

Corresponding author: Walker, L.R. (walker@unlv.nevada.edu).
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Glossary

Competition: the negative influence of one plant on its neighbors, usually attributed to a reduction of resources; competitive inhibition can slow species turnover (decelerating succession) whereas competitive displacement can increase species turnover (accelerating succession).
Constraint: an ecological process that provides boundaries to the possible states of a process that occurs at a shorter temporal scale.
Disturbance: a relatively abrupt loss of biomass, structure, or function which, when of sufficient severity, has the capacity to initiate or redirect succession.
Driver: an ecological process that provides a mechanistic explanation of another process that occurs at a longer temporal scale.
Facilitation: the positive influence of one plant on another; facilitation of new species can accelerate succession.
Global change: changes that have impacts at the global level, which includes human-induced shifts in land use, nutrient status, climate, and biological invasions and extinctions.
Hierarchical approach: the study of multi-scalar influences using drivers and constraints to understand how processes at several relevant scales affect a given scale of interest.
Plant succession: the change in species composition in a community following a disturbance that occurs over time spans approximating ten times the life span of the dominant species, from months for herbs to millennia for trees [1] and that is characterized initially by a progressive phase of accumulation of plant biomass, sometimes followed by a retrogressive phase (see 'Retrogression').
Restoration: the manipulation of community composition, structure, function, and successional turnover to a desired state following a disturbance.
Retrogression: the decline phase of succession in the long-term absence of disturbance that is characterized by decreasing levels of plant biomass, soil fertility, and often soil permeability [6].
Successional rates and trajectories: the speed at which species change occurs and the directional shifts in species composition, often in relation to other successional sequences (i.e., parallel, convergent, divergent) [1].
Temporal framework: a conceptual approach to understand relationships among processes that occur at different temporal scales.

Within the framework of temporal linkages presented in Figure 1, we address how the most common biotic and abiotic processes interact to affect succession. First, we discuss the effects that short-term processes (operating on time scales from seconds to decades) have on succession. We consider these to be drivers in the sense that they provide mechanistic explanations of a focal process [18]. Next, we explore the influences that longer-term processes (operating at scales of thousands to millions of years) have on succession. We consider these to be constraints in the sense that they provide boundaries to possible states of a focal process [18]. We do not indicate all possible links in Figure 1 (e.g., between geology and macro-evolution) and do not imply directionality of any of the 'gears'. Finally, we discuss how global change phenomena and restoration influence short-term drivers and longer-term constraints of succession. Our interpretation of succession as a product of temporal processes at all ecological scales helps expand our conceptual framework for understanding temporal processes in ecology.

Short-term processes drive successional dynamics

Processes occurring at micro time scales (seconds to days), such as plant physiological responses to fast nutrient fluxes, influence processes that operate at local time scales (days to years), such as plant life cycles and herbivory. These longer processes influence the first several decades of succession when colonizers substantially alter trajectories, which in turn determine the first several centuries of succession during which biomass and soil organic matter accumulate (Figures 1 and 2).

Nutrient supply rates from the soil, governed by biogeochemical processes that operate over seconds to days, influence the relative success of different colonizing plant

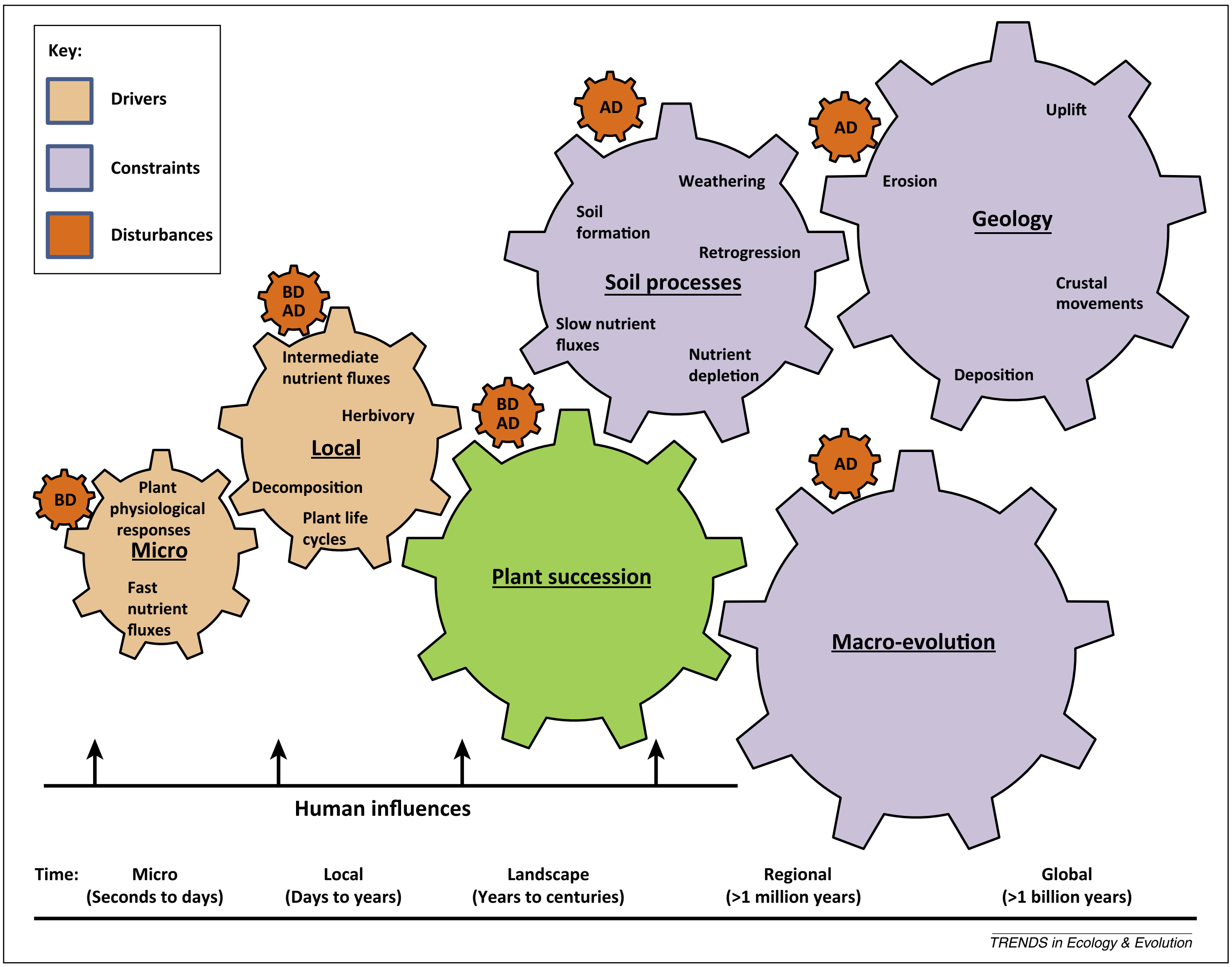

Figure 1. Plant succession as an integrator of ecological processes. Placing plant succession (green) in a broader context can illustrate how succession is driven by shorter-term processes at micro and local scales (beige-colored drivers) and constrained by longer-term ones at regional and global scales (blue-colored constraints). Drivers provide mechanistic explanations and constraints provide boundaries to possible states (e.g., trajectories) of succession; neither implies a directional influence on rates of succession. Spatial terminology is suitable for describing temporal scales because of the strong correlation between spatial and temporal scales [18]. Categories of temporal scales are approximate because of the extensive overlap among ecological processes (e.g., plant life cycles encompass weeks to centuries; soil formation occurs over years to millennia). Biotic (BD) and abiotic (AD) disturbances (dark-brown-colored) alter the influences of these processes on succession. Human influences both drive and constrain succession at many temporal scales. We do not indicate all possible links (e.g., between geology and macro-evolution) and do not imply directionality of any of the 'gears', instead focusing on major drivers or constraints of succession. Paleoecological time scales are also not within the scope of this paper, but can be conceived as historical iterations (layers) of Figure 1.

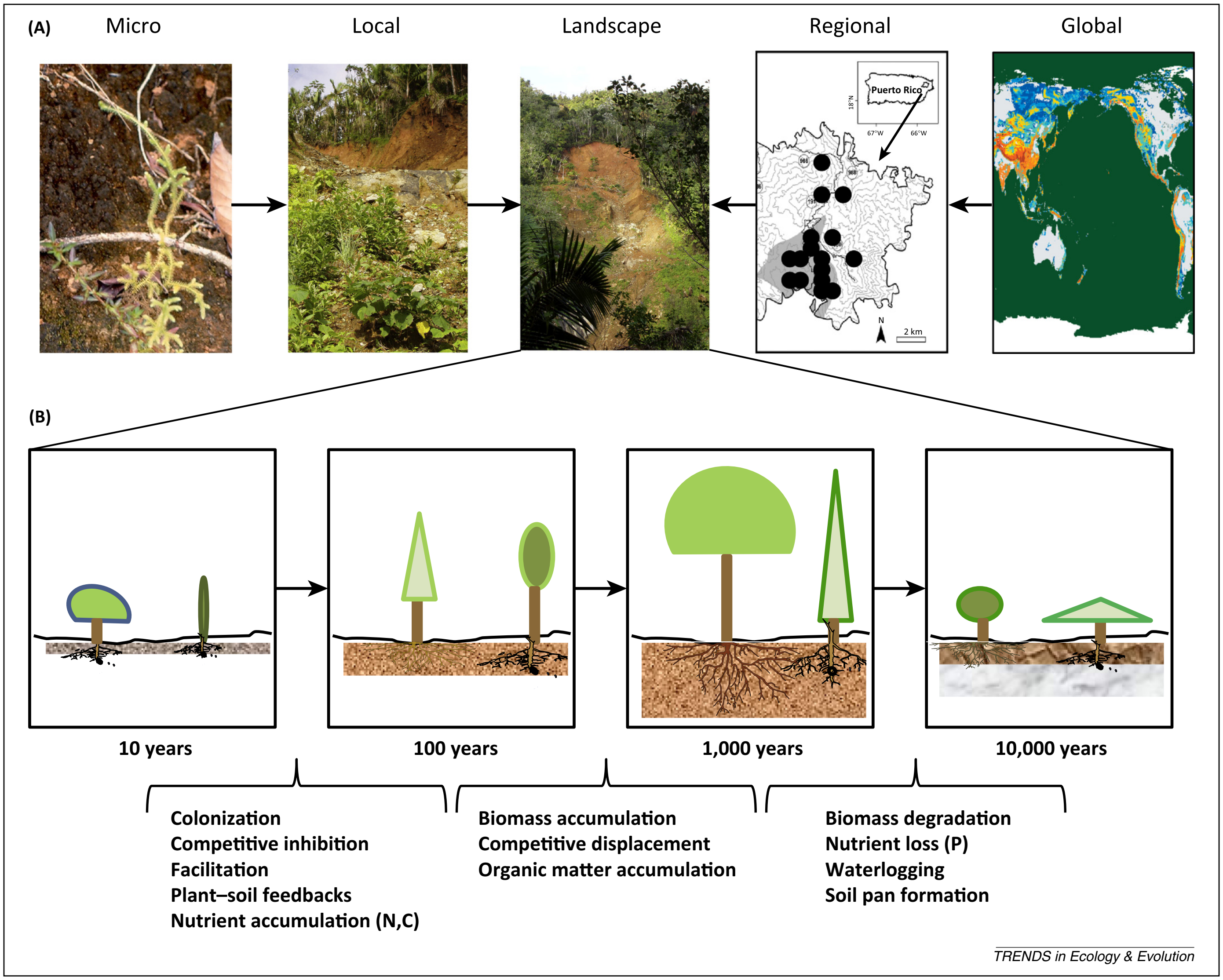

Figure 2. Illustrations of scales affecting succession. **(A)** Images of the range of temporal processes from micro to global scales in relation to landslides in Puerto Rico. Illustrations from left to right: micro, cryptobiotic crust and club moss; local, pioneer plants; landscape, a landslide covering an entire slope; regional, landslide locations ($n = 4$ per dot) from 2003 to 2004 in the Luquillo Experimental Forest; 69% of the 68 landslides >60 m^2 are found on the more erosive diorite soil (shaded), 31% on the volcaniclastic soils (unshaded) [65]; global, locations of highest global incidence of landslides (orange and red shading). Processes at the sub-landscape scale (micro and local) drive plant succession whereas those at larger scales (regional and global) constrain it, as indicated by arrows. **(B)** Most successional studies focus on landscape-level changes that last decades to millennia. Plant biomass and the rates of belowground processes (e.g., nutrient fluxes) increase throughout the progressive phase of succession, then decline during retrogression. The grey color in the last panel indicates impermeable iron or clay pans that can develop over thousands of years in the absence of large disturbances. The regional image is from [65]; the global image is from satellite imagery by the US National Aeronautics and Space Administration.

species, and species replacements during succession (Figure 1). Importantly, plant species also regulate soil biogeochemical processes that regulate nutrient supply, which sets a feedback in motion between plants and biogeochemical processes, although the importance of this feedback and its relevance for understanding succession is seldom explicitly studied [4,19]. One example where such a feedback has been addressed is in studies on Dutch foredunes that reveal how the poor quality litter that the colonist *Erica tetralix* (cross-leaved heath) produces leads to organic matter build-up and ultimately a net release of mineral nitrogen. This habitat amelioration promotes ingress by *Molinia caerulea* (purple moor grass) that then competitively displaces *E. tetralix* over successional time [20]. Other examples involve increasing domination by plant species that produce high levels of polyphenolic compounds that sequester soil nitrogen, thus enabling them to replace species that require access to mineral nitrogen, and in turn promoting succession [19,21].

Feedbacks between plants and consumer biota that operate over timescales from days to years can serve as powerful drivers of longer-term successional processes (Figure 1). Despite considerable recent focus on feedbacks between plants and soil biota [4], such feedbacks have rarely been considered in a successional context [22,23]. However, early successional species can enter negative feedbacks with soil biota (e.g., pathogens) that facilitate species replacement, whereas later successional species can enter positive feedbacks (e.g., with mycorrhizal fungi) that impede species replacement [23]. Feedbacks involving plants and aboveground consumers also play an important role, and several studies show that herbivores delay species replacement in fertile conditions and promote it in infertile conditions [24]. These effects of herbivory, which may be transient, have important legacies both aboveground and via the soil that are relevant over much longer successional time scales. For example, exclusion of deer from New Zealand rainforests on decadal time frames influences soil properties, which then differentially affect seedlings of plant species of contrasting successional status [25].

Plant–plant interactions are principal drivers of succession, with implications extending beyond the life span of the interacting individuals to that of the entire successional sequence (Figure 1), although such a successional connection is rarely made [1]. Plants that survive a disturbance or colonize immediately afterward often dominate propagule pools and resource patches [26], giving them a competitive advantage (e.g., through priority effects) [27] and leading to a successional trajectory that depends on their particular life history characteristics [28]. The colonists can accelerate succession if they are short-lived or promote their own demise [29], or can arrest succession if they form inhibitory thickets or are long-lived [30]. For example, succession on landslides colonized in Puerto Rico by grasses and forbs remained arrested, whereas tree pioneers led to later successional forested stages [31].

The balance between dominance by competitive versus facilitative interactions among species in the early stages of succession can influence later successional dynamics. This balance has been linked to N:P ratios of plants, soils, and dead organic matter in a study of post-volcanic succession on Mount St Helens (WA, USA) [32]. Plant life forms and functional roles can also influence this balance. Nitrogen-fixing woody plants are typical facilitators [33], but their facilitative role can occur either during their lifetime or only after they die [34], leading to variable successional outcomes. Plants that initially facilitate can eventually be outcompeted by the plants that they once nursed [29]. The implications for successional trajectories are largely missing from recent literature on facilitation [7,33], but facilitative interactions generally accelerate succession and promote convergent trajectories [1,35]. Competitive inhibition of later colonists can arrest succession [30] and promote convergence, whereas competitive displacement of an existing dominant can accelerate succession and lead to divergence [1,35]. Therefore, the net effects of species interactions on succession are still unclear.

Long-term processes constrain successional trajectories

Succession occurs in the context of processes that operate at much longer time scales (thousands to millions of years) and that constrain potential rates and trajectories of succession. These processes include geological forces that determine substrate stability and soil conditions, soil processes that influence nutrient and water status, and macro-evolution that provides the species pools available for succession (Figures 1 and 2).

Geological forces can constrain succession through two principal means. First, they determine the composition of the parent material; this impacts on succession primarily indirectly through influencing the properties of soils formed from the material (e.g., soil fertility, mineralogy, hydrological properties), although more direct effects can occur when plants and their mycorrhizal associates access mineral nutrients directly from rocks [36]. In particular, the fact that major rock types vary more than 30-fold in their phosphorus concentrations has important implications for soil fertility and ultimately for successional pathways [37]. Second, geological forces determine the extent to which succession is interrupted or reset by disturbance regimes that lead to access to new parent material, tectonic uplift that exposes new surfaces, and erosion that involves loss of soil [38].

Both these effects of geological forces determine soil fertility and stability, which act as constraints on succession (Figure 1). It is well established that newly formed surfaces are initially nitrogen- rather than phosphorus-limited, but that this balance reverses as organic matter and nitrogen accumulate while phosphorus sourced from the parent material becomes depleted over many thousands of years. In the absence of major geological disturbances over millennial time scales, this phosphorus depletion leads to retrogression [6,39], which is characterized by reduced vegetation stature [39], altered functional composition of the vegetation and plant trait spectra [40], increased plant diversity [41], and slowed rates of succession [6]. Considerable periods (e.g., millions of years) without extensive disturbances that expose parent material can lead to severely phosphorus-depleted ecosystems and the development of a flora that is especially adapted for these conditions, as is the case for much of Australia [42].

Macro-evolution regulates the pool of colonizing species, but that pool is dynamic, changing as species adapt to new abiotic (e.g., weathering) and biotic (e.g., competition) filters [9]. These filters select colonizers with different tolerances along and responses to environmental gradients [43], thereby constraining succession by limiting its possible rates and trajectories. Macro-evolution also determines various species traits that influence community turnover. For example, community phylogenetic patterns in a New Guinea lowland rain forest shifted during succession from random, to clustered, and then to over-dispersed [44]. This trend may reflect, in sequence, stochastic colonization of pioneer species, environmental filtering favoring rapidly growing and competitive species, and greater environmental heterogeneity favoring species coexistence. Macro-evolution further constrains the rates and trajectories of succession by controlling the adaptability of species to changes in soil conditions, for example through selecting for species that have high phosphorus use efficiency in low-phosphorus ecosystems that have undergone retrogression in the extended absence of major disturbance [6]. Shorter-term evolutionary processes (micro-evolution) also affect succession (as drivers in our terminology), for example through their influence on soil organisms [45] or via herbivore resistance [46], but their longer-term temporal implications are still poorly understood.

Global change and restoration

Human-induced global environmental changes are well-recognized as having powerful influences on the structure and function of ecosystems, but their temporal implications are unclear. Global change influences operate at both shorter (e.g., land use and biological invasions) and similar

Table 1. Effects of human influences operating at contrasting time scales on plant succession

Human influence	Time scale relevant to succession			Effect on rate of succession	Effect on trajectory of succession	Effect on species composition	Effect on alpha diversity
	Shorter	Similar	Longer				
Higher disturbance frequency/severity	X			Decelerates/stops	Shortens trajectory/ promotes convergence	Promotes pioneers	Variable
Biological invasions	X	X		Variable	Redirects	Often promotes pioneers and new mixes	Usually increases
More extensive grazing	X	X		Decelerates	Shortens	Promotes short forbs, grasses	Increases if low intensity
Restoration		X		Accelerates to desired stage, then stops	Targets shortest to goal or redirects	Mimics original	Variable, depending on intent
Nitrogen enrichment	X	X	X	Decelerates	Shortens	Promotes pioneers	Decreases
CO_2 enrichment		X	X	Variable, depending on dominant species	Redirects	Variable, depending on original composition	Variable, depending on level
Global warming[a]		X	X	Variable	New directions	New mixes	Variable

[a]We do not address the many other aspects of climate change (e.g., sea level rise, increased frequency of extreme climatic events, increased variability in precipitation regimes) because of their varied and unresolved effects on plant succession.

to longer (e.g., CO_2 enrichment and global warming) time scales than succession, and alter drivers or constraints of succession, respectively (Table 1). A temporal approach to ecology therefore has much to offer in terms of understanding and predicting the impacts of human-induced global change over successional time scales.

Human land use can alter successional trajectories over a much longer time scale than that at which the land use itself occurs. For example, forest succession after agricultural abandonment throughout Europe and North America often involves fewer species and altered understory composition as a result of species pool depletion [47]; and historic, low-intensity land use by Sami in northern Sweden has led to domination by plant species characteristic of fertile environments more than a century after abandonment [48]. Enhanced nitrogen availability, from either land use intensification or atmospheric deposition, also has powerful longer-term effects that are relevant at decadal to century-long successional time scales, such as when nitrophilous herbaceous vegetation is promoted at the expense of successional change to heath vegetation [49]. Further studies of land use effects on successional trajectories can help to prioritize current land management decisions.

Invasions by non-native plant species can similarly influence succession over a much longer time scale than the invasion event itself, both through their contribution to the species pool [17], and their longer-term effects on native species. These effects depend on the attributes of both the invasive and native plants present, and can result in accelerated succession through competitive displacement of early successional plant species [50], decelerated or arrested succession through competitive inhibition of later successional species [51], and deflection of successional trajectories. This latter effect is especially apparent when the invasive plant greatly modifies environmental conditions. For example, in Hawaii, enhanced soil fertility resulting from invasion by the nitrogen-fixing tree *Falcataria moluccana* (albizia) leads to successional pathways dominated by non-native rather than native plant species [52], and invasive grasses promote a fire regime that leads to successional dominance by grasses rather than woody vegetation [53]. Too few studies of invasive species have addressed successional trajectories to enable us to make robust predictions about their long-term ecosystem consequences.

Human-induced increases in atmospheric CO_2 concentrations, such as have occurred over the past several centuries, can constrain successional processes. Although higher CO_2 levels generally increase plant growth, ecosystem-level responses can include altered rates of decomposition or increased N limitation [54], with variable consequences for successional pathways. Short-term experiments suggest that increased CO_2 concentration can arrest succession when it favors fast-growing, early successional species [55]; or accelerate succession when it reduces plant longevities [56], alters plant forms (e.g., when woody plants invade grasslands [57]), or changes plant functions (e.g., when N-fixing plants invade [54]). However, longer-term experiments are needed to determine the successional implications of species changes brought about by increasing CO_2 concentrations.

The alterations in global climate (e.g., increased temperatures and increased variability in precipitation regimes) accompanying atmospheric CO_2 increases will also likely constrain succession. Early successional communities are favored when the frequency and severity of disturbance (e.g., fires, floods, and hurricanes) are increased [58], and where there is an increasing mismatch between climate and plant communities that alters species migration, competitive balance, soil development, and evolutionary processes [59]. For example, secondary forest succession in the eastern USA may be delayed considerably by climate change owing to loss of sensitive species, alteration of competitive regimes, and delay in immigration of late successional species subject to novel dispersal barriers [59]. Landscape-scale spatial and temporal effects are still hard to predict, especially as phenological shifts [60] and ecotonal adjustments [61] will also alter successional responses to climate change in unpredictable ways, although effects of temperature changes are better understood than effects of increased variability of precipitation regimes (Table 1).

Ecological restoration is the manipulation of succession to a desired stage to optimize biodiversity conservation and/or ecosystem services [10,62]. Restoration is too often conducted with little reference to successional dynamics [62]. However, restoration activities can provide valuable insights into temporal drivers and constraints of successional rates and trajectories (Table 1), whereas successional studies can in turn improve restoration effectiveness. Experimental additions associated with restoration activities have helped clarify how phenomena that operate over short-term time scales such as nutrient enrichment, aboveground–belowground feedbacks, and plant life cycles have consequences that are apparent at longer, successional time scales [1,10,11]. For example, successful stabilization of eroded slopes over decades to centuries requires knowledge of the consequences of soil amendments, plant introductions, and competitive interactions [63]. Restoration successes and failures in adjusting to short-term drivers such as land use and invasive species, and long-term constraints such as management legacies and global climate change, help us understand how processes that operate at vastly contrasting temporal scales alter succession [11,64]. In turn, maximal restoration effectiveness can be achieved by its integration into a larger temporal framework of ecological processes.

Concluding remarks and the way forward

We have shown how placing succession in a larger temporal context can help explain some of the complexities of this phenomenon. Succession is an integrator of a range of phenomena that operate over both much shorter and longer time scales than the successional process itself. Although in this article we have focused explicitly on succession, we suggest that the study of any ecological phenomenon can potentially benefit from considering it in an explicit temporal framework, because they are each impacted to a varying extent by processes that occur at different time scales. The application of such a temporal framework for understanding ecological process should recognize the clear positive correlation between temporal and spatial scales [18], as well as the influences of other processes that occur over shorter temporal scales that act as drivers of that process, or those that occur over longer time scales that act as constraints. In particular, succession and other ecological processes of intermediate temporal scale such as intermediate to slow nutrient fluxes and soil formation provide critical linkages between short-term and long-term phenomena that do not have any direct or obvious connection with one another (Figure 1). We know of no other attempts to link major ecological processes across time, nor any that suggest a mechanism through which those links are made.

More generally, we suggest that a greater focus on the role of temporal scale has much to contribute to our understanding of patterns and processes in nature. First, our understanding of processes that have been studied by ecologists at short time scales, including multi-trophic interactions and plant–soil feedbacks, could be greatly enhanced by a more explicit focus on their consequences for longer-term processes such as succession [23]. Similarly, our knowledge of phenomena such as geological processes and macro-evolution that operate over very long time scales can benefit through an enhanced focus on how they impact on shorter-term processes. Second, despite a growing recent focus on ecological networks in which spatial and temporal scales dynamically interact [3], we have yet to develop a clear understanding of the feedbacks that occur between processes that operate at contrasting temporal scales within such networks. Third, our understanding remains incomplete of how succession is influenced by global change phenomena that occur at time scales that are both shorter- and longer-term than succession itself. Therefore, an enhanced understanding of the ecology of global change will benefit by a more explicit integration of this field with that of plant succession. Ultimately, temporal frameworks that draw from multiple disciplines that collectively encompass a broad spectrum of scales over time and space have considerable potential to clarify ecological processes and their responses to a changing global environment.

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