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A comprehensive framework for vegetation succession

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Abstract

Succession is defined as a directional change in species populations, the community, and the ecosystem at a site following a disturbance. Succession is a fundamental concept in ecology as it links different disciplines. An improved understanding of succession is urgently needed in the Anthropocene to predict the widespread effects of global change on succession and ecosystem recovery, but a comprehensive successional framework (CSF) is lacking. A CSF is needed to synthesize results, draw generalizations, advance successional theory, and make improved decisions for ecosystem restoration. We first show that succession is an integral part of socio-ecological system dynamics and that it is driven by social and ecological factors operating at different spatial scales, ranging from the patch to the globe. We then present a CSF at the local scale (patch and landscape) at which succession takes place and explain the underlying successional processes and mechanisms operating at that scale. The CSF reflects the increasingly broader perspective on succession and includes recent theoretical advances by not only focusing on species replacement but also on ecosystem development, considering succession as part of a socio-ecological system, and taking the effect of past and current land use, the landscape context, biotic interactions, and feedback loops into account. We discuss how the CSF can be used to integrate and synthesize successional studies, and its implications for ecosystem restoration.

KEYWORDS
biotic interactions, community, conceptual model, disturbance, ecosystem, land use intensity, landscape, socio-ecological system, spatial scale, succession

INTRODUCTION

Succession can be defined as a directional change in species populations, the community, and the ecosystem at a site over time after a disturbance has deposited a new substrate (i.e., primary succession) or removed (part of) the vegetation and soil (i.e., secondary succession). It is a fundamental concept in ecology because it explains ecosystem development over time, and because it links and integrates different ecological disciplines such as functional, population, community, systems, and landscape ecology (Pickett et al., 2011). This concept has become more crucial in the Anthropocene because widespread global change, including land use change and climate change, modifies environmental conditions and disturbance regimes, thus leading to vegetation change (Walker & Wardle, 2014). An improved understanding of succession is, therefore, urgently needed to predict the effects of global change on succession and ecosystem recovery. Such an improved understanding provides the basis for ecosystem restoration because it allows us to predict where natural regeneration and succession are possible within a reasonable time frame, where assisted regeneration is needed to accelerate succession, and how restoration practices can be tailored to local site conditions using ecological principles (Temperton et al., 2004; but see Rapson, 2023).

Succession has been studied for over a century, and since the pioneering work of Clements (1916), significant conceptual and empirical advances have been made, which have been summarized in excellent reviews that have focused on succession in general (Glenn-Lewin et al., 1992), successional theories (Pickett et al., 2011; Poorter et al., 2023), empirical evidence (Connell & Slatyer, 1977; Drury & Nisbet, 1973), feedback loops and variation in successional pathways (van Breugel et al., 2024), primary succession (Walker & Del Moral, 2003), temperate old-field succession (Meiners, Pickett, et al., 2015), tropical grassland succession (Peterson & Carson, 2008), and different disturbance types across the world (Prach & Walker, 2020). Over time, there has been a gradual development in our thinking of succession. Four broad periods can be distinguished, reflecting the main(stream) view of succession of that time (Poorter et al., 2023). The four successional views are succession of plants (from 1910 onwards), succession of communities and ecosystems (from 1965 onwards), succession in landscapes (from 2000 onwards), and succession with people (from 2015 onwards). These views increase in organizational and spatial scale and scope, and reflect the increasingly broader perspective and understanding of succession over time.

Despite these important conceptual advances, a comprehensive successional theory is currently lacking. This is partly because of the heterogeneous nature of succession, where many factors are involved and many different successional pathways are observed across different ecosystems (Clements, 1916; Prach & Walker, 2020) and within sites (Norden et al., 2015; Vandermeer et al., 2004). Part of the heterogeneity of successional pathways is because succession is not only driven by nature, but also by humans, who have a large impact on succession but are often ignored by ecologists. Succession is therefore the result of a complexity of factors that can be best evaluated using a socio-ecological system (SES) approach (Balvanera et al., 2021). Part of the successional heterogeneity can also be explained by the fact that succession is not only driven by proximate factors that directly affect succession in the field, but also by ultimate social and ecological factors that operate at different spatial scales, and that provide the different templates within which successional development unfolds (Meiners, Cadotte, et al., 2015). A comprehensive theory is also lacking because researchers have focused on different successional processes, on different ecosystems that are characterized by other disturbance factors and environmental constraints, have measured different response variables, and used different terminology. As a result, scholars have fundamentally different views on succession (Pickett et al., 1987b). The use of a common, comprehensive successional framework (CSF) is a prerequisite to combine the different views and advance successional theory. It will help to identify the key drivers of succession in different ecosystems, make explicit what part of the successional process is studied, and what not, increase comparability across studies, and serve as a vehicle for integration and synthesis (Pickett et al., 1987b). From a practical viewpoint, a CSF can be used to identify the main ecological and socioeconomic bottlenecks constraining succession, the main drivers accelerating succession, and which key management interventions can steer successional development toward the desired management goals (Temperton et al., 2004).

This study aims to present a CSF that reflects a broadening perspective on succession. First, we present a broader view of how succession is shaped by the SES, in which social and ecological factors operating at different spatial scales (from the globe to the patch) determine together successional development (Figures 1 and 2). Second, we zoom in on the local scales (landscape and patch) where vegetation succession actually takes place and present a CSF that explains the underlying processes and mechanisms operating at that scale (Figure 3). To this end, we build on the hierarchical framework of Pickett et al. because it focuses on the three main drivers of succession, and because of its flexible nature, it can provide both generalization and local realism. We expand the framework by including recent advances and elements from different successional theories and explain how different mechanisms may affect the pace and direction of succession. Finally, we discuss how this framework can be used to integrate and synthesize successional studies, and its implications for ecosystem restoration. The successional framework is generally applicable to all types of succession, but we illustrate it using forest succession as an example, because it encompasses a long and complete successional trajectory from annual herbs up to trees. We enrich this using important successional examples from other ecosystems.

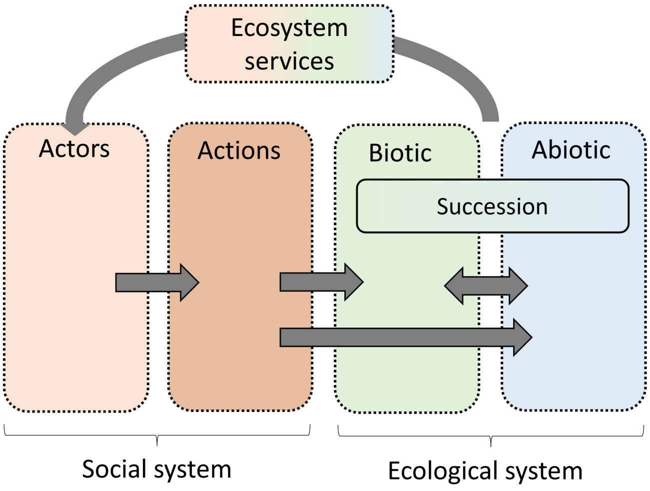

FIGURE 1 Succession is the consequence of dynamics in a socio-ecological system (SES). The SES consists of different systems (dotted boxes): a social system (orange, left), and an ecological system with biotic (green, middle) and abiotic components (blue, right). Human actions ("actions," brown box) affect the ecological system, and the ecological system provides ecosystem services (also known as nature's contributions to people, orange–green–blue box) to the social system. Interactions among the systems are indicated by arrows.

A CSF: INTEGRATING ECOLOGY AND SOCIETY

In this section, we provide the bigger picture of succession. Succession is a natural process occurring at the patch and landscape scale. It can perfectly occur without human intervention, following a natural disturbance. Yet, to better understand how humans affect ecosystem recovery in the Anthropocene, we first explain that it is important to consider succession as an integral part of SES dynamics (Figure 1) and then how succession is driven by ecological factors (Figure 2, right side) and social factors (Figure 2, left side) operating at different spatial scales.

Succession is an integral part of the dynamics of a SES

A SES (e.g., Díaz et al., 2011; Ostrom, 2009) consists of a social system and an ecological system that are interdependent and connected by complex interactions. The social system includes actors (Figure 1, pink box) and actions (brown box), and the ecological system includes the biotic components (green box) and abiotic components (blue box) (Figure 1). Succession is an integral part of SES dynamics because human actions, such as land use change and management interventions, affect the ecological system, leading to the availability of new sites where succession can take place (i.e., with the original biotic community partially removed) or to changes in the biotic and abiotic environment, which may change the course of succession. Even new sites that are only the result of natural disturbances (e.g., volcanic eruptions, landslides) may be soon influenced by human activities. Human actions can either facilitate succession, through land abandonment and restoration, or constrain succession, through overexploitation and degradation. Succession, in turn, as part of the ecological system, provides specific ecosystem services (also known as nature's contributions to people, pink-green-blue box) or disservices (shade, weeds, pests) to the actors in the social subsystem. Four types of ecosystem services can be distinguished: supporting services, which provide habitat to different species; regulatory services, which regulate the microclimate and carbon, water, and nutrient cycles; provisioning services, which provide goods and services to people; and cultural services, which comprise recreational, spiritual, and educational values to people (Díaz et al., 2019). Many of the human actions in the ecological subsystem, as well as the kind of

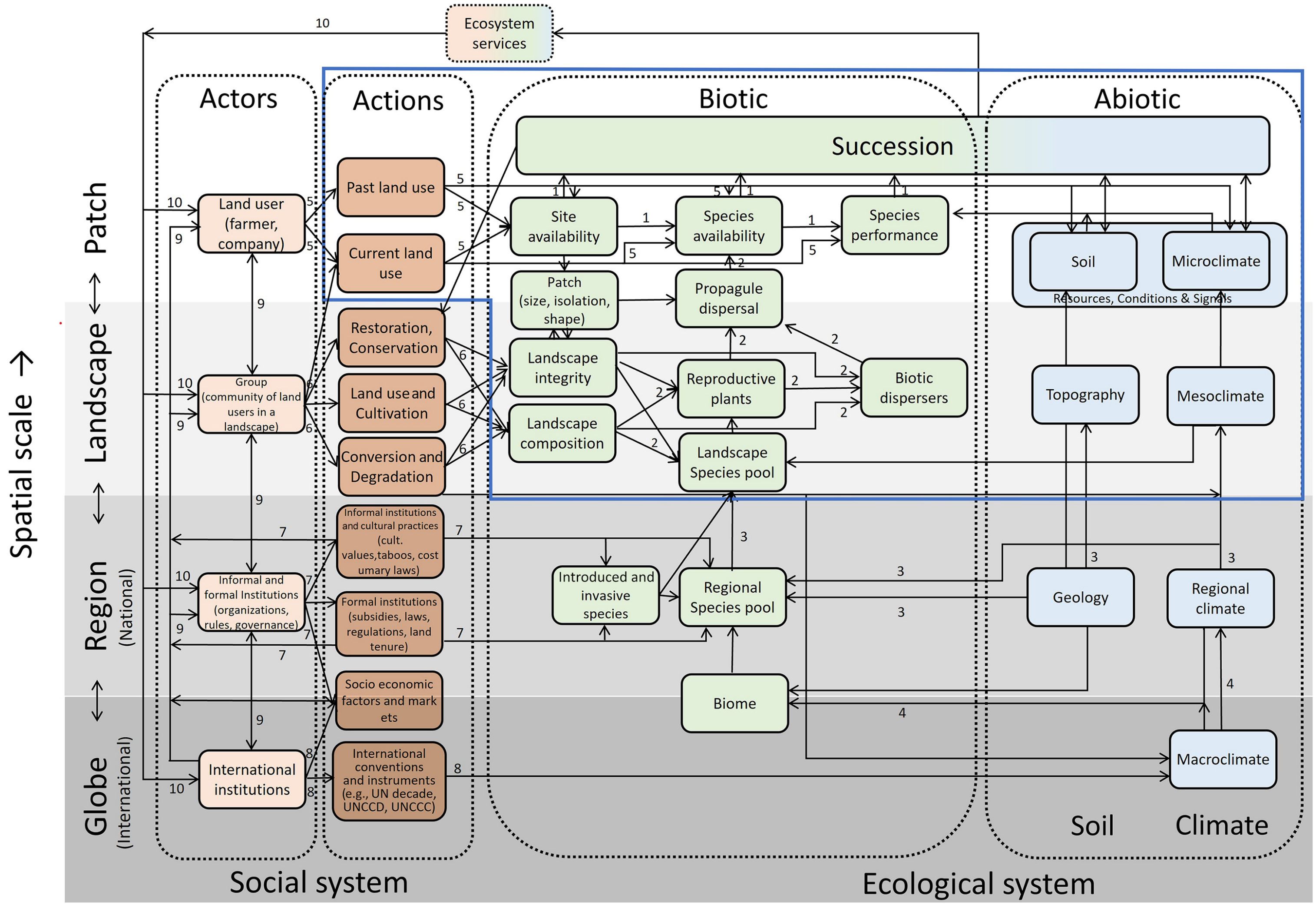

FIGURE 2 Succession is driven by proximate and ultimate factors in a socio-ecological system (SES) operating at different spatial scales. The SES consists of different systems (dotted boxes): a social system (orange, left), and an ecological system with biotic components (green, middle) and abiotic components (blue, right). Human actions ("actions," brown boxes) affect the ecological system, and the ecological system provides ecosystem services (also known as nature's contributions to people, orange–green–blue box) to the social system. Interactions among the systems are indicated by arrows. Succession takes place at the patch and landscape scales, but it is also driven by societal and ecological factors operating across larger spatial scales (*y*-axis). Spatial scales refer to the global, regional, landscape, and patch scales (from bottom to top, gray-shaded bands) at which actors, factors, and processes are operating. Human actions affect the ecological subsystem ("actions," brown boxes), and the ecological subsystem provides ecosystem services to the social subsystem at different spatial scales. Actions can be carried out at all spatial scales. Interactions are discussed in the text, referring to the numbers provided. Based on this overview, we present in Figure 3 a comprehensive successional framework that zooms in on the patch and landscape scales (the blue frame).

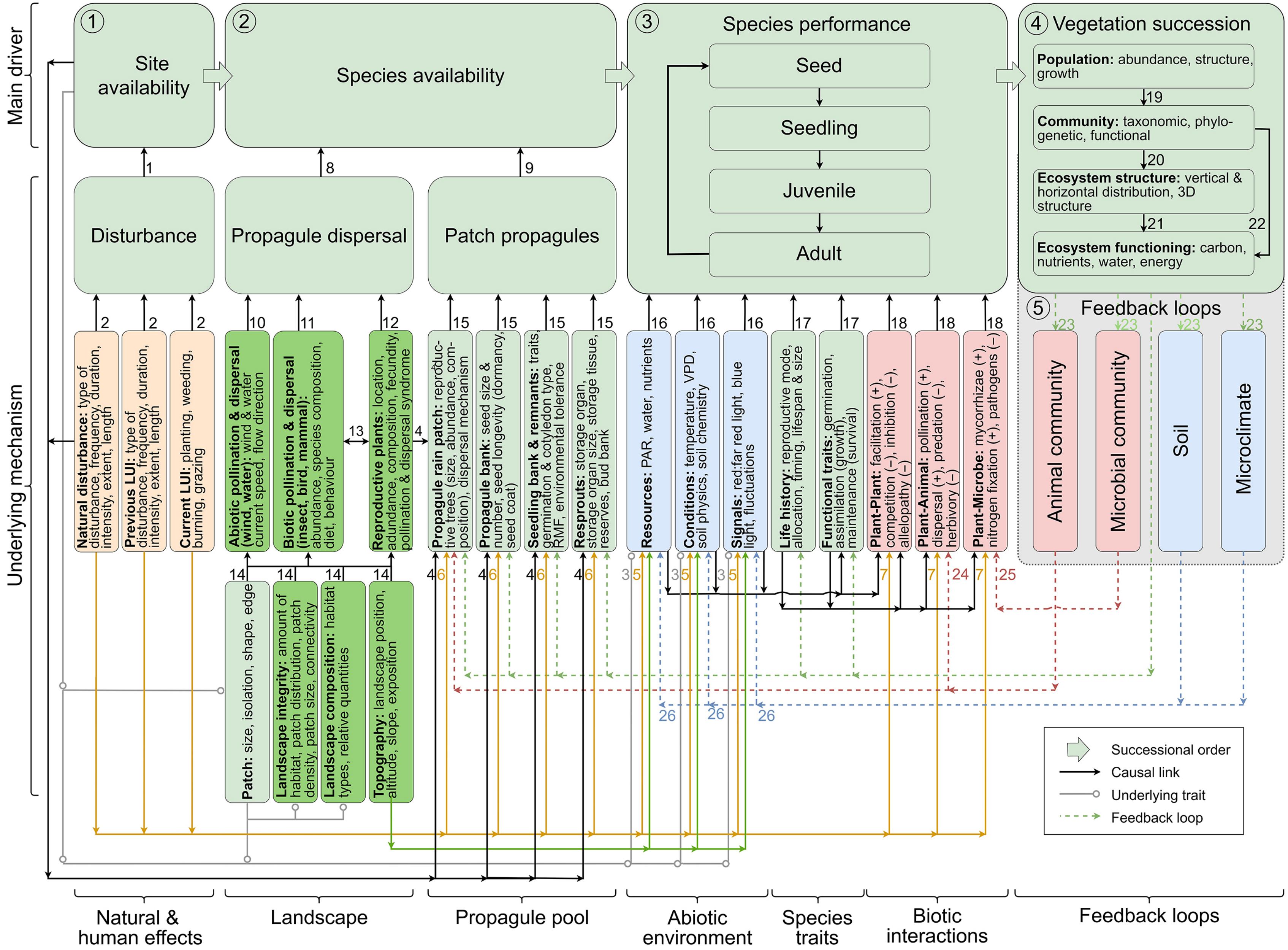

FIGURE 3 Legend on next page.

FIGURE 3 A comprehensive successional framework focusing on the patch and landscape scales. Vegetation succession in a patch is the result of three general drivers that initially operate sequentially over time: (1) site availability, (2) species availability, and (3) species performance (top-level light-green boxes). Each of these drivers is affected by underlying mechanisms (lower level light-green boxes). Site availability is determined by natural or human disturbances before and after the onset of succession (orange boxes). Species availability is determined by propagule dispersal to the patch, which is determined by factors operating at the landscape scale (darker green boxes), and by propagule availability in the patch. Species performance refers to performance at different stages of a plant's life cycle (seed, seedling, juvenile, and adult; top box). Species performance is determined by the abiotic environment (resources, conditions, and signals; blue boxes), species traits (life history, and other functional traits; light-green boxes), and biotic interactions (plant–plant, plant–animal, and plant–microbe; red boxes). Differences in species availability and species performance lead to (4) vegetation succession at different organizational scales (population, community, and ecosystem structure and functioning). Successional changes in the vegetation are associated with successional changes in the biotic environment (animal community, microbial community; red boxes) and the abiotic environment (soil, microclimate; blue boxes). These cause (5) feedback loops (dashed lines) affecting different parts of the system, thus accelerating or inhibiting successional change. Large arrows indicate the main causes of succession. Small arrows indicate cause–effect relationships, while lines ending with open dots indicate associated variables. Arrows are color-coded in the same way as the factors where they are coming from. The numbers next to the arrows refer to relationships that are referred to in the text. See Appendix S1: Figure S1 for a simplified version of the conceptual diagram for communication purposes.

actions, are motivated by the type of ecosystem services they want to obtain.

Succession is driven by ecological factors operating at different spatial scales

Succession is driven by socio-ecological factors operating at different spatial scales, ranging from the patch to the globe. Here, we group the different spatial scales into four categories: the patch, landscape, regional, and global scales (Figure 2, from top to bottom, gray-shaded bands) at which factors, actors, and processes are operating. Succession occurs at the patch scale (several square meters to hectares) when disturbance creates an open space followed by regrowth of the vegetation (Figure 2, arrows 1). Patches may range from a few square meters in the case of a small canopy gap disturbance to hectares in the case of a large-scale fire disturbance. Succession is directly influenced by the landscape scale (hectares to several square kilometers) where the vegetation surrounding the patch determines the amount and diversity of reproductive plants and the frequency and behavior of dispersal vectors such as mammals and wind that enable seed dispersal into the patch (Figure 2, arrows 2). Succession is indirectly influenced by factors operating at the regional scale (hundreds to thousands of square kilometers) where regional climate, geology, and biogeography determine the regional species pool and productivity (e.g., the rate of regrowth). Together, these factors provide the biophysical setting in which succession occurs (Figure 2, arrows 3). Different settings lead to different successional pathways, as the abiotic conditions, available resources, and species traits set the magnitude, pace, and direction of succession (Meiners, Cadotte, et al., 2015; Odum, 1969). As a result, successional pathways vary widely along broadscale environmental gradients, even within the same vegetation type, such as temperate grasslands (Prach et al., 2014; Wright & Fridley, 2010) or tropical forests (Poorter et al., 2019, 2021). Finally, at the global scale (150 million km^2), the macroclimate varies because of latitude, elevation, and continentality. Human-induced climate change triggers shifts in the distribution of individual species or entire biomes and disturbance regimes, with large consequences for succession (Figure 2, arrows 4).

Succession is driven by social factors operating at different spatial scales

Succession is driven by proximate causes that directly affect succession at the patch scale (e.g., management decisions) and by ultimate causes, that is, the socioeconomic factors and processes that underlie the proximate causes (e.g., national or international policies, and the market price of commodities). This social dimension is especially important in the Anthropocene when human actors operating at local to global scales significantly impact all aquatic and terrestrial ecosystems. Our SES approach to succession recognizes that people affect the ecological subsystem through their actions, and that the ecological subsystem provides ecosystem services (Figure 2, dark green box) to actors at different spatial scales. Understanding the social dimension is also important to comprehend and evaluate the outcome and effectiveness of conservation and restoration initiatives that aim to bend the curve of biodiversity loss (Leclère et al., 2020), restore ecosystems, and mitigate climate change.

For example, at the patch scale, land users such as small holders or agricultural enterprises may facilitate succession through land abandonment, tree planting and protection, or constrain succession when past or current land use was or is intense or when agrochemical and fire use was or is too high (Jakovac et al., 2021) (Figure 2, arrows 5).

At the landscape scale, groups of land users, such as local communities or interest groups, decide or steer land use and management. They either transform the natural ecosystem and cultivate the land (thus affecting site availability); manage natural ecosystems to facilitate succession through conservation and restoration; or inhibit or constrain succession through vegetation conversion or degradation (Figure 2, arrows 6). Land use decisions are often regulated through informal institutions and cultural practices, such as customary use laws (e.g., local agreements on land use rights, Figure 2, arrow 7) and through nongovernmental organizations, which coregulate and impact the activities of groups and land users. All these land use decisions shape landscape composition (i.e., different land use types and their relative cover area) and landscape integrity (i.e., the quality, size, and connectivity of the patches), which influence the landscape species pool. Intact landscapes consisting of natural vegetation may have a species pool dominated by many (late-successional) habitat specialists, whereas fragmented landscapes with little, scattered natural vegetation may have a species pool dominated by a smaller group of (early-successional) habitat generalists (Arroyo-Rodriguez et al., 2017) (Figure 2, arrows 2). Fragmented landscapes may also have more non-native invasive species due to (un)planned species introductions and because frequent disturbances and bare soil provide many opportunities for the establishment and spread of invasive species, which affect species composition and even ecosystem functioning at the patch and landscape scales (Meiners, Pickett, et al., 2015).

At the regional scale, institutions such as organizations, rules (laws and regulations), or governance regulate human actions. The regional level often coincides with the national level and may therefore include formal national governmental institutions and their rules and incentives (subsidies).

Finally, at the global scale, international institutions such as the United Nations (UN) foster international conventions and instruments, such as the United Nations Framework Conference on Climate Change, the Sustainable Development Goals, the Decade of Ecosystem Restoration, the Convention of Biological Diversity, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, and the Bonn Challenge. These initiatives aim to mitigate climate change through forest and landscape restoration, and to bend the curve of biodiversity loss through restoration (Figure 2, arrows 8, 9).

Although local actors are the proximate drivers of succession, they are influenced by actors who operate at higher levels of organization such as industries, governments, or international organizations (Figure 2, arrows 9). Generally, actors at higher levels of governance influence local actors by setting the legal framework (e.g., policies and regulations) that enables or constrains local actors from conducting certain activities on their land, and by shaping the socioeconomic conditions that affect local livelihood options (e.g., by fostering specific productive activities, imposing trade barriers and agreements, tariffs and markets, migration by socioeconomic instability). Local actors also influence higher level governance by social movements that act collectively, several examples of which are now appearing in the context of locally led restoration, for example, regreening in the Sahel (Reij et al., 2009), or the agroecology movement in Zona da Mata in Brazil (Cardoso et al., 2001). Generally, top-down effects are stronger than bottom-up ones because of asymmetries in power, knowledge, capital, and influence (Giller et al., 2008). Often, actors operating at different levels are interested in different ecosystem services (Figure 2, arrows 10) (Schweizer et al., 2019). Local land users and groups are mainly interested in production services (such as agriculture, timber, and non-timber forest products), in the regulatory services that underpin it (i.e., healthy productive soils and water availability), and in the cultural services as certain landscapes provide them with a sense of belonging. In contrast, regional and global organizations that focus on sustainability are more interested in habitat services (biodiversity conservation), climate regulation at the regional scale (e.g., the Amazon Forest re-transpiring water, thus providing orographic rainfall to the Andes), and climate change mitigation at the global scale (i.e., carbon storage and sequestration). There is therefore often a misalignment in the interests, narratives, and distribution of costs and benefits among actors operating at different spatial scales, which hampers the successful implementation of ecosystem restoration (Schweizer et al., 2019). Interactions between social and ecological systems may be strongest when they occur at the same spatial scale (i.e., horizontal arrows), and policy interventions should therefore be carried out at the appropriate scale of interest.

CSF AT THE PATCH AND LANDSCAPE SCALES

Zooming in on the blue frame in Figure 2, we now present a CSF to study succession at the patch- and landscape scales, as these are the spatial scales at which succession takes place. We further develop the conceptual framework of Pickett et al. (1987a, 1987b, 2011, 2013) and expand it to include recent advances that have broadened the concept of succession and better explain the underlying mechanisms. See Meiners, Pickett, et al. (2015) for an example of temperate old-field succession. We use Pickett's framework as a starting point because it (1) provides a rather broad understanding of succession, (2) is straightforward and simple because it focuses on the three main sequential causes of succession (site availability, species availability, and species performance), (3) is universally applicable, (4) can easily be adjusted by selecting that subset of factors that is relevant for local succession, (5) is sufficiently general to include multiple (sub)theories and to accommodate new ones, and (6) allows to go for both generality and local realism (i.e., site- and situation specific). We expand the framework by including elements from different successional theories and recent advances. For example, we include the effects of different spatial scales (Arroyo-Rodriguez et al., 2017), organizational scales such as the ecosystem and SES (Balvanera et al., 2021; Odum, 1969), time scales (Meiners, Cadotte, et al., 2015; Walker & Wardle, 2014), and land use and management (Jakovac et al., 2021). We will incorporate the human dimension by including the role of past and current land use, and by including the landscape context, which is often modified by humans. The framework is generally applicable to vegetation succession, and we will use forest succession to illustrate how the framework can be applied because it presents one of the longest successional gradients (>100 years) with a complete turnover in life forms, from annual herbs to trees. We specifically use examples from tropical forests because they often present more complex successional dynamics due to their high species diversity and structural complexity, and stronger coevolution between plants, pollinators, and dispersers. Where relevant, we also use examples from other ecosystems.

Vegetation succession is a process that results from three main proximate drivers that initially operate sequentially over time: (1) site availability, (2) species availability, and (3) species performance (Figure 3, top row). These three drivers ultimately lead to changes in (4) populations, the community, and ecosystem, and hence to vegetation succession. Successional changes in abiotic conditions and the biotic community lead to (5) feedback loops, which fuel or constrain the speed of succession and modify successional pathways. Each of these three main drivers is driven by underlying mechanisms and factors, as indicated in the lower level boxes (Figure 3, bottom rows). A mechanism indicates the cause of change (e.g., propagule dispersal), whereas a factor is an independent variable that drives change (e.g., landscape forest cover, which affects seed dispersers). In Appendix S1, we present a simplified version of the CSF which is easier to use for educational purposes.

SITE AVAILABILITY

Site availability is determined by disturbances (Figure 3, arrow 1). Disturbances can be classified as natural disturbances such as windstorms and landslides (pink box, arrow 2), and human disturbances such as past and current land use (pink box, arrow 2). New sites can become available through a disturbance, followed by its cessation (e.g., land use followed by land abandonment).

Disturbance

A disturbance is defined as a sudden, discrete event such as a windstorm, fire, herbivory, or clearing for agriculture that removes part of the aboveground vegetation and or soil, which changes the site and, hence, the abiotic conditions (i.e., more light reaches the soil, more nutrients become available when leaf and stem litter decompose; Figure 3, arrow 3). This creates new open sites available for plant establishment. The succession that follows is called *secondary succession* because there was vegetation before and many legacies of the previous vegetation are present, such as soil development and propagules. Secondary succession is in general a relatively fast process because these legacies can kick-start succession, although in some cases, succession can get arrested when a single life form dominates the patch (ferns, grasses, lianas), thus preventing species replacement. In contrast, when disturbances lead to the deposition of new substrate (such as volcanic lava streams, meandering rivers, or coastal dune formation) or remove soil material resulting in newly exposed substrates (such as landslides, retreating glaciers), then little or no legacies are present (Walker & Del Moral, 2003). The succession that follows is called *primary succession* because it starts from scratch on bare parent material. Primary succession is generally a much slower process because it depends on species immigration and soil formation (Walker & Del Moral, 2003). In reality, the distinction between primary and secondary succession is not so clear-cut, as there is a continuum in disturbances that result in a continuum of legacies (ranging from 0 to nearly 100%) (Walker & Del Moral, 2003). For example, lava flows may not affect the whole area but may leave some ridges untouched, resulting in a fine-scale mosaic of vegetated and unvegetated patches. Disturbances can have natural causes or human causes (see below). Disturbances can not only vary in type, but also in the size, intensity, frequency, timing, and temporal pattern, leading to different abiotic conditions in the newly available site (Figure 3, arrow 3) that allow different species from the propagule pool to establish and dominate the patch (arrows 4, a propagule refers to a plant reproductive unit), thus resulting in different successional pathways (cf. Bazzaz, 1984). The timing of disturbance is especially important in more seasonal or variable environments (spring vs. fall, dry vs. wet period, dry vs. wet years) where it strongly determines abiotic conditions (arrow 3), resource availability (arrow 3), and species availability (arrows 3 and 4) of the newly available site, thus leading to different successional pathways (Meiners, Pickett, et al., 2015). Temporal patterns in disturbances can be classified as pulses, presses, and ramps (Lake, 2000). Pulses are short-term and sharply delineated disturbances, such as a windthrow or a fire. Presses are disturbances that may arise sharply, and then reach a plateau that is maintained, such as sedimentation by rivers. Ramps may steadily increase over time, such as the cumulative effect of a prolonged drought (Lake, 2000). Similarly, plant and vegetation responses may show a pulse, press, or ramp shape over time (cf. Lake, 2000). In plant ecology, presses and ramps are often considered stressors, which reduce plant growth and performance (Grime, 2006), and may gradually but not abruptly lead to mortality.

Natural disturbances

Natural disturbances are caused by the elements (earth, wind, fire, water) and by the biotic community (e.g., through defoliation by insects or grazing by ungulates). Natural disturbances that lead to primary succession are volcanic eruptions, lava flows, glacier retreat, landslides, dune formation, and meandering rivers (Prach & Walker, 2020). Natural disturbances that lead to secondary succession are windstorms, fires, floods, herbivory by grazers (e.g., ungulates), or insect pests (e.g., bark beetle leading to forest dieback). These different disturbance types vary in frequency, scale, and intensity and have therefore different impacts on succession. For reviews, see Walker and Del Moral (2003) for primary succession, Chazdon (2014) for tropical forest succession, and Prach and Walker (2020) for succession in different biomes across the world. The absence of disturbance can also affect succession. For example, in fire-prone regions, fire suppression can lead to buildup of fuel load, larger stand-replacing disturbances once there is a fire, and different successional pathways afterwards. Because human activities at different spatial scales lead to climate change and land use change (Figure 2), the natural disturbance regimes are also shifting, leading to different successional pathways.

Previous land use intensity

Humans affect succession through previous and current land use intensity (LUI, pink boxes). LUI is the extent to which the original abiotic and biotic environment is being used and modified and is the main way the social system directly affects succession in the ecological system (Figures 1 and 2). There are several types of human disturbances that sometimes lead to novel habitats, as is the case of mining. For a review, see Prach and Walker (2020). Here we focus on agriculture (e.g., crop fields, cattle ranching) as the most widespread type of land use, comprising one third of the terrestrial land cover (Watson et al., 2019). Past LUI increases with the duration of use (years since first use), extent (in hectares), frequency (e.g., number of crop production cycles, frequency of plowing or burning), intensity (e.g., the amount of external inputs such as fertilizers, irrigation, machinery, herbicides and pesticides, or the stocking density), and length (months per year that crops are cultivated or that the pasture is grazed by cattle) (Jakovac et al., 2021). Low LUI, such as extensive rangeland grazing, may retain remnant forest species along streams and as scattered trees, while moderate LUI may increase soil functioning, for example, when litter and exudates by grassroots increase the soil organic carbon in pastures (Veldkamp et al., 2020). However, a high LUI may generally further degrade the environment (eutrophication, acidification, aridification, desiccation, erosion, degradation, and contamination) (Figure 3, arrows 5) and deplete the patch propagule pool, such as the seedbank, seedling bank, and resprouts (arrows 6). This may slow down or arrest succession for years to decades (Goosem et al., 2016; Suazo-Ortuño et al., 2015) and result in deviating (deflected) successional pathways (Jakovac et al., 2016) or only partial recovery in ecosystem functioning (Bauters et al., 2022). In general, in shifting cultivation systems, soils recover faster from agricultural use in productive areas (high rainfall, soils with active clays) compared with less productive areas (low rainfall, soils with inactive clay), and when the previous land use has been less intense (e.g., small-scale crop fields that have been used for a short period of time rather than pastures that have been used for a long time) (van der Sande, Powers, et al., 2023).

Current LUI

Land users often do not completely abandon their lands, resulting in secondary forests that are actively managed and used. For example, in many tropical shifting cultivation systems, there is a gradual transition from the agricultural phase to the fallow phase, in which the first trees and herbaceous plants establish naturally while people are still actively using the land. Later successional stages are also often used for the collection of fuelwood, medicinal plants, or cattle grazing (Lohbeck et al., 2020). Although often overlooked by field ecologists, these current land use practices may strongly shape succession. For example, farmers may affect patch propagules by unintentionally dispersing seeds through fruit consumption or by introducing domesticated species (Figure 3, arrows 6); also, they intervene in plant–plant interactions by weeding competing species, promote the growth of desired species by pruning, affect plant–animal interactions through herbivory by grazing livestock or burning of pastures, and modify plant–microbe interactions by inoculating the soil with mutualistic mycorrhizal fungi (Levis et al., 2018) (Figure 3, arrows 7). Consequently, farmers may actively modify the composition of regenerating species with their land use (Lohbeck et al., 2020).

SPECIES AVAILABILITY

The second main driver of succession is species availability. The speed and direction of succession are generally more strongly determined by species availability than by the environmental requirements of the plant species (Gleason, 1926; Palma et al., 2021). Species availability is determined by propagule dispersal to the patch (Figure 3, arrow 8) and by the propagules in the patch that have survived the disturbance event (arrow 9). The order of species colonization is important, as it may determine the sequence of facilitative, neutral, or inhibitory actions, and such priority effects of arrival may therefore determine subsequent successional pathways, and the heterogeneity in successional pathways observed within a site (Fukami, 2015; Pickett et al., 2011; van Breugel et al., 2024).

Propagule dispersal

Species arrive in the patch through dispersal of their propagules (i.e., reproductive units such as seeds and spores). Propagule dispersal from surrounding areas to the successional patch is determined by factors operating at the landscape scale (dark green boxes) and depends on the presence, abundance, and productivity of reproductive plants (Figure 3, arrow 11), the biotic (arrow 12) and abiotic (arrow 10) pollination of the flowers, the availability of dispersal agents, and on landscape factors (arrows 14).

Reproductive plants

Reproductive plants provide the propagules coming from outside the patch (arrow 12). Propagule availability depends on the species composition in the landscape, and increases with species abundance, plant fecundity (i.e., number of propagules produced per plant), and proximity to the patch. Seed formation depends on successful pollination, the pollinator availability in the landscape (arrow 13), and the plant pollination syndrome. The spatial and temporal display and arrangement of flower features and rewards attract or facilitate specific pollination vectors such as wind, insects, birds, or bats. Subsequent seed dispersal depends on the plant dispersal syndrome (i.e., the display and arrangement of fruit features and rewards) that attracts or facilitates specific abiotic and or biotic dispersal vectors (Figure 3, arrow 13).

Biotic pollination and dispersal

Biotic pollination is done by coevolved organisms and guarantees successful pollination and outcrossing. Pollination is generally done by smaller organisms such as insects (bees, trips, wasps, beetles) that also have smaller home ranges, but also often by larger sized birds and bats. Biotic dispersal can be done through ingestion (endozoochory), the external attachment of seeds to the animal body (exozoochory), or through scatter-hoarding (synzoochory). The mutualistic relationship between plants and dispersers is generally less tight than the relationship with pollinators, as fruits can be eaten by many species, although larger frugivores tend to consume larger fruits (Figure 3, arrow 13). Biotic pollination and dispersal are especially important in tropical forests, where plant species occur in low densities, food sources are available year-round, and where there has been strong coevolution because of an evolutionary stable environment. In temperate zones, insect pollinators become important after a few years of succession when perennial herbs dominate the vegetation, whereas biotic dispersal becomes more important when woody lianas, shrubs, and trees dominate the vegetation (Meiners, Pickett, et al., 2015). Disperser success is determined by the abundance, composition, behavior, dietary preferences, and seed-depositing behavior of biotic dispersal vectors (Dennis & Westcott, 2006; Dent & Estrada-Villegas, 2021). The interaction between seed plants and dispersers then depends on the fruit traits of the plants and the traits of the animal species, such as gape width (i.e., the internal width of the bill), dietary preferences, and body size (arrow 13) (Dent & Estrada-Villegas, 2021; Lambert et al., 2005). The importance of animal dispersers for succession has been emphasized during the last decades, as the global decline of habitat area, landscape integrity, and animal abundance has made people more aware of the importance of dispersers for plant community assembly. During temperate and tropical forest succession, the contribution of animal dispersers increases over time, as animals need habitat structure for food, perching (in the case of birds), or protection (Meiners, Pickett, et al., 2015). In tropical forests, the relative importance of different dispersal modes is predicted to change during succession: bats are especially effective in open environments, and their importance declines during succession. In contrast, birds and nonvolant mammals prefer a structurally more complex habitat and later successional plant species as their food source, and their contribution to the seed rain increases during succession (de la Peña-Domene et al., 2014; Dent & Estrada-Villegas, 2021).

Abiotic pollination and propagule dispersal

Wind pollination and wind dispersal are common phenomena among mosses, ferns, gymnosperms, grasses, and temperate plant species. Wind speed and dispersal distance tend to be higher in open landscapes and forest edges, and as a result, wind dispersal is important early in succession when the vegetation is dominated by annual herbs and grasses, and declines over time when the vegetation becomes more dense (Meiners, Pickett, et al., 2015). Vegetation patches with locally low canopy height result in updraft wind, a larger chance to escape the canopy, and larger dispersal distances (Bohrer et al., 2008). Water dispersal depends on buoyancy (the time the seed is able to float) and flooding frequency and duration.

Landscape factors

The abundance and composition of reproductive plants and biotic pollination and dispersal vectors are, in turn, determined by landscape characteristics (Figure 3, arrows 14). *Patch characteristics*, such as patch size and patch proximity to other habitats, determine the likelihood of arrival of different species and ultimately the rate at which succession occurs (Sloan et al., 2016). The *landscape composition*, such as the amount of different habitats (e.g., natural and anthropogenic) and their relative area, determines the habitat suitability for different plant and animal species. The *landscape integrity*, such as the number and size of patches and their connectivity indicates how easy it is to move across these landscapes for mammals, birds, and insects with different body sizes and determines wind speed and, hence, abiotic dispersal. The *topography* is also important, as the water availability and climatic exposure determine the suitability of the habitat for different species, and the slope and landscape position of the patch determine the easiness with which vectors can move through the landscape. In general, flower pollination, seed dispersal, and successional speed increase when the patch is larger, the landscape composition consists of more natural habitats, and the landscape integrity is high (Arroyo-Rodriguez et al., 2017).

Propagule availability in the patch

Species availability within the successional patch depends not only on propagule dispersal from surrounding areas to the patch, but also on the propagule pool that survived disturbance and is therefore already present in the patch. The propagule pool at the patch level consists of the local propagule rain from within the patch, the seed bank, the seedling bank, resprouts, and other remnant plants (Figure 3, arrows 15).

Propagule rain within the patch

Local seed rain from within the patch increases over time when individuals attain a reproductive size and start to reproduce. Short-lived light-demanding herbaceous and woody pioneer species are the earliest ones to reproduce, but they often have specific requirements for germination and establishment (Grime, 2006). Although they may account for a large share of the local seed rain, they will contribute over time increasingly less to regeneration, because the environmental conditions have changed, and become inappropriate for the establishment of early-successional pioneers (Connell & Slatyer, 1977).

Instead, seeds produced by these pioneer species may contribute to regeneration elsewhere in space or time, for example, at the edge of the expanding patch. The seed rain of longer lived shade-tolerant tree species will increase more slowly over time, but these seeds will contribute more to local regeneration in the long term.

Propagule bank

The seed bank tends to be dominated by small-seeded pioneer species that produce seeds in massive numbers. Hence, these pioneer species do not only disperse in space but also in time (i.e., when they persist in the seedbank), which enhances their chance to be present once a canopy gap in the vegetation is formed. Entrance in the seed bank is enhanced by small, compact, and smooth seeds that facilitate seed burial and the escape from seed predators (Thompson et al., 1993). Seed longevity and persistence in the seed bank are facilitated by a hard seed coat, desiccation tolerance, dormancy, and special germination triggers (see below). Some tree pioneer seeds can persist in the seed bank and stay alive for up to 50 years (Dalling & John, 2008) or their seed bank is maintained through continuous seed input. Seed banks are especially important for herbaceous plants (e.g., annuals, grasses) and in (temperate) seasonal environments where seeds survive the harsh seasons in dormant stage, and only start to germinate when environmental conditions are favorable (such as winter and spring annuals and therophytes) (Grime, 2006).

Seedling bank and remnant plants

In closed forest communities, many seedlings wait and persist in the understory as advanced regeneration until a disturbance creates a canopy gap. This seedling bank gives those species a size advantage and a head start over plants that germinate only after the disturbance. Species that rely on such advanced regeneration tend to be more shade-tolerant, have a slow metabolism, and have storage reserves in large seeds (hypogeal germination), storage cotyledons, and a large belowground root system as reflected in a high plant biomass fraction in roots (root mass fraction—RMF). Additionally, adult nurse plants, such as remnant shrubs or trees, may facilitate regeneration in open landscapes and abandoned fields. They improve the microclimate through shading, water availability through hydraulic lift, soil carbon and nutrients through leaf and root litter production, and attract a diversity of animal dispersers (birds, bats) that perch on the trees and defecate the seeds (Olff et al., 1999). Remnant shrubs and trees are therefore important components of human-modified open landscapes, and may therefore speed up succession (Amani et al., 2022), especially of later successional, animal-dispersed tree species that else would take a long time to arrive (Guevara et al., 1986; Holl et al., 2020).

Resprouting

Resprouting is a vegetative form of regeneration; it occurs when plants are damaged, apical dominance is lost, and dormant buds start to resprout. Resprouting plants rely on reserves that are often stored in stolons or in specialized belowground storage organs (such as roots, rhizomes, lignotubers, and bulbs) that have a lower risk of being damaged or lost during disturbance. Resprouting ability increases with the storage organ size (i.e., a large root system), specialized storage tissue (a relatively large amount of parenchyma cells), and large concentrations of nonstructural carbohydrates (starch, sugar) (Poorter et al., 2010), and lipids and nutrients that are stored in the vacuoles. The number of sprouts depends on the bud bank; plants with small leaves and internodes tend to have many axillary buds, and therefore also many sprouts (Poorter et al., 2010). Vine and lianas can grow vegetatively from basal nodes and tubers, which can increase their capacity to colonize young successional forests adjacent to remnants. In fire-prone ecosystems such as savannas and Mediterranean woodlands, resprouting may become the most important source of species for succession. Because resprouting is triggered by disturbance-driven biomass removal, it is an important mode of regeneration early in succession.

Disturbance intensity determines the mode of regeneration and what component of the propagule pool is released (arrows 4). With increasing size, intensity, and frequency of the disturbance, the mode of regeneration will shift from advanced regeneration in the seedling bank to resprouts when some damage has occurred to plants, via mobilization of the seed bank (when environmental conditions have been modified sufficiently to trigger germination), to relying exclusively on the external seed rain in case of a severe disturbance event (Bazzaz, 1984).

SPECIES PERFORMANCE

The third general driver of succession is species performance. Species performance refers to vital rates (germination, growth, survival, and reproduction) of plants in the relevant stages of the plant's life cycle (seed, seedling, juvenile, and adult) (Figure 3, light-green upper box). Species performance affects the transition from one life cycle stage to the next and is determined by the interplay between the abiotic environment (resources, conditions, and signals; Figure 3, blue boxes, arrows 16), species traits (life history and other functional traits; green boxes, arrows 17), and biotic interactions (plant–plant, plant–animal, and plant–microbe; red boxes, arrows 18).

Abiotic environment

Species performance is strongly influenced by the abiotic environment (Figure 3, arrows 16), which comprises resources, conditions, and signals. Plant *resources* refer to the elements needed by plants to construct biomass. They consist of irradiance (photosynthetically active radiation—PAR), CO_2, macro- and micronutrients, and water. Sometimes space is also considered a resource, as it is temporarily occupied, or "consumed" by a plant. *Conditions* are environmental factors that modify resource uptake, such as temperature that controls metabolic activity and vapor pressure deficit (VPD) that controls transpiration and water flow. Soil chemistry (pH) influences the availability of essential nutrients (P, base cations) and toxic compounds (Al), while soil physics such as bulk density determinse the aggregate structure, aeration, and water-holding capacity of the soil. *Signals* inform the plant about the environment. For example, red light is preferentially absorbed by leaves over far-red light for photosynthesis. Both a high red (667 nm) to far-red (730 nm) ratio of light and a large temperature fluctuation indicate a canopy gap and, hence, a safe environment for germination.

Abiotic conditions are an inherently dynamic component of successional systems, as during succession, there is a gradual change in the resources, conditions, and signals when the vegetation builds up; the PAR (Matsuo et al., 2021) and Red:Far-Red ratio near the soil surface tend to decline, the microclimate becomes cooler and therefore the VPD reduces, and the temperature fluctuations weaken (Lebrija-Trejos et al., 2011). In general, the soil becomes more acidic due to the partial decomposition of organic material, and the nutrient concentration in the soil builds up due to biological nitrogen fixation and litter input, while the soil bulk density decreases (van der Sande, Powers, et al., 2023) due to increased root growth, litter input, and bioperturbation. For the soil parameters, the successional direction may vary, depending on the initial conditions (fertile or infertile soils, high input or low input agriculture), the type of succession (primary or secondary), and the peculiarities of plant priority effects and plant–soil feedbacks (Van der Putten et al., 2013). Initial soil conditions determine the course of succession. In 19 central Europe seres, succession proceeded in most cases from open vegetation with widespread species (ruderals and weeds) to woodland within 20 years (Prach et al., 2014). In contrast, in very dry habitats (dry sandy or rocky sites) and wet sites, succession proceeded toward an open dry grassland or wetland vegetation with many habitat specialists.

Species traits

Species traits can be divided into life history traits and other functional traits. Together, they determine species performance (Figure 3, arrows 17) under certain environmental conditions.

Life history

Life history refers to the pattern of survival and reproduction of an organism and has a strong impact on its fitness. Life history traits include: (1) the allocation of carbohydrates and nutrients to survival and growth versus reproduction; (2) the reproductive mode: monocarpic plants that reproduce once in a lifetime (such as annual or biennial herbs, but also some long-lived trees and succulent plants such as *Agave*), or polycarpic plants that reproduce several times during their lifetime; (3) the age or size at reproduction and longevity; (4) the frequency of reproduction (continuous, annual, or multi-annual, such as episodic mass fruiting); and (5) fecundity (i.e., the amount of seeds produced per plant at a given size and age). In general, early-successional species have a fast reproductive lifestyle with a large allocation to reproduction, early and continuous reproduction, with a high fecundity (Salguero-Gómez et al., 2016) and relatively low levels of defenses (Coley, 1983). As a result, early-successional species live, grow, and reproduce fast, and die young after which they disperse in space or time to colonize new early-successional habitats. During succession, small species with fast life history traits (*r*-strategists) are therefore replaced by taller species with slow life history traits (*K*-strategists) (Pianka, 1970). For example, life history traits drive species replacement on temperate abandoned fields, where first summer annuals dominate (which germinate in spring, mature in summer, and die in late summer/autumn) followed by winter annuals (which germinate late in the growing season, overwinter as rosettes, and reproduce in spring), and biennials (which germinate in one year, overwinter often as rosettes, and reproduce the second year) until they are replaced by longer lived woody species (Meiners, Pickett, et al., 2015).

Functional traits

Functional traits refer to morphological, chemical, physiological, and phenological characteristics of an individual that affect its performance in terms of germination, growth, survival, or reproduction (Violle et al., 2007). The reproductive traits have been discussed above under life history traits. Díaz et al. (2016) identified two global spectra of plant form and function, in which species vary in their economic- and size-related traits. Plant species show a spectrum from fast to slow returns on investments of carbon, water, and nutrients in plant tissues. Such economic spectra have been shown for leaf (Wright et al., 2004), stem (Yang et al., 2022), and whole plant traits (Freschet et al., 2010). This suggests a similarity and alignment in trait spectra across plant organs (Reich, 2014), although for root traits this may be different as roots have to acquire multiple resources and face multiple pressures (Weemstra et al., 2016). Roots show two spectra: one spectrum related to root economics and another spectrum that ranges from thin roots that increase resource uptake by the plant to thick roots that facilitate mycorrhizal development and increase resource uptake by mycorrhizal fungi (Bergmann et al., 2020). In general, plants from productive (and early-successional) environments have “fast” “acquisitive” trait values that increase resource uptake and growth, whereas plants from unproductive (and later successional) environments have “slow” “conservative” trait values that increase resource conservation, survival, and persistence (Diaz et al., 2004; Garnier et al., 2004; Lambers & Poorter, 1992; Laughlin, 2023; Poorter & Bongers, 2006; Shipley et al., 2006). Although in productive, mesic environments, succession proceeds from species with fast to species with slow trait values; this pattern may be fundamentally different in dry and nutrient-poor environments. Here, species with slow trait values may dominate early in succession, and they are replaced by species with fast trait values when vegetation cover builds up and the environment becomes more benign (Poorter et al., 2019, 2021).

Biotic interactions

Biotic interactions refer to the interaction between plants and other organisms of various trophic levels, such as plant–plant, plant–animal, and plant–microbe interactions (Figure 3, red boxes). These biotic interactions can be positive or negative for plants, and therefore have a direct effect on plant species performance and abundance (Figure 3, arrows 18). The outcome of biotic interactions can leave important environmental legacies that affect succession.

Plant–Plant

Plant–plant interactions can have positive effects on a target plant (in the case of facilitation) or negative effects (in the case of competition, inhibition, and allelopathy) (arrows 18). *Facilitation* occurs when the presence of plants favors the establishment, growth, and survival of other species. Facilitation occurs when nurse plants provide shelter against harsh climatic conditions (cold, freezing, aridity), improve resource availability below their crown through litter input, hydraulic uplift, or symbiotic nitrogen fixation (Callaway, 2007), or provide protection against herbivores with their spines, thorns, and bushy habit (Olff et al., 1999; Smit et al., 2007). Facilitation is an important process during primary succession when mineral soils are still developing, or early in secondary succession when climatic conditions tend to be harsh. In general, facilitation speeds up succession and leads to convergent vegetation development (Walker & Wardle, 2014). *Competition* occurs when plants compete for the same resources that are in limiting supply. In temperate regions, herbaceous species may preempt resources by beginning growth early in the season, and the phenological niche is therefore important. Competition is likely to shift in intensity and scope during succession; competition may initially be weak when vegetation cover is sparse but increases over time when the vegetation builds up. Plants may compete initially for belowground resources as water and nutrients are often in limited supply but compete later for aboveground resources when the vegetation builds up and light becomes limiting (Tilman, 1985). Early in succession, clonal plants such as grasses, sedges, ferns, and large-leaved herbs are good competitors because they can mobilize their storage reserves, spread quickly horizontally through their runners (stolons and rhizomes), preempt the space, and form dense swards, making the establishment of other species virtually impossible (Grime, 2006; Meiners, Pickett, et al., 2015). As the vegetation canopy closes, plants start to compete for vertical rather than for horizontal space. As light tends to come from above, there is a strong asymmetric competition for light and a strong advantage of height growth. Grasses and ferns are initially efficient light competitors, as with their newly developed and coiled leaf or fern frond they can easily penetrate the dense vegetation and unfold their leaves above the vegetation canopy. During succession, there is therefore a predictable replacement from smaller short-lived to taller long-lived growth forms, from lichens, mosses, herbs, grasses, shrubs, and trees. This growth form replacement is one of the most general patterns in succession (Clements, 1916; Finegan, 1996; Meiners, Pickett, et al., 2015). *Inhibition* occurs when a plant occupies a site and prevents the establishment of another plant because of space limitation. Once a pioneer plant dies, it can be replaced by another pioneer or by a later successional species. Because pioneers are short-lived, they will be replaced more often than long-lived later successional species. As a result, pioneers will decline and long-lived species will increase in abundance during succession (Connell & Slatyer, 1977). Inhibition in combination with species longevity can, therefore, partially explain successional patterns in community composition. Early-successional communities are dominated by species with short life span, leading to fast community turnover and higher invasibility for exotic species. In contrast, later successional communities are dominated by longer lived species, which result in less community turnover, slowing down the pace of succession (Meiners, Pickett, et al., 2015). *Allelopathy* refers to the production of secondary metabolites by plants that negatively affect the growth and development of other plants. For example, allelopathic effects by *Solidago*, *Aster*, and grasses inhibit *Prunus* tree regeneration and prevent succession from temperate grass savannas to later successional stages (Horsley, 1977).

Plant–animal

Plant–animal interactions can be positive for plant fitness, in the case of pollination and dispersal, or negative, in the case of seed predation and herbivory (Figure 3, arrows 18). For a discussion on biotic *pollination* and *dispersal*, see the section on "Propagule dispersal." *Seed predation*, that is, the partial or complete consumption of seeds, can be done by insects, birds, and small rodents. In tropical rainforest, tree seed predation rates are highest early in succession when dense liana tangles provide small rodents habitat and shelter, and decline with stand age (Peña-Claros & De Boo, 2002). Seed predation rates varied from 50% to 100% across tree species, indicating that predation can strongly steer species succession. *Herbivory* is the removal of plant material by insects or animals, such as wildlife or cattle. It can be divided into grazing and browsing, where grazing refers to the consumption of grass and herbs and browsing to the consumption of twigs and leaves. The spatial–temporal pattern of herbivory is an important regulator of successional dynamics (Meiners, Pickett, et al., 2015; Olff et al., 1999). Herbivory rates tend to be higher for herbaceous plants compared with woody plants because of their higher nutritional value. Herbivory rates are higher for early-successional species compared with late-successional species, as they are more nutritious (higher leaf nutrient concentrations), more palatable (less fibers and higher water content), and less defended (less thorns, spines, and chemical defenses) (Coley, 1983; Poorter et al., 2004). In fertile systems, herbivores can maintain the vegetation in an early-successional stage when they consume a large part of the net primary productivity and return nutrients as labile feces to the soil, which stimulates the growth of early-successional species (Wardle et al., 2004). In contrast, in infertile systems, herbivores may accelerate succession when they consume a small part of the primary productivity, remove preferentially palatable species, and favor unpalatable plant species with poor leaf and litter quality (Wardle et al., 2004). Plant–animal interactions and, hence, successional pathways depend strongly on herbivore densities. This is related to LUI in the case of livestock density, or related to landscape integrity and conservation status in the case of wild herbivore populations (arrows 14). A relatively small set of insect species (mostly bark beetles and moths) can cause stand-replacing disturbance events by killing most canopy trees in a short time (Thomas, 2023). As insects tend to be specialized, such stand-replacing disturbance events only occur in boreal and northern temperate forests where only few tree species coexist (Thomas, 2023). Examples are the mountain pine beetle that impacts *Pinus contorta* in the United States, or the European spruce bark beetle that impacts *Picea abies* in Europe.

Plant–microbe

Microbes are viruses and organisms of microscopic size (bacteria and fungi). Plant–microbe interactions can be positive in the case of nitrogen-fixing symbionts and nutrient- and water-acquiring mycorrhizal fungi, or negative in the case of pathogenic viruses, bacteria, and fungi (arrow 18). In general, early in succession, there is a lower microbial abundance and diversity because of the physical impact of disturbance and because fewer plant hosts are available. Microbial diversity and abundance will increase over time with microbial colonization and when more plant hosts become available (Meiners, Cadotte, et al., 2015) and their overall effect on the plant community is thought to be positive early in succession and negative later in succession (Reynolds et al., 2003), but see Kardol et al. (2007). *Nitrogen fixation* is a mutualistic relationship between plants and *Rhizobium* bacteria (in the case of the Fabaceae) or *Frankia* bacteria (in the case of eight other plant families). The bacteria occur in root nodules and are capable of fixing atmospheric nitrogen for the plant, while the plant delivers assimilates to the bacteria. N-fixers are therefore crucial and abundant during the initial stages of primary succession, when they can increase N availability in the system and facilitate the establishment of other species (Chapin et al., 1994) and during the initial stages of secondary succession when they can restore the nitrogen stock of degraded soils (Batterman et al., 2013). At the same time, nitrogen fixation acidifies the soil, which further accelerates the successional process (Chapin et al., 1994). *Mycorrhiza* refers to a symbiotic association between a fungus and a plant in the plant root. Mycorrhizal fungi make extensive networks of thin hyphae that take up water and nutrients for the plant. Mycorrhizae are especially important for the uptake of P, which is relatively immobile in the soil. Ectomycorrhizae do not penetrate the plant cell but construct a sheet around the roots that protects the plant against soil pathogens. Ectomycorrhizae are found in only 10% of the plant families (mostly tree families), dominate in cold environments, and can break down and use organic sources of soil nutrients, especially nitrogen (Steidinger et al., 2019). Endomycorrhizae form tree-like (arbuscular) structures in the cell membrane, thus facilitating nutrient exchange. They occur in 70% of the plant species and dominate in warm environments where decomposition rates and nutrient cycling are high (Steidinger et al., 2019). Mycorrhizal fungi abundance increases rapidly during succession because they tend to be generalists and because of their positive feedback loop with plants (Meiners, Cadotte, et al., 2015). Initial studies suggest that there is a continuum in successional strategies of mycorrhizal fungi that may parallel the continuum in plant successional strategies (Chagnon et al., 2013). Early-successional fast-growing plant species are less defended and can suffer therefore from a negative feedback loop with pathogenic soil biota (Hannula et al., 2017; Kardol et al., 2007) or root-feeding invertebrates (De Deyn et al., 2003), which accelerates plant species replacement and succession. In contrast, later successional plant species can have a positive feedback loop with soil biota (e.g., with mycorrhizal fungi) that slows down plant species replacement and succession (Kardol et al., 2013; Walker & Wardle, 2014). *Pathogenic bacteria and fungi* can lead to plant disease and death and tend to be very plant species specific. Because of their plant host specificity, such antagonistic microbes are likely to build up more slowly during succession than the mutualistic microbes (Meiners, Cadotte, et al., 2015). Pathogens build up over time in the root zone around plants, which leads to inhibition of plant regeneration (i.e., a negative plant–soil feedback loop) that accelerates species replacement and succession. For example, in foredune succession in the Netherlands, reciprocal transplant experiments have shown that the two dominant, sand-stabilizing species *Ammophila arenaria* and *Hippophaë rhamnoides* disappear from sites where the soil has become colonized with species-specific growth-depressing microorganisms. This paves the way for the establishment and dominance of later successional plant species (Van der Putten et al., 1993). Such pathogen-mediated plant–soil feedbacks are very common, and given the specificity of these relationships, this may lead to many different successional pathways (Fukami, 2015; van Breugel et al., 2024).

VEGETATION SUCCESSION

Traditionally, vegetation succession has only focused on species replacement (e.g., Pickett et al., 1987b). Yet, differences in species performance lead to vegetation succession at different organizational scales: changes in species populations lead to changes in plant communities (Figure 3, arrow 19), which, in turn, lead to changes in ecosystem structure (arrow 20) and functioning (arrow 21). We therefore take a broader view on succession by considering successional changes in all these organizational scales.

A population (Figure 3, box 4) refers to all individuals of a plant species in a patch. Populations can vary in density, size structure, and growth rate. During succession, often extended periods of low abundance precede or follow peak abundances in population size (Pickett et al., 2013). Early- and mid-successional species show hump-shaped patterns in abundance and biomass over time, which depends both on the time of species arrival and the successional changes in environmental conditions. The vital rates of seedlings and juveniles define the period of population increase and the timing of species' maximum abundance, whereas the mortality rate of mature individuals determines how long each species persists during succession (Martínez-Ramos et al., 2021).

A community (Figure 3, box 4) refers to all the plant species that co-occur in a patch. Depending on the species relative abundances, communities can vary in taxonomic diversity (richness, evenness), phylogenetic diversity (i.e., the phylogenetic relatedness of species in a community as for example expressed by their summed phylogenetic branch lengths), and functional diversity (the distribution of trait values in the community, for example, expressed in the skewness and kurtosis) (Gross et al., 2021). In general, species diversity increases during succession (Prach & Walker, 2019, 2020) due to the gradual arrival of new plant species and the development of a taller and more complex vegetation structure (with increased vertical stratification and spatial heterogeneity) that physically can harbor more species and offers increased establishment opportunities for more species with different niches. Early in succession, there may be phylogenetic and functional convergence (i.e., clustering) because of strong abiotic filtering for a small set of pioneer species from closely related lineages with similar trait values (Meiners, Cadotte, et al., 2015; Norden et al., 2012). Later in succession, there may be phylogenetic and functional divergence (i.e., overdispersion) because of limiting similarity, niche differentiation, and because more species with different trait values can establish and persist under relatively benign late-successional conditions. Return toward the original species composition is more likely in colder biomes and at higher latitudes, because these contain fewer (late) successional species and succession is therefore also more predictable (Prach & Walker, 2019, 2020).

Ecosystem structure (Figure 3, box 4) is defined here as the physical, three-dimensional structure of the vegetation. It can be described in terms of the size (i.e., total) and variation (i.e., the horizontal and vertical distribution) of plant height, leaf area, root length, and biomass. In general, the size (height, leaf area index, rooting depth, and above- and belowground biomass) increases during succession due to cumulative growth and asymmetric competition for resources. The structural heterogeneity increases over time because (1) continuous plant recruitment changes the plant community from an even-aged toward an uneven-aged structure, (2) plants accrue in size, resulting, for example, in big veteran trees, (3) different species attain a different maximal size, which results in vertical stratification and layering of crowns and roots, and (4) senescence or small-scale disturbance events result in plant mortality, which creates gaps in the canopy and root zone (Oliver, 1980).

Ecosystem functioning (Figure 3, box 4), or ecosystem processes, refers to the changes in ecosystem states over time due to the combined activities and interactions of all organisms in an ecosystem and the abiotic environment. Ecosystem functioning can be described in terms of carbon, water and nutrient cycling, and energy fluxes. In general, gross primary productivity increases over time due to buildup of vegetation, but because of increased maintenance costs, the respiration catches up, leading to a mid-successional peak in net primary productivity and an asymptotic increase in aboveground biomass over time (Odum, 1969). Nutrient uptake rate from the soil is initially fast because of fast plant growth but decreases over time when plant growth slows down. Nutrient cycles become more closed as mature systems have greater capacity to entrap and hold nutrients (Morriën et al., 2017) with denser and deeper root systems (Odum, 1969). With the accumulation of biomass, detritus becomes more important for nutrient cycling. Finally, the food chain is thought to change from linear, grazing-dominated plant–herbivore–carnivore chains in open herbaceous vegetation, to complex web-like food chains dominated by detritivores in closed forest vegetation (Odum, 1969). Most ecosystem processes are driven by vegetation quantity (Figure 3, arrow 21) rather than vegetation quality (Lohbeck et al., 2016), because biomass is the main driver of assimilation, transpiration, and respiration, and associated nutrient and energy fluxes. Ecosystem processes are therefore also driven by the traits of the dominant species because they make up most of the community biomass (arrow 22), which is also known as the mass ratio hypothesis (Grime, 1998). Finally, species and trait diversity may increase ecosystem functioning (arrow 22) because of complementarity in resource use in space or time (Loreau & Hector, 2001), or because of pathogen dilution (Schnitzer et al., 2011), or the inclusion of particularly productive species (which is also known as the selection effect). During succession, there may be a shift from vegetation quantity to vegetation quality driving succession, because early in succession, stands vary more in biomass than in functional composition (i.e., the distribution of plant trait values in a community) (Lohbeck et al., 2015). During succession, there may also be a shift in the biodiversity-related mechanisms that contribute to ecosystem functioning. For example, a forest modeling study showed that soon after disturbance, complementary effects prevail, whereas later in succession, selection effects prevail when more competitive species dominate the community (Schmitt et al., 2020).

SUCCESSIONAL CHANGES IN THE BIOTIC AND ABIOTIC ENVIRONMENT CAUSE FEEDBACK LOOPS

Successional changes in the vegetation are associated with successional changes in the biotic environment (animal community, microbial community, red boxes) and the abiotic environment (soil, microclimate, blue boxes) (Figure 3, arrows 23). For example, during succession, the *animal community* (Figure 3, box 5) changes generally from a few, early-successional generalists to a diversity of later successional specialists (Ramos-Fabiel et al., 2019), although biodiversity may peak during succession when early- and late-successional species coexist (Connell, 1978). The direction or shape of successional patterns may vary with taxonomic or functional group where some prefer open, disturbed environments (e.g., geese, bats, ungulate grazers), whereas others prefer a later successional, closed environment (e.g., ungulate browsers) (van Andel et al., 1993). For tropical forests regrowing on abandoned lands, the species richness of ants, amphibians, reptiles, birds, and mammals generally increases rapidly during succession, whereas the similarity with old-growth species composition increases more slowly (Acevedo-Charry & Aide, 2019; Dunn, 2004). The *microbial community* (Figure 3, box 5) may build up over time because more carbon-based energy sources become available and may change in composition because of changes in substrate quality. For example, during 30 years of temperate grassland succession on abandoned, intensively managed crop fields, the active microbial community changes from bacteria-dominated to fungi-dominated (Hannula et al., 2017). The fungal community changed from pathogenic fungi and fast-growing unicellular sugar-feeding fungi, via saprophytic fungi to slower growing hyphal arbuscular fungi and molds. In response, the fungi feeding fauna changed from protists and nematodes, via springtails, to mites (Hannula et al., 2017). As a result, the soil network of microbes and soil fauna became more connected, leading to a higher soil carbon uptake (Morriën et al., 2017) and carbon and nitrogen mineralization rates (Holtkamp et al., 2011). During succession, there is an increase in recalcitrant litter, which increases the abundance of detritus fragmenters (e.g., earthworms, millipedes, and woodlice) and wood-degrading fungi (Morriën, 2016). In addition, vegetation and plant species modify the *microclimate and soil conditions* (Figure 3, box 5) because of shelter, root exudates, and resource uptake and loss (arrows 23).

These biotic and abiotic changes cause feedback loops (Figure 3, Box 5, dotted lines) affecting different parts of the successional process, thus fueling, retarding, or inhibiting successional change (van Breugel et al., 2024). For example, changes in the animal community directly impact plant–animal interactions (arrow 24), changes in the microbial community directly affect the magnitude and nature of plant–microbe interactions (arrow 25), and changes in soil and microclimate modify resources, conditions, and signals (arrows 26) and, hence, plant performance. These feedback loops can be species specific. For example, plant species modify the microclimate and soil in different ways, due to their difference in canopy and root architecture (Mejía-Domínguez et al., 2011), and differences in resource uptake and loss (van Breugel et al., 2024). As plant–animal interactions and especially plant–microbe interactions can be very species specific, this gives rise to a multitude of different successional pathways for plant, animal, and microbial communities. For example, inoculating early-successional vegetation on abandoned agricultural fields with specific late-successional beneficial soil organisms can steer succession toward either grassland or heathland communities (Wubs et al., 2016). Because microbes stay in the soil, they may have important, long-term legacies on the direction and speed of succession.

The order and timing in which plant species arrive during succession determines their impact on later arriving species (which is also known as the "priority effect") and therefore community assembly and successional pathways (which is also known as "historical contingency") (Fukami, 2015). As the arrival of species is to some extent a stochastic process driven by dispersal limitation, this may further diversify the potential number of successional pathways. Succession may therefore have both predictable and unpredictable components (Norden et al., 2015), which may vary with spatial scale. Unpredictable stochastic processes, such as arrival of woody species, lead within abandoned fields to divergence in abundance-weighted species composition over time, as it is a chance process where exactly the first woody species will establish (Li et al., 2016). Predictable, deterministic processes such as light competition lead to convergence in abundance-weighted species composition across abandoned fields over time, when small species are replaced by taller species that are better competitors for light (Li et al., 2016). Hence, the taxonomic predictability of succession increases when larger spatial scales and longer temporal timescales are considered (Meiners, Pickett, et al., 2015), whereas the unpredictability of succession is likely to increase in more diverse (tropical) systems (Prach & Walker, 2020), where there is a larger opportunity for dispersal limitation, priority effects, and pairwise interactions between different types of organisms and species.

DISCUSSION AND IMPLICATIONS

We have advanced successional theory in two ways. First, we show that succession occurs within the context of a SES, where social and ecological factors operating at different spatial scales have large consequences for local succession (Figures 1 and 2), and second, we present a CSF to understand succession at the local (patch and landscape) scale (Figure 3). Here we first discuss how the successional framework can be used, and then the implications of this broader view and the CSF for ecosystem restoration.

How to use the successional framework

Our framework addresses succession at the patch and landscape scales (Figure 3). It improves our mechanistic understanding of succession and can be used to study succession worldwide. Although the framework is comprehensive (Figure 3), it does not require all components to be studied at the same time and in all cases. Instead, it can be used to study specific successional processes in more detail. Quantifying all processes and mechanisms of this successional framework is clearly a daunting task, and even doing so for a single site would require a large team effort or a lifetime career. So how can this framework be used?

Which components?

Because the framework provides a complete overview, it may help researchers to think more broadly about their study system and about the potential factors they may have not studied or overseen. The framework can also be used to focus and identify a priori the most relevant successional factors and drivers to be analyzed in a given study system, based on preliminary or general knowledge of the ecosystem. For example, in seasonally dry tropical forest, the most important factors for species availability may be abiotic wind dispersal and resprouts, whereas in wet tropical forests, it may be biotic bat dispersal and the seedling bank. For published studies, it makes more explicit which components of the successional processes are being studied and which are being overlooked. Finally, in meta-analyses, the studies can be mapped on the framework. This reveals which components, drivers, and processes are being over- and understudied, and allows to identify knowledge gaps and priorities for future research.

Shifts in steering factors

The framework can be used to evaluate how the relative importance of successional steering factors shifts during succession or across environmental gradients. Because succession is initially a sequential process, it is likely that early in succession the factors that determine the first steps of succession are important (Figure 3, the left part of the scheme), such as previous LUI, current LUI, and species availability. The relative importance of these factors may decline over time. In contrast, it is likely that later in succession the later successional steps are important, like, for example, plant–microbe interactions that determine plant performance and feedback loops (Figure 3, the right part of the scheme). Successional steering factors may also shift along climatic gradients. For example, in dry forests, succession may be more strongly determined by abiotic drivers (heat, drought), whereas in wet forests, it may be more strongly determined by biotic factors (biotic dispersal, plant–animal and plant–microbe interactions). The framework can therefore be used to develop and test new hypotheses.

A tool for synthesis

The framework can be used as a comparative tool to evaluate the role of a specific successional factor across different (published) studies. Most successional studies have quantified the shape of the relationship between community attributes (e.g., species richness) or ecosystem attributes (e.g., aboveground biomass) and time since disturbance cessation (plot abandonment). Yet, it is equally important to quantify the shape of the relationship between these vegetation attributes and the underlying drivers, for example, by evaluating the effect of landscape integrity on species richness.

Testing the framework

The successional framework can be tested by combining three complementary approaches: empirical field studies, experiments, and modeling (cf. Chang & Turner, 2019; van der Sande et al., 2017). Empirical field studies can quantify succession, provide firm evidence for real-world patterns, and generate new hypotheses. For example, longitudinal field studies can monitor community assembly over time and quantify variation in successional pathways, while chronosequence studies can provide a long-term perspective on succession. Longitudinal paleoecological studies can provide a deep time perspective (from decades to millennia) on succession in the same region, using, for example, functional traits to infer directional change in species composition (van der Sande, Bush, et al., 2023), or isotopes to infer successional patterns in biogeochemical cycling (Dunnette et al., 2014). Experimental studies can control the large number of confounding factors and really test hypotheses and the underlying mechanisms, for example, by adding or removing environmental factors, biota, or plants in different life history stages. Process-based modeling studies not only remove confounding factors, but also integrate different mechanisms, and can scale up across space and time, thus providing a longer time perspective on succession. Process-based models allow to do sensitivity analysis about the relative importance of different factors, do scenario analysis, and make quantitative predictions about how succession may vary due to anthropogenic and environmental change (Pacala et al., 1996; Schmitt et al., 2020; Shugart & West, 1980).

Implications for ecosystem restoration

With the 30 × 30 debate (30% of the terrestrial area set aside for conservation by 2030), and initiatives to bend the curve of biodiversity loss, and restore the productivity of degraded landscapes, there is an increased interest in ecosystem restoration. This is also reflected in the UN Decade 2020–2030 on Ecosystem Restoration (UNEA, 2019). Succession is a nature-based solution for ecosystem restoration, which, alongside restoration planting, is receiving increased attention. Yet, the successional pathways and, therefore, the restoration outcomes can be very diverse in both restoration speed and directionality, and in the resulting composition and functionality. It is therefore important not only to consider the proximate drivers (Figure 3), but also the ultimate drivers of succession (Figure 2). Applying our framework (Figure 3) to seres across broadscale social gradients in livelihoods, and environmental gradients in precipitation, temperature, elevation, soil fertility, and disturbance (Figure 2), allows for a better insight into what successional processes matter under what conditions (cf. Prach & Walker, 2020). This will help to formulate and test successional hypotheses, advance successional theory, increase the predictability of successional outcomes, and make locally relevant restoration decisions. Restoration is a human endeavor (Holl, 2020). Using a broader SES perspective (Figures 1 and 2) allows us not only to understand the proximate drivers of succession, but also the ultimate drivers of succession that are influenced by people's decisions. This is especially important in the Anthropocene, where we need to understand the reasons underlying widespread degradation and the opportunities for widespread natural recovery and ecosystem restoration in order to optimize and prioritize restoration planning (Brancalion et al., 2019; Strassburg et al., 2020). This framework may further be used when constructing a theory of change for landscapes undergoing restoration activities. In addition, by zooming into the ecological subsystem (Figure 3), the successional framework helps to identify the most important factors that steer succession, and hence relevant intervention points for active (i.e., planting) or passive (i.e., natural regeneration) ecosystem restoration, or combinations of both (de la Peña-Domene et al., 2014). These insights can be used for restoration practices that intervene in the three main drivers of succession, by either controlling disturbance (site availability), enhancing colonization (species availability), or directing competition (species performance) (Pickett et al., 2009; Rosenberg & Freedman, 1984).

AUTHOR CONTRIBUTIONS

All authors contributed to conceptual development. Lourens Poorter wrote the first draft; all co-authors edited the manuscript and provided comments. Jazz Kok made the visualization.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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