Feedback loops drive ecological succession; towards a unified conceptual framework

Authors: Michiel van Breugel[1,2,3*], Frans Bongers[4], Natalia Norden[5], Jorge A. Meave[6], Lucy Amissah[7], Wirong Chanthorn[8], Robin Chazdon[9], Dylan Craven[10], Caroline Farrior[11], Jefferson S. Hall[3], Bruno Hérault[12], Catarina Jakovac[13], Edwin Lebrija-Trejos[14], Miguel Martínez-Ramos[15], Rodrigo Muñoz[4], Lourens Poorter[4], Nadja Rüger[3,16,17], Masha van der Sande[4], Daisy Dent[3,18,19]

[1] Department of Geography, National University of Singapore, Arts Link, #03-01 Block AS2, Singapore 117570
[2] Yale-NUS College, 16 #01-220, 16 College Ave West, 138527, Singapore
[3] Smithsonian Tropical Research Institute, Roosevelt Ave. Tupper Building – 401, Panama City 0843-03092, Panama.
[4] Wageningen University & Research, PO Box 47, 6700 AH Wageningen, The Netherlands.
[5] Centro de Estudios Socioecológicos y Cambio Global, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia
[6] Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México. Circuito Exterior s/n, Ciudad Universitaria, Coyoacán, Ciudad de México, C.P. 04510, Mexico.
[7] CSIR-Forestry Research Institute of Ghana UP.O,Box 63 Kumasi, Ghana
[8] Department of Environmental Technology and Management, Faculty of Environment, Kasetsart University, 50 Ngamwongwan Road, Jatujak District, 10900, Thailand
[9] Tropical Forests and People Research Centre, University of the Sunshine Coast, 90 Sippy Downs Road, Sippy Downs, Queensland, Australia
[10] Centro de Modelación y Monitoreo de Ecosistemas, Facultad de Ciencias, José Toribio Medina 29, Universidad Mayor, Santiago, Chile / Data Observatory Foundation, Santiago, Chile.
[11] Department of Integrative Biology, University of Texas at Austin, 2415 Speedway, Stop C0930, Austin, TX 78705, USA
[12] CIRAD, UPR Forêts et Sociétés, F-34398 Montpellier, France & Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France
[13] Departamento de Fitotecnia, Centro de Ciências Agrárias, Universidade Federal de Santa Catarina, Rod. Admar Gonzaga, 1346, 88034-000 Florianópolis, Brazil
[14] Department of Biology and Environment, University of Haifa–Oranim, Israel
[15] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Campus Morelia, Antigua Carretera a Pátzcuaro # 8701, Col. Ex-Hacienda de San José de la Huerta, CP 58190, Morelia, Michoacán, Mexico
[16] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[17] Department of Economics, Institute of Empirical Economic Research, University of Leipzig, Leipzig, Germany
[18] ETH Zürich, Department of Environmental Systems Science, Zürich, Switzerland
[19] Max Planck Institute for Animal Behavior, Konstanz, Germany

Corresponding author: Email: mvbreugel@gmail.com. Tel: +65 98621006

Abstract

The core principle shared by most theories and models of succession is that plant-environment (PE) feedback dynamics drive a directional change in the plant community, following a major disturbance. The most commonly studied feedback loops are those in which the regrowth of the plant community causes changes to the biotic (e.g., dispersers) or abiotic (e.g., soil nutrients) environment, which differentially affect species availability or performance. This, in turn, leads to shifts in the species composition of the plant community. However, there are many other PE feedback loops that potentially drive succession, each of which can be considered a model of succession.

While plant-environment feedback loops in principle generate predictable successional trajectories, succession is generally observed to be highly variable. Factors contributing to this variability are the stochastic processes involved in feedback dynamics, such as individual mortality and seed dispersal, and extrinsic causes of succession, that are not affected by changes in the plant community but do affect species performance or availability. Both can lead to variation in the identity of dominant species within communities. This, in turn, leads to further contingencies if these species differ in their effect on their environment (priority effects). Predictability and variability are thus intrinsically linked features of ecological succession.

We present a novel conceptual framework of ecological succession that integrates the propositions discussed above. This framework defines seven general causes: landscape context, disturbance and land-use, biotic factors, abiotic factors, differential species availability and performance, and the plant community. When involved in a feedback loop, these general causes drive succession and when not, they are extrinsic causes that create variability in successional trajectories and dynamics. The proposed framework provides a guide for linking these general causes into causal pathways that represent specific models of succession.

Our framework represents a systematic approach to identifying the main feedback processes and causes of variation at different successional stages. It can be used for systematic comparisons among study sites and along environmental gradients, to conceptualize studies, guide the formulation of research questions and design of field studies. Mapping an extensive field study onto our conceptual framework revealed that the pathways representing the study's empirical outcomes and conceptual model had important differences, underlining the need to move beyond the conceptual models that currently dominate in our specific fields and to find ways to examine the importance of and interactions among alternative causal pathways of succession. To further this work, we argue for integrating long-term studies across environmental and anthropogenic gradients, combined with controlled experiments and dynamic modeling.

Key words: ecological succession, plant-environment feedback loops, causes of variability, landscape context, biotic and physical environment, disturbance and land use, conceptual framework

Contents

1. Introduction

Ecological succession is a term used to describe the process of change in a plant community after a disturbance event or human land use has removed some or all of the original vegetation (secondary succession) or created newly exposed substrate (primary succession)(Pickett, Meiners & Cadenasso, 2011; Prach & Walker, 2019). These changes are most frequently defined in terms of biomass, canopy architecture, species composition, environmental conditions, and ecosystem functions. Traditionally, succession was viewed as a deterministic process where changes in the physical (e.g. light) or biotic environment (e.g. soil biota), induced by the regrowth of the plant community, drive a turnover of plant species with different functional characteristics (e.g., Horn, 1974; Tilman, 1985; Huston & Smith, 1987). Yet, despite the apparent clarity of the concept, views on succession differ strongly among researchers (Poorter *et al.*, n.d.). There are several reasons for this. Causes and mechanisms of succession are manifold, complex and vary across ecosystems (Arroyo-Rodríguez *et al.*, 2017). Studies take place in different ecosystems, focus on different components of the successional process and on vastly different spatial-temporal scales, and examine different ecological processes (e.g., resource competition versus dispersal) and variables (e.g., species composition versus biomass).

Here we propose that there is one core principle common to most theories and models of ecological succession: feedback dynamics between plants and their environment (Kulmatiski *et al.*, 2008; Meiners *et al.*, 2015). This feedback involves vegetation-driven changes in the plant community's environment, which, in turn, differentially affect the availability or performance of the plant species in the local species pool (e.g., Horn, 1974; Finegan, 1984; Tilman, 1985; Smith & Huston, 1989). 'Environment' is here defined broadly as the aggregate of all anthropogenic and natural variables that affect plants within a community, at local and landscape scale. The number of specific variables that potentially play a role in succession is overwhelmingly large (Arroyo-Rodríguez *et al.*, 2017), but can be classified into a few categories or 'general causes' (Pickett, Collins & Armesto, 1987a). We define these here as landscape context, historical and current disturbance or land use, and biotic and abiotic factors (Fig. 1). In summary, succession can be defined as a process of concomitant changes in a plant community and its environment, with a clear starting point in time relating to a major **disturbance event** or the **abandonment of the previous land-use** and subsequent **directional change** in species composition over time driven by **plant-environment feedback dynamics.**

While successional trajectories are often directional, they usually vary among sites (Norden *et al.*, 2015). This has generated a long-running debate about the role of chance and determinism in succession

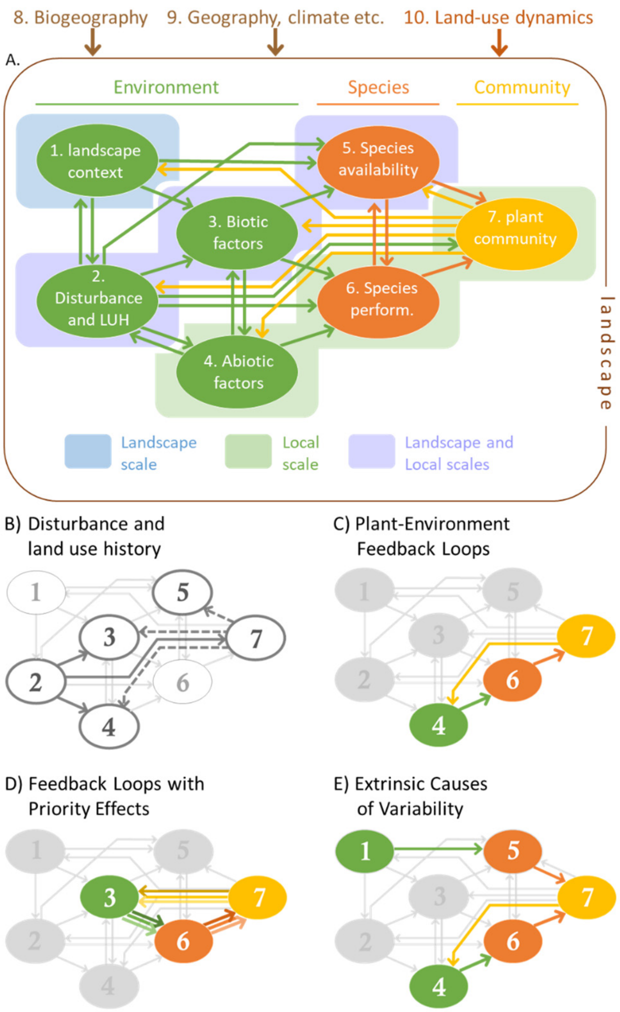


Figure 1. A conceptual framework of succession. **A**) **Full conceptual framework**. Our framework consists of four categories of causal factors that represent different aspects of the environment (green circles), at the landscape scale (blue background), the local scale (green background), or both (purple background) (①-④). Interspecific variation in species' life histories, in interaction with changes in other causal factors, drive shifts in species availability at the local and landscape scale (⑤) and in species performance at the local scale (⑥) (orange circles). This, in turn, drives changes in species abundance and composition of the plant community (⑦, yellow circle). At larger spatial scales, differences in biogeography, climate, soils, landscape configuration, disturbance regimes or land-use dynamics (⑧-⑩) can cause variation in successional dynamics among landscapes. Causal factors can be linked in causal pathways that represent models or hypotheses of ecological succession. These causal pathways need to include plant-environment feedback loops, as these are the fundamental drivers of succession, and can further include causal factors that are thought to be important drivers of variability in the successional dynamics of the study system. **B**) **Before succession: disturbance and land-use history**. Succession starts after previous land-use or a disturbance event modified the local biotic and abiotic factors indirectly because of the removal or modification of the plant community (②→⑦→③ or ②→⑦→④) and possibly directly as well (②→③ or ②→④). In addition, the removal of seed plants directly affects species availability (②→⑦→⑤). The newly created conditions constitute the starting point of – and will be modified over the course of – succession. **C**) **Plant-environment feedback loops**. The simplest models of succession describe single and clearly defined plant-environment feedback loops that, in principle, would be sufficient for a directional change in species composition to occur. In this example, interspecific

variation in species performance in response to changes in local abiotic factors causes shifts in the species composition (④→⑥→⑦) as succession proceeds. Changes in the vegetation, in turn, drive further changes in abiotic factors (⑦→④). **D**) **Priority effects.** Feedback loops can cause variability in succession if, in contrast to what was assumed in the previous model, species differ in how they affect their environment (indicated by the multiple arrows). For example, when plants accumulate species-specific assemblages of soil pathogens in their rhizosphere, differences in the composition of the (dominant) species will cause differences in the soil biome (⑦⇉③), which in turn differentially affect the performance of co-occurring or later arriving species (③⇉⑥). This, then, leads to further variability in species composition across plant communities in a landscape or across neighborhoods within a plant community (priority effects)(⑥⇉⑦). **E**) **Extrinsic causes of variability**. Variability in the successional dynamics of the plant communities within a landscape can be resulting from causal factors that differentially affect species, but are themselves not affected by changes in the plant community (within the time frame of the study). For example, diversity in seed source variation across the landscape would directly cause variation in species availability, leading to differences in species composition across sites (①→⑤→⑦). More complex models of plant community succession can be constructed by combining multiple causal pathways. This framework can be used as a guide to identifying and defining the causal pathways that are thought to be most relevant within the context of a specific study or restoration project.

(Chase & Myers, 2011; Dini-Andreote *et al.*, 2015; Estrada-Villegas *et al.*, 2020). However, one of the foundational papers of succession already comprehensively discussed how predictability and variability are intrinsically linked features of ecological succession (Gleason, 1926, 1927). Environmental variables may produce temporal gradients in the plant community and its environment through plant-environment feedback dynamics, but spatial and temporal variation in these variables may also be unrelated to vegetation change; in these cases environmental variables will not be part of a feedback loop, but they will externally influence the successional feedback dynamics and drive variability among plant communities (Guichard & Steenweg, 2008). Moreover, the probabilistic nature of many of the processes involved in successional feedback dynamics, such as local dispersal, introduce a measure of variability in succession (Clark, LaDeau & Ibanez, 2004; e.g., Richter-Heitmann *et al.*, 2020). Finally, the feedback dynamics themselves may cause contingency when spatial variation in causal factors or stochastic processes lead to different species dominating the plant communities (van de Voorde, van der Putten & Bezemer, 2011).

We present a conceptual framework that is structured around the idea of a hierarchy of causes (Pickett *et al.*, 1987a) with multiple plant-environment feedback loops as the principal drivers of spatial and temporal variation in successional plant communities. This framework defines seven general causes that can be linked in feedback loops and causal pathways of various levels of complexity, each representing a model of succession (Fig. 1). The framework can aid broad comparative studies that synthesize causal pathways of succession across different study systems. In the context of local sites, specific variables can be substituted for the general causes in this framework, to define and examine further causal pathways that represent system-specific models of succession.

In the following section, we first examine the concept of plant-environment feedback loops as drivers of succession (section 2). Second, we explore how extrinsic causes of variability and plant-environment feedback loops interact to drive spatial variability in the successional dynamics of plant communities within a landscape (section 3). Finally, we illustrate how to use the proposed framework to identify, synthesize and compare the main causal pathways underpinning succession; both in terms of theoretical ideas and real study sites, where the framework can help us to identify key factors and relationships at the site and make critical decisions about data collection and study design (section 4).

2. Feedback loops as drivers of succession

Succession can be viewed as a process where a series of interacting feedback loops drive concomitant changes in the plant community (Fig. 1, ⑦) as well as in landscape context, disturbance and land-use, biotic factors and/or abiotic factors (causal factors ①-④) over time. For brevity, we will hereafter refer to these four causal factors as the ‘environment‘ in a broad sense. Models of successional feedback loops share two fundamental assumptions. The first is that, as successional plant communities develop over time, they alter their environment (Fig. 1, ⑦→①, ②, ③ and/or ④). The second is that plant species differ in their response to changes in their environment, either in terms of species availability, i.e. the availability of seeds, or in terms of species performance, i.e. the germination, establishment, growth, survival, and reproduction of plants (⑤-⑥). Both assumptions need to be true for ecological succession to occur, as combined they create the temporal and interspecific variation in demographic rates that ultimately drive succession (Pickett, Collins & Armesto, 1987b; Rüger *et al.*, 2023). Without interspecific variation in species responses, i.e., in the absence of meaningful life history variation, community level changes in plant composition over succession would not be directional (Hubbell, 2005; Gravel *et al.*, 2006). Note that our framework does not include direct species or plant-plant interactions. Instead, plant availability and performance are affected by the integrated effects of the plants in the neighborhood or larger surroundings on the environment, rather than through direct plant-plant interaction (parasitic plants are a notable exception, Bouwmeester, Sinha & Scholes, 2021). Feedback loops are the core of all successional theories and models. They are the focus of, for example, studies on plant-soil interactions (van der Putten *et al.*, 2013) or many process-based models (Larocque *et al.*, 2016), but they are often

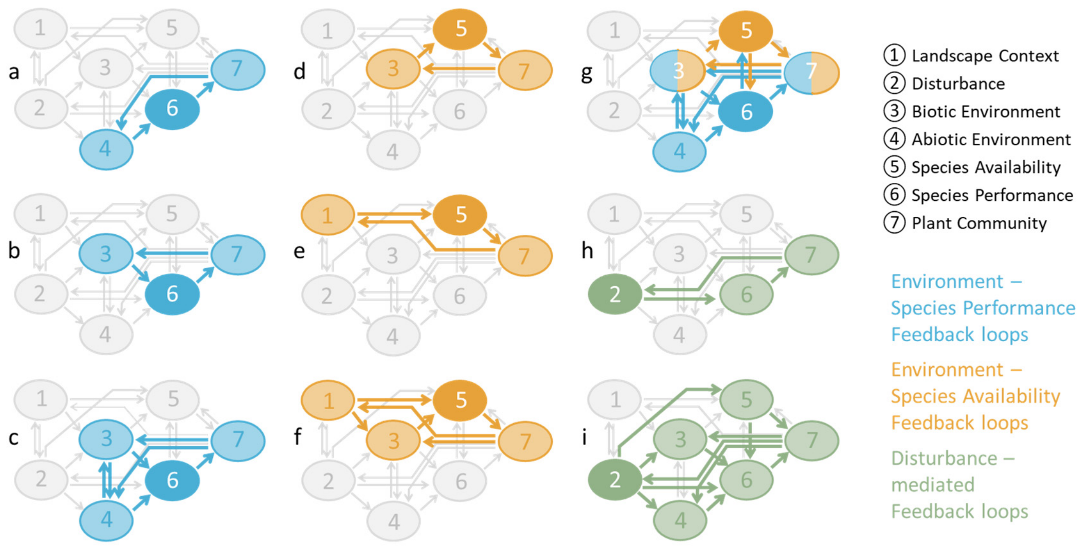


Figure 2. Examples of plant-environment feedback loops that represent models of succession, with numbers as in figure 1. **a, b, d, e, h**) The five feedback loops in the overall framework that include one single environmental factor. **c, f, g, i**) Examples of models that integrate multiple interacting feedback loops. For example, in the case of (c) those are ⑦→④→⑥→⑦; ⑦→③→⑥→⑦; ⑦→③→④→⑥→⑦; and ⑦→④→③→⑥→⑦. **a-c**) Environment-**species performance feedback loops.** Changes in the plant community drive shifts in abiotic factors (a), in biotic factors (b) or in both, including their interactions (c), which differentially affects plant species performance and hence drives changes in the plant community. **c**) These species performance feedback loops are discussed in section 2.1. **d-f)** E**nvironment-species availability feedback loops**. Changes in the plant community drive shifts in biotic factors (d), in landscape context (e), or in both (f), which differentially affects plant species availability and hence drives changes in the plant community. Discussed in section 2.2. **g**) Shifts in the plant community drive changes in both species performance and availability via impacts on abiotic and biotic factors. Both feedback loops involved are coupled through interactions between biotic and abiotic environmental factors and through trade-offs between life history attributes that relate to both species availability and performance. Discussed in section 2.4. **h-i**) **Disturbance-mediated feedback loops. h)** Disturbances differentially affect species performances, leading to changes in the plant community that subsequently increase the likelihood of recurring disturbances, and/*or* their frequency, intensity, severity, spatial pattern or scale. **i)** Effect of reoccurring disturbances may be complex, as they can differentially affect the performance or availability of species of local species pool either directly (e.g., ②→⑤) or through direct effects (e.g., ②→④→⑥) or indirect effects (e.g., ②→⑦→④→⑥) on biotic or abiotic factors. Discussed in section 3.2.

not explicitly recognized as the fundamental drivers of succession in verbally formulated models or empirical studies. There are many plant-environment feedback loops that could drive succession (Fig. 1, 2), although only a few dominate the literature (section 2.1 and 2.2). The three most commonly studied feedback loops are those between environment and species performance, environment and species availability, and disturbance and species performance. The Environment-Species-Performance (ESP) feedback loop (discussed in section 2.1) describes one of the simplest models of succession where local biotic and/or abiotic factors select for a subset of plant species that can establish and become abundant; these plant species then modify their local environment, which in turn, differentially affects plant species performance (including conspecifics) and, in consequence, plant community composition (Fig. 2a-c). The Environment-Species-Availability (ESA) feedback loop (discussed in section 2.2) describes how changes in the plant community can be driven by the interaction between species availability and the biotic environment and/or landscape context (Figs. 1, 2d-f). For example, the interaction between plant pollinators and seed dispersers at the landscape-scale drives the availability of viable seeds shaping the regeneration of the plant community (Verheyen & Hermy, 2001; Piotto *et al.*, 2019; Dent & Estrada-Villegas, 2021). The Disturbance-mediated feedback loop (DM) involves successional interactions between recurring disturbances, local environment and species performance and availability (Fig. 2h, i). When disturbances affect early successional species more than late successional species, they accelerate succession (e.g., Ross *et al.*, 2001). However, when dominance by a specific group of disturbance-adapted species increases the likelihood or intensity of recurring disturbances, this can lead to arrested succession. Because this feedback loop involves species-specific effects, variation in the identity of the early colonizers matters. Therefore, the DM feedback loop is discussed in more detail in section 3.2, in the context of priority effects and arrested succession. We further discuss some simple alternative models of feedback loop-driven species replacement (section 2.3) and how more complex models of succession can integrate multiple causal factors and interactions between the different feedback loops in section 2.4.

2.1 Species performance feedback loops

Most succession models are variants of a feedback loop that involves species performance and local environment, which we refer to as: the Environment-Species-Performance (ESP) feedback loop (Fig. 2a-c). This feedback loop applies when species colonize a recently disturbed area and, once established, modify the local abiotic and/or biotic environment. Over time, the environment becomes less habitable for the initial colonizing species and/or more habitable for other species with different environmental requirements and life-history traits. The most well-studied example is the feedback between forest plant communities and light availability (Fig. 2a) (Bazzaz & Pickett, 1980; Ross, Flanagan & Roi, 1986; Nicotra, Chazdon & Iriarte, 1999). In forest succession, the tree species that initiate succession are typically fast-growing, light-demanding species. As these trees grow and the forest canopy develops over succession, light levels in the understory decrease (van Breugel *et al.*, 2013; Matsuo *et al.*, 2021). This reduction in light availability increases seedling mortality of light-demanding species, limits the recruitment of light demanding species and favors the recruitment of more shade-tolerant species (Lin *et al.*, 2014; Lai *et al.*, 2021).

Another widely studied group of successional feedback loops is between plants and soils. Plant communities influence chemical, physical, and biological soil processes and properties, such as soil nutrient concentrations (Fig. 2a)(Tilman, 1985), soil moisture levels and paludification (Fig. 2a)(Ross *et al.*, 2001; Jacobs *et al.*, 2015; Schaffhauser *et al.*, 2017), the soil microbiome (Fig. 2b)(van der Putten, Dijk & Peters, 1993; Kardol *et al.*, 2007), soil invertebrates (Fig. 2b)(Deyn *et al.*, 2003) and the biogeochemical processes that regulate nutrient supply (Fig. 2a,b)(Epihov *et al.*, 2021). Soil properties then differentially influence the success of colonizing plant species, which sets in motion further plant-soil feedbacks that can speed up or slow down plant species replacement over succession (van der Putten *et al.*, 2013). Succession in an European heathland illustrates this plant-soil feedback; the early colonizing shrub species, *Erica tetralix*, produces poor-quality litter that leads to organic matter build up and release of mineral nitrogen, favoring competitive replacement by the grass species *Molinia caerulea* (Berendse, 1998).

The feedback between plants and soil microbes (i.e., fungi, bacteria, archaea, protists, and viruses) can involve positive or negative impacts on subsets of plant species, and both can drive species replacement (van der Putten *et al.*, 2013). For example, the buildup of species-specific microbial pathogens in the rhizosphere of early colonizing plants can exclude early-successional species and select for more pathogen-resistant late-successional species (van der Putten *et al.*, 1993; Kardol, Bezemer & van der Putten, 2006; Kardol *et al.*, 2007). Early successional species may also have weaker defenses and suffer more negative feedbacks from pathogenic soil bacteria and fungi than later successional species, or can be negatively affected by soil biota associated with later successional species (Grime & Jeffrey, 1965; Kulmatiski *et al.*, 2008; van de Voorde *et al.*, 2011; Zhang *et al.*, 2021). Positive feedbacks between plants and their microbial mutualists may also drive shifts in community composition over time, via a feedback loop between the biotic (bacteria or fungi) and abiotic soil environment and species performance (Fig. 2c). In that case, positive plant-soil feedbacks need to be more common among late-successional species; otherwise, these positive feedbacks would not drive predictable replacement of early- by late-successional species. For example, changes in the dominance and composition of mycorrhizal fungi during secondary forest succession can promote shifts in tree species composition by preferentially improving the performance of late-successional plants over early successional species

(Wubs *et al.*, 2016; Sulman *et al.*, 2017). Mycorrhizal fungi have been shown to both trigger succession and drive longer-term changes in plant composition in various ecosystems, such as temperate forest in coastal dune areas and temperate grassland succession on an abandoned coalmine (Allen & Allen, 1988; Ashkannejhad & Horton, 2006).

Generally, several ESP feedback loops interact simultaneously to shape succession. For example, while change in light availability in the understory is considered a key driver of species turnover in forest succession (Finegan, 1984), recent trait-based studies suggest that soil conditions may also contribute to the shift from resource acquisitive to more conservative ecological strategies during forest succession (both Fig. 2a)(Pinho *et al.*, 2018; Caplan *et al.*, 2019; Hogan *et al.*, 2020). In arid systems, characterized by heat and drought stress, stress-tolerant nurse pioneer plants ameliorate the microclimate and facilitate the establishment of later-successional species, which subsequently outcompete the less competitive nurse pioneers for resources such as light and water (both Fig. 2a)(Gómez-Aparicio *et al.*, 2004; Lebrija-Trejos *et al.*, 2010; Badano *et al.*, 2016). In another example from Mount St Helens, USA, multiple interacting feedback loops define primary succession on volcanic substrates (Fagan, Bishop & Schade, 2004; del Moral & Rozzell, 2005). First, the nitrogen-fixing forb *Lupinus lepidus* colonizes early, and increases soil organic matter, total N and microbial activity (Halvorson, Smith & Franz, 1991; Halvorson, Smith & Kennedy, 2005; Fagan *et al.*, 2004), promoting the recruitment, growth and diversity of other plant species (Fig. 2a)(Morris & Wood, 1989; Titus & Del Moral, 1998; del Moral & Rozzell, 2005). At the same time, the increasing abundance of *L. lepidus* attracts higher densities of species-specific lepidopteran herbivores, which can reduce its growth and fecundity and levels of abundance (Fig. 2b)(Fagan *et al.*, 2005). Thus the plant-herbivore feedback loop can alter the pace and pattern of primary succession by impacting the plant-soil feedback loop and slowing down soil formation (Bishop, 2002)

2.2 Species availability feedback loops

In regrowing vegetation, successional changes in the plant community can drive shifts in pollination and propagule dispersal through changes in the abundance, composition and fecundity of flowering and fruiting plants (source limitation; Clark et al. 2007; Schupp et al. 2019) as well as in that of their pollination and dispersal vectors (pollinator and disperser limitation; Ghazoul, 2005; Zwolak, 2018). As these factors alter the availability of plant species, we define this as the Environment-Species-Availability (ESA) feedback loop (Fig. 2d-f). The abundance and species composition of plants and their pollination and dispersal vectors are strongly determined by past and current variation in landscape composition, configuration and connectivity (Mitchell et al., 2015). For example, agricultural landscapes support low densities of seed sources (Fig. 2e), as well as depauperate communities of pollinators and dispersers whose abundance and movement is limited by an inhospitable landscape matrix (Fig. 2d)(Breitbach *et al.*, 2012; Caughlin, Elliott & Lichstein, 2016). Although the effect of fragmentation on succession has been well studied (see Arroyo-Rodríguez et al., 2017), the underlying processes, i.e. pollination and propagule dispersal, are still relatively overlooked (Dent & Estrada-Villegas, 2021).

At the patch scale, dispersal could drive successional feedback loops via shifts in the successional plant community that differentially affect pollinators and dispersers and thus alter dispersal of pollen and seeds into the same community. For example, in fragmented forest landscapes, the diversity and density of tree seeds declines sharply with distance from forest edge (Cubina & Aide, 2001), and seed rain in open fields is dominated by a small number of species dispersed by wind, frugivorous bats and small birds (Duncan & Chapman, 1999; Wijdeven & Kuzee, 2000), typically generalist and light-demanding plant species. Forests regenerating within these contexts gain height and structural complexity over succession, attracting a higher number, diversity and size range of frugivorous birds, bats and ground-dwelling mammals (Fig. 2d)(Carrara *et al.*, 2015; Deere *et al.*, 2020; Estrada-Villegas *et al.*, 2022; Coddington *et al.*, 2023.). These animals disperse seeds from a greater diversity of species (Parrotta, Knowles & Wunderle, 1997; Piotto *et al.*, 2019). In addition, the structure of older successional forests may be less attractive to early-successional bird and bat species (Carrara *et al.*, 2015) and may act as a barrier to wind dispersal (Qin *et al.*, 2022) resulting in a shift in the dominant seed dispersal mechanisms (Dent & Estrada-Villegas, 2021). Ultimately, forest succession not only alters the composition of seeds dispersed into the site from elsewhere, but also the production of seeds within the resident plant community (Fig. 2f, ⑤→⑦→⑤)(Bischoff, Warthemann & Klotz, 2009). With successional age, the proportion of locally produced seeds from large-seeded, shade-tolerant species in seed rain increases while the proportion of seeds from outside the patch decreases (Huanca Nuñez, Chazdon & Russo, 2021). Combined, these processes create a feedback loop that can lead to predictable shifts in the composition of the plant community (Dent & Estrada-Villegas, 2021).

At the landscape scale, successional plant communities on abandoned fields increase the abundance of native plant species in the meta-community (Fig. 2e), provide wildlife habitat (Fig. 2d) and improve landscape connectivity (Fig. 2f, ⑦→①→③→⑤→⑦), exerting a positive influence on the abundance, diversity and movement of animal pollinators and dispersers (Fig. 2f)(Alonso *et al.*, 2010; de la Pena-Domene, Minor & Howe, 2016; Bennett *et al.*, 2020; Eeraerts *et al.*, 2021). This, in turn, positively affects species availability in local plant communities. These feedback dynamics will drive a directional shift in species composition if regeneration of plant communities positively impacts late-successional specialists more strongly than disturbance-adapted or generalist pollinator and disperser species (Carrara *et al.*, 2015), thus improving the fecundity and dispersal of their co-dependent plant species relative to that of other plant species (Rodger *et al.*, 2021). In summary, succession can be caused by feedback dynamics where the changing composition of plant communities drives changes in the abundance and composition of the seed disperser and pollinator communities and vice versa (Fiedler, Landis & Arduser, 2012; Dent & Estrada-Villegas, 2021).

2.3 Mechanisms of successional species replacement

Inherent to all plant-environment feedback loops is the premise that vegetation-driven changes in causal factors 1-4 lead to successional species replacement, where a subset of species is benefited or hindered *relative* to other species in the local species pool (Fig. 3). At the most basic level, one can imagine three simple mechanisms of successional species replacement. Each of these mechanisms can be driven by most or all plant-environment feedback loops (Fig. 3) and all three are related to classic concepts of succession such as the relay and initial floristic models (Egler, 1954) or facilitation, tolerance and inhibition models (Connell, Noble & Slatyer, 1987). Because ecologists often differ in how they interpret these verbal models (Finegan, 1984; Wilson *et al.*, 1992; McCook, 1994), we will refrain from a direct comparison (for an critical comparison of species replacement concepts, see: Pickett *et al.*, 1987b). For the first mechanism, we assume favorable local conditions early in succession, such that all species from the local species pool are able to arrive and establish soon after disturbance. This first cohort then creates environmental conditions that some species cannot tolerate. At the landscape scale, *later* successional communities therefore would be composed of a subset of species present in earlier successional communities (***Fig. 3a***). Alternatively, we can assume that only a subset of plant species (or their pollinators or dispersers) tolerate the environmental conditions characteristic of early successional sites, e.g., no plant cover, high irradiance and temperatures, water stress, and compacted or nutrient-depleted soils. As these early colonizers modify local conditions, new species are enabled to arrive or establish (Halvorson *et al.*, 2005; Brooker *et al.*, 2008; Koffel *et al.*, 2018). In this case, early successional communities are a subset of species found in later successional communities (***Fig. 3b***). This process may be especially important in ecosystems with strong biotic and abiotic stressors, such as many dry

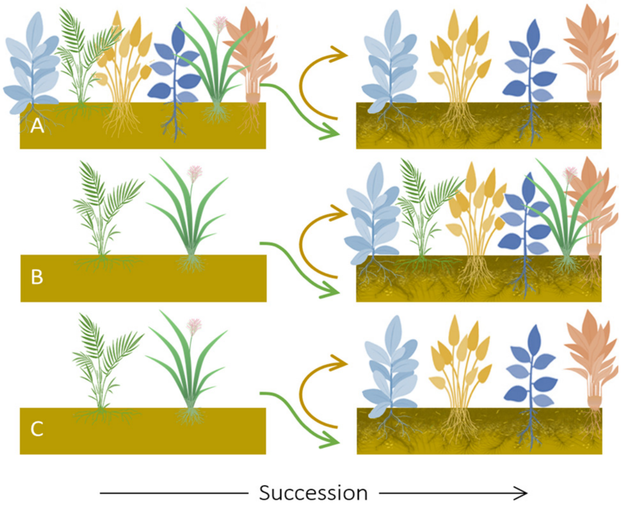


Figure 3. The three simplest mechanisms of successional species replacement in which plants affect their environment (for example, edaphic conditions; green arrows) and these changes in their environment, in turn, benefit or adversely affect the performance of a subset of species relative to that of the other species (brown arrows). **A**) All species of the landscape species pool are able to establish under early successional conditions, but only a subset of plant species tolerate the later successional conditions. **B**) Only a subset of plant species tolerate the adverse environmental conditions early in succession. Upon establishment, they ameliorate the local environment and thus enable all species in the landscape species pool to establish. **C**) The third option requires life-history tradeoffs between superior performance under- or tolerance of early versus late successional conditions. For all three mechanisms, the same line of reasoning can be applied with regard to species availability. The different plant types in the figure are best interpreted as functional groups of plant species, each with a specific suite of functional traits, rather than as individual species. See section 2.3 for further details.

ecosystems where low water availability, high temperatures, hard soil crusts and grazing limit plant recruitment, growth and survival early in succession (Rousset & Lepart, 1999; Lebrija-Trejos *et al.*, 2011).

In most theoretical models of succession, species replacement is driven by life history tradeoffs, whereby some species are better adapted to- or better able to take advantage of early successional conditions than other species, which are better adapted to later successional conditions. Shifts in plant community composition will reflect those tradeoffs (***Fig. 3c***). The most widely studied life history trade-offs are those between resource conservation and hign survival on the one hand and resource capture and fast growth (Wright *et al.*, 2004) and/or early and high fecundity (Muller-Landau, 2010) on the other hand (Díaz *et al.*, 2016; Maynard *et al.*, 2022). Evidence for these tradeoffs has been found across a wide range of vegetation types (Bruelheide *et al.*, 2018). Recently additional trade-offs have been shown to play important roles in different vegetation types, for instance the trade-off between stature and recruitment in secondary forest succession in dry and moist Neotropical regions (Rüger *et al.*, 2023), or the trait-based fungal collaboration trade-off where do-it-yourself resource uptake is contrasted to outsourcing of resource uptake to mycorrhizal fungi (Bergmann *et al.*, 2020).

Life history trade-offs relate to interspecific differences in resource allocation to specific functions and their associated traits (Wright *et al.*, 2004; Chave *et al.*, 2009; Reich, 2014), where some species allocate more resources to traits that promote resource acquisition, rapid growth or early and copious reproduction under favorable conditions, while others allocate more to traits that reduce mortality under stressful conditions (Westoby *et al.*, 2002; Wright *et al.*, 2010). From this perspective, successional shifts in species are the result of a shift from species with traits in balance with the earlier environment to species with traits in balance with the later environment (Lebrija-Trejos *et al.*, 2010; Craven *et al.*, 2015; Kelemen *et al.*, 2017).

The three species replacement mechanisms (Figure 3) predict different patterns of trait composition and diversities (Raevel, Violle & Munoz, 2012; Boersma *et al.*, 2016). In the first species replacement mechanism (‘***wide-to-narrow trait range***’, Fig. 3a), species with all trait combinations from the trait space of the local species pool can colonize due to benign local environmental conditions. As the plant community develops over time, increasing competition leads to limitation of one or more resources, which increasingly restricts the range of viable trait combinations and selects for communities dominated by traits associated with resource conservation, such as low specific leaf area, leaf N and P levels and high wood density, leaf toughness and chemicals that defend against enemies. This has been found in, e.g., temperate grassland and forest succession (Strandberg, Kristiansen & Tybirk, 2005; Shipley *et al.*, 2006; Hédl, Kopecký & Komárek, 2010; Lasky *et al.*, 2014). The second species replacement mechanism (***‘narrow-to-wide trait range’***, Fig. 3b) illustrates an opposite trajectory, where communities characterized by traits that reflect adaptations to environmental stress and resource conservation shift to communities exhibiting a functional composition representative of the entire local species pool. This has been found in, e.g. dry tropical forest succession (Poorter *et al.*, 2019). The third species replacement mechanism (‘***trade-off***’, Fig. 3c) predicts a shift in functional composition from trait values associated with high fecundity, efficient dispersal and/or resource acquisition towards trait values associated with resource conservation (Bazzaz, 1979; Finegan, 1996). Because in general only a small proportion of the species pool has species with life history strategies specifically adapted to take advantage of large disturbances (Turner, 2008), a further prediction of the third mechanism is that of increasing functional diversity in parallel with the predicted shift in functional composition. The combination of these two patterns has been observed in various vegetation types, such as temperate herbaceous plant communities (Backhaus *et al.*, 2021) and humid tropical forests (Poorter *et al.*, 2021).

The three mechanisms are best conceptualized in terms of gradual shifts in species-specific arrival, establishment and survival probabilities along a successional gradient defined by multiple environmental variables, rather than in terms of discrete groups and successional stages. Moreover, different species replacement mechanisms may act at a given time and different mechanisms may dominate different 'phases' of succession. The same species may partake in different species replacement mechanisms at different times along the successional gradient (Pickett *et al.*, 1987b). What this section highlights is that species replacement mechanisms are all, ultimately, variants of the same fundamental mechanism of succession: plant-environment feedback loops.

2.4 Interacting feedback loops and endpoints to succession

Studies on plant community succession typically investigate single feedback loops, (e.g., plant-light) yet it seems likely that succession is influenced or shaped by multiple interacting feedback loops (Pickett *et al.*, 2011). Integrating multiple feedback loops into more complex causal pathways can thus help us to design studies that (i) assess the relative importance of different feedback loops in shaping successional dynamics and (ii) that improve our ability to predict successional processes. An example is a causal pathway that includes both the Environment-Species-Availability and the Environment-Species-Performance feedback loops (Fig. 2g)(Pacala & Rees, 1998). In this pathway, successional changes in the plant community affect local scale processes that affect both species performance (e.g. forest canopy closure selecting for shade-tolerant species; Fig. 2g, ⑦→④→⑥) and species-availability processes (e.g. increasing canopy complexity attracts more dispersers; Fig. 2f, ⑦→③→⑤) to shape succession in the long term. In this context, widely dispersed plant species with high fecundity often initiate succession (van Breugel *et al.*, 2013; Makoto & Wilson, 2019; Martínez-Ramos *et al.*, 2021). The two feedback loops in this causal pathway are further linked through life history trade-offs: traits that promote species availability often trade off against traits that promote tolerance and persistence in stressful habitats (Fig. 2g, ③ ⇄ ④)(Turnbull *et al.*, 2004; Muller-Landau, 2010; Beckman, Bullock & Salguero-Gómez, 2018).

Viewing succession as a process involving multiple concurrent and interacting plant-environment feedback loops also may clarify why succession can continue long after a particular feedback loop has ended. For example, during forest succession, if understory light levels stop declining after canopy closure (van Breugel *et al.*, 2013; Matsuo *et al.*, 2021), the feedback loop between the plant community, understory light levels and seedling recruitment (Fig. 1a) (Montgomery & Chazdon, 2002) ceases to be the primary driver of successional change at the stand level (but may still operate as part of gap dynamics). It will then still take centuries until the forest structure and composition become similar to old-growth forests, due to the longevity of trees (Rüger *et al.*, 2020; Poorter *et al.*, 2021). During that time, other feedback loops may become more important for ongoing successional change in the seedling community, such as a plant-disperser feedback loop (Fig. 1b; Huanca Nuñez *et al.*, 2021). This suggests that studies of succession need to consider multiple feedback loops that capture the temporally overlapping mechanisms driving succession, and that we may view successional change through the lens of multiple feedback loops.

Often, succession is considered to have reached an endpoint when the plant community has arrived at a climax or equilibrium state defined by climate, edaphic conditions and biotic environment (Clements, 1936; Perry, 2002; Van Der Valk, 2013). A common approach for determining how close the successional plant community is to its endpoint is a comparison with a reference site that is (1) similar in terms of edaphic conditions, climate and species pool and (2) undisturbed and thus assumed to be a typical representation of the local steady state or equilibrium vegetation (e.g., Anderson, 2007; Johnson & Miyanishi, 2008; Poorter *et al.*, 2021). The theoretical and practical issues with this approach have been extensively discussed elsewhere (Gibson, 1996; Chazdon, 2014). Our framework implies a more process-oriented view of the endpoint to succession where succession continues as long as a change in the plant community drives a change in the environmental variable(s) and *vice versa*. Individual successional feedback loops have an endpoint, which is defined as when change in the plant community ceases to drive a directional and continuous change in the environment. This implies that succession ends when the last of the successional plant-environment feedback loops stops operating at the community level, i.e. when species turnover reaches a stable state ('stationary'; Wolkovich et al., 2014).

3. Variability in succession

Successional plant communities within a landscape can exhibit highly variable trajectories, even when disturbance and land-use histories, environmental factors and landscape context are very similar, (Norden *et al.*, 2015). Therefore, we need to answer two fundamental questions to understand the successional dynamics of plant communities within a landscape,: (1) what are the (dominant) feedback processes that drive similar successional trajectories among the plant communities within the meta-community (Fig. 4, green arrow), and (2) what are the causes of spatial variability in successional

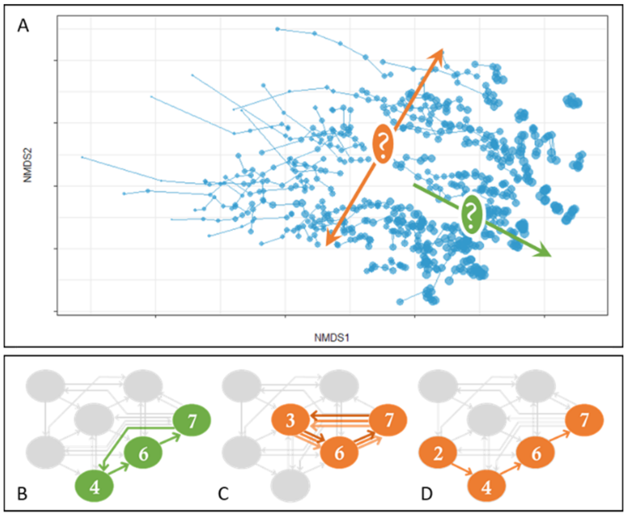


Figure 4. Predictability and variability in successional dynamics across plant communities in a landscape. **A**) The NMDS plot shows shifts in the species composition of 0-32 year old secondary forests over a period of 8 years. Dots connected by a line represent the same plot but different censuses, and dot size is proportional to stand basal area (van Breugel & Hall, unpublished data). The arrows represent the idea of two main axes of variation in the species composition of the plant communities: a common directional shift over time (green arrow), and spatial variability (orange arrow). **B-D**) Examples of processes that drive directionality and variability in succession. In our framework, the driver of directionality is a plant-environment feedback loop (example: B), while the drivers of variability are either plant-environment feedback loops with priority effects (example: C), extrinsic causal factors that themselves are not part of the feedback loop (example: D) or a combination of interacting extrinsic factors and feedback loops.

dynamics (Fig. 4, orange arrow)? These two questions are inextricably intertwined, an insight that was already key to the foundational work of Gleason (1926, 1927). Plant-environment feedback loops rely on deterministic mechanisms that, in principle, drive predictable shifts in the plant community (section 2).

However, because they involve stochastic processes, such as mortality and seed dispersal, there will always be a degree of variability in the successional dynamics of plant communities (Clark *et al.*, 2004; e.g., Richter-Heitmann *et al.*, 2020). Feedback loops can drive further variability if the identity of the dominant species among the early colonizers varies among plant communities (Kardol, Souza & Classen, 2013; Weidlich *et al.*, 2021). If the dominant species differ in their resource use, how they modify the local environment, or simply in longevity, plant-environmental feedback loops themselves may bring about variability in succession through '***priority effects'*** (Fig. 4c)(Fukami, 2015). We discuss this in sections 3.1 and 3.2. When environmental factors (Fig. 1, causal factors 1-4) differentially affect plant species performance or availability, but are not affected by successional changes in the plant community themselves, then they are ***extrinsic causes*** of variability in succession. These extrinsic causes may create spatial heterogeneity among similar-aged plant communities within the same landscape (discussed in section 3.3) or variation in successional trajectories among landscapes along environmental or anthropogenic gradients at much larger spatial scales (Fig. 1, causal factors 8-10)(e.g., Wright & Fridley, 2010; Poorter *et al.*, 2019; Prach & Walker, 2020; Coradini, Krejčová & Frouz, 2022). Finally, extrinsic causal factors such as previous land-use may cause differences in the identity and dominance of the early colonizers, which may lead to priority effects (section 3.4).

3.1 Feedback loops with priority effects as drivers of variability

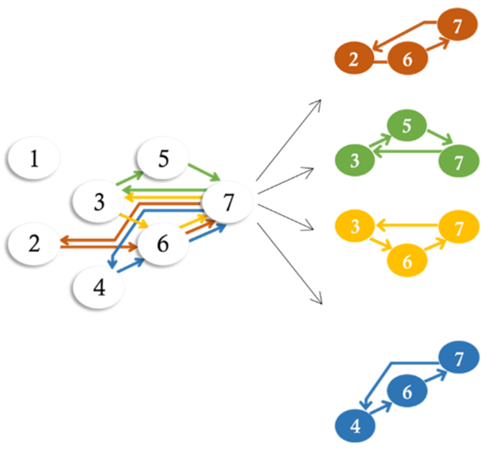
Variation in the composition of initial colonizers may directly influence the recruitment of other species from the local species pool and thus trigger historically contingent successional trajectories through priority effects (Fig. 4b). This is best understood in contrast with the alternative option, where early colonizing species do ***not*** substantially differ in their effect on the environment or in their demographic characteristics, such as longevity, and so shifts in local site conditions occur independently of initial species composition and are instead driven by community-level vegetation changes, including above- and below-ground biomass, leaf area index, and canopy height. Most simulation models of forest succession are primarily concerned with these stand-level environmental feedbacks (Huston & Smith, 1987; Pacala *et al.*, 1996; Larocque *et al.*, 2016). For priority effects to result in contingent successional trajectories, reassembling plant communities across a landscape must be dominated by different subsets of species that differ in their effects on the environment (see section 2.3; Mouillot *et al.*, 2013; Avolio *et al.*, 2019). Empirical evidence for ESP feedback loops with priority effects as drivers of variability in succession mostly comes from controlled experiments or plant communities involving limited numbers of mostly short-lived species in temperate grassland and herb-dominated ecosystems (Kardol *et al.*, 2007, 2013; Sikes, Hawkes & Fukami, 2016). From a theoretical perspective, the resource ratio hypothesis (Tilman, 1985) predicts that differential resource use by the first colonizers causes variation in the relative availability of two or more limiting resources. This, in turn, will determine the identity of the species that replace these initial colonizers, leading to divergent successional trajectories.

Priority effects may also result from feedback loops between plants and their biotic environment. Different plant assemblages have different soil microbiomes, and this may lead to differential performance among late colonizers, potentially promoting variation in floristic composition over succession (Kardol *et al.*, 2007; van de Voorde *et al.*, 2011). Studies on the effects of plant-herbivore feedback interactions on primary succession on Mount St. Helens (NW USA; Bishop, 2002; Fagan *et al.*, 2004) show that not only the timing of plant species' arrival, but any process that affects abundance early in succession, could lead to priority effects. For instance, the timing of herbivore arrival after *Lupinus lepidus* plants – a nitigen-fixing herb species that facilitates succession – established varied across the landscape, causing spatial heterogeneity in the extent to which herbivory slowed down or even reversed the growth of *L. lepidus* patches, thereby influencing successional trajectories (Fagan *et al.*, 2005). Priority effects may have long-lasting soil legacy effects that influence plant re-assembly processes long after the initial colonizers have disappeared (Helsen, Hermy & Honnay, 2016; Pickett *et al.*, 2019)

At larger scales, priority effects can also develop if early colonizers differentially affect pollination and dispersal, and thus species availability, through their (facilitative) effects on the abundance and movement of pollination and dispersal agents (ESA feedback loop, section 2.3). Some plant species may attract high numbers of pollinators (for instance by massive synchronous flowering) which, in turn, may reduce pollen limitation and increase the diversity of natural recruitment in successional plant assemblages (Fontaine *et al.*, 2005). Similarly, some plant species are particularly attractive to seed dispersers because they produce nutritionally rewarding fruit crops, or because at the population level they fruit at times of the year that other fruits are not available. In tropical forests, for instance, fruiting trees of the genus *Ficus* often attract a wide diversity of bats, birds and mammals, which can promote the assembly of more diverse seedling communities later in succession relative to locations without fig trees (de la Peña-Domene, Martinez-Garza & Howe, 2013; Cottee-Jones *et al.*, 2016). This priority effect is often an important consideration in ecological restoration strategies, and restoration practitioners often select species for active seeding or planting based on their perceived attractiveness to pollinators or dispersers (Menz *et al.*, 2011; Jones & Davidson, 2016; Holl, Joyce & Reid, 2022).

3.2 Feedback loops leading to arrested succession

Arrested succession results in a plant community that is stalled in an early successional state for a prolonged period of time. In our framework, we identify two types of causal pathways that can drive arrested succession. The first is the ***disturbance - mediated (DM) feedback loop*** (Fig. 2h, i). For example, in human-modified landscapes, invasive grasses can prevent the establishment of forest tree species by facilitating recurring anthropogenic dry season fires (Hooper, Legendre & Condit, 2005). While these fires kill tree seedlings and saplings, grasses have well protected buds and can resprout quickly using the reserves in their belowground stolons or rhizomes, thus outcompeting tree seedlings and preventing the progression of forest succession (Styger *et al.*, 2007; Saltonstall & Bonnett, 2012).



Bracken stands facilitate recurring and high-intensity fires, resulting in very low tree seedling survival[1,2].

Lower densities of seed dispersers in bracken negatively affect seed dispersal (lower seed rain)[3,4]

Higher densities of seed predators leading to low rates of seed survival and seedling establishment[4,5]. Relatively low palatability[6].

Differential effects on seedling establishment and survival through physical inference by decomposing fronds and litter[9,10, but see 10], through shading by frond canopy[5,8,10], soil acidification[11], or allelopathy[12-15 but see 5].

References: [1]Adie *et al*. 2011; [2]Roos et al. 2010; [3]Maya-Elizarrarás & Schondube 2015; [4]Ssali *et al*. 2018; [5]Den Ouden 2000; [6]Vetter 2009; [7]Cooper-Driver *et al*. 1977; [8]Humphrey & Swaine 1997; [9]Dolling 1996; [10]Ssali *et al*. 2019; [11]Johnson-Maynard et al., 1998; [12]García-Jorgensen et al. 2021; [13]Mira et al. 2021; [14] Jatoba *et al*. 2016; [15]Dolling et al. 1994

Figure 5. Bracken fern (*Pteridium aquilinum* [L.]) has been found to slow down or arrest forest succession across a wide range of forest biomes, and different positive feedback loops have been hypothesized to explain this. In reality, tree regeneration in bracken fern stands seems to be affected by the simultaneous operation and interaction of multiple feedback loops (upper-left diagram), with the relative importance of each single positive feedback loop (single-colored diagrams) depending on the specifics of the particular site. Numbered ovals are as in figure 1. In-text numbers refer to the references in the lower box, which are examples of empirical studies that addressed the proposed feedback loops.

The second feedback loop causing arrested succession is the ***ESP feedback loop*** with ***strong priority effects***, in which a specific (group of) early successional species affect their environment in a way that ultimately benefits their own persistence relative to that of other species, or inhibits the establishment of other species (Weidlich *et al.*, 2021). For example, studies of landslides in Puerto Rico found that initial colonization by ferns inhibited forest succession, while early colonization of landslides by fast-growing trees led to successional replacement by more shade tolerant, longer-lived tree species over time (Walker *et al.*, 2010a). Succession on these landslides thus depends on the identity of plant species that initially colonize and dominate the site, with one of the trajectories (fern colonization) leading to a form of arrested succession (Slocum *et al.*, 2004).

Arrested succession is often the result of multiple, co-occurring DM and ESP feedback loops, which is nicely illustrated by the extensively studied case of bracken fern (*Pteridium* sp.; Fig. 5). Dense stands of this fern species have been shown to inhibit tree regeneration across a wide range of forest ecosystems and through a variety of mechanisms, including resource competition, as physical barriers to dispersal, by harboring high densities of seed predators, or allelopathy (den Ouden, 2000; Marrs *et al.*, 2000; Ssali, Moe & Sheil, 2018). Feedback loops often reinforce each other in keeping plant communities in early successional states. For example, in many temperate forests, disturbances such as fire or logging favor highly competitive invasive herbaceous species (strong resource competition) and also lead to higher browsing pressure of ungulates on tree seedlings and saplings (which can be considered a form of chronic and selective biotic disturbance) that, combined, strongly impacts tree regeneration (Vavra, Parks & Wisdom, 2007; Laskurain *et al.*, 2013; Maxwell, Rhodes & St. Clair, 2019; Hanberry & Faison, 2023).

3.3 Spatial variation in extrinsic causal factors

Variability in the successional trajectories of plant communities can also be driven by ***extrinsic factors*** that differentially affect plant species performance or availability, but that act outside of the plant-environment feedback loops (Figs. 4d). Perhaps the simplest conceptual model reflecting this is that of a hierarchical series of dispersal and environmental filters that vary across a landscape and filter out different subsets of species from a larger species pool (Weiher & Keddy, 1995). Variation in the floristic composition of similar-aged successional communities within a landscape has been related to characteristics of and legacies from the prior land use (Jakovac *et al.*, 2021), differences in soil type and fertility (Pinho *et al.*, 2018; van Breugel *et al.*, 2019), patch size (Phillips & Shure, 1990; Shumway & Bertness, 1994), surrounding vegetation cover, and landscape connectivity (Damschen & Brudvig, 2012; Arroyo-Rodríguez *et al.*, 2017). At larger spatial scales (regional to continental), successional trajectories are constrained by natural and anthropogenic factors and processes (Walker & Wardle, 2014), such as climate (e.g., Poorter *et al.*, 2016), soil types (e.g., Sande *et al.*, 2022), biogeography (Jakovac *et al.*, 2022), hunting pressure (Chritz *et al.*, 2016), and landscape transformation (Pérez-Cárdenas *et al.*, 2021).

The importance of extrinsic factors in driving species replacement may shift as succession proceeds. For example, a study on tropical forest succession in Panama found that spatial heterogeneity in soil fertility caused variability in species composition, but this relationship weakened over the course of succession as the canopy closed and light became the dominant limiting factor (van Breugel *et al.*, 2019). Environmental gradients may also cause variation in the nature of successional feedback loops (Bazzaz, 1979; Wright & Fridley, 2010). For example, it has been postulated that the intensity of facilitation and competition for different resources, which drive different interacting ESP feedback loops, shift along soil resource gradients (Keddy, 2001; Koffel *et al.*, 2018). Facilitation tends to be important in stressful environments, and therefore also early in succession, while facilitation is less important in benign environments or later in succession (Brooker *et al.*, 2008). The dominant competition processes can change across gradients of soil fertility, and shift from competition for belowground resources on nutrient poor soils to aboveground competition for light on fertile soils (Putz & Canham, 1992; Wilson, 1999). Similarly, the relative importance of the ESP and ESA feedback loops can be expected to shift along gradients of environmental conditions (Fraaije *et al.*, 2015), landscape context (van Breugel *et al.*, 2019; Sonnier, Johnson & Waller, 2020) and land-use dynamics (Jakovac *et al.*, 2021). Thus spatial variability in extrinsic causal factors can be reflected in the relative strength of different feedback loops and variables, leading to spatial variation in successional dynamics and trajectories across the landscape.

3.4 Land-use dynamics as an ultimate driver of variability

In human-modified landscapes, spatial-temporal land use dynamics are an important source of variability in succession (Arroyo-Rodríguez *et al.*, 2017; Jakovac *et al.*, 2021). At the local scale, variation in land use practices (Fig. 1, ②, e.g., use of fertilizer, herbicides and pesticides, livestock management, tilling or ploughing, hunting, or slash-and-burn management) will determine species availability and species performance directly (⑤ and ⑥; e.g., seed bank survival) or through its effect on biotic factors (③; e.g., soil biota, wildlife) and abiotic factors (④; e.g., soil bulk density, hydraulic conductance and soil fertility)(Barnes *et al.*, 2017; Veldkamp *et al.*, 2020). At the landscape scale, land-use dynamics determine the spatial-temporal distribution of patches of native vegetation and agriculture, which affects habitat availability and connectivity, and hence the abundance and spatial distribution of propagule sources (①→⑤) and their pollinators and biotic seed dispersal vectors (①→③)(Pérez-Cárdenas *et al.*, 2021). Land use dynamics also shape the abundance and distribution of pathogens and herbivores and, hence, species performance (①→③→⑥)(Szefer *et al.*, 2020). Moreover, land use characteristics and landscape context may co-vary within or across landscapes (⑩→①+②)(Lawrence, Peart & Leighton, 1998; Lawrence, Suma & Mogea, 2005), in which case it is difficult to disentangle their effects on succession. The impacts of land-use on succession thus involve multiple interconnected feedback loops and extrinsic causes of variability. A major challenge when studying vegetation succession is to identify those causal pathways that are responsible for most of the variation within or across landscapes (Fig. 6) or, from a management perspective, identify pathways that can feasibly be targeted with specific restoration measures.

In diverse plant communities such as tropical forests or temperate grasslands, previous and current land use, spatial heterogeneity in environmental factors and priority effects may all affect succession (e.g., Clark, Knops & Tilman, 2019; Jakovac *et al.*, 2021). For example, variation in disturbance history or edaphic conditions may lead to local species assemblages that are dominated by different subsets of

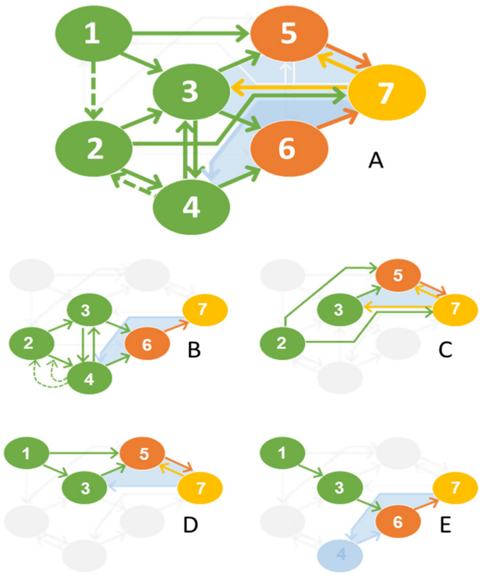


Figure 6. Complex effects of land-use on succession. **A**) A complex model of land use as a driver of variability in forest succession. This model can be deconstructed into four causal pathways that originate in either land use history (B, C) or landscape context (D, E). **B**) Land-use alters physical, chemical and biological soil variables through multiple interacting causal pathways (②→(③⍰ ④)→⑥). Although this pathways implies that land-use and soil attributes are the ultimate and proximate causes of variation in species performance, the other way around edaphic factors may drive land use decisions (④⍰ ②) and moderate the effects of land-use on abiotic and biotic soil attributes (④⍰ (②→④)). **C**) land-use drives variation in the local availability of propagule sources through its impact on the soil seed bank and root stock (②→⑤) or because of differences in the number and identities of the trees that were conserved or introduced as land-use components. These trees can be direct seed sources (②→⑦→⑤) or affect species availability by attracting dispersers (②→⑦→③→⑤). **D**) Landscape context determines the proximity to and abundance of seed sources (①→⑤) and affects the abundance and movement of dispersers and pollinators, which affects species availability (①→③→⑤). **E**) Landscape context affects species performance by influencing the prevalence and movement of herbivores and pathogens. Numbers as in figure 1. Ovals and arrows indicate pathways driving variability and blue shaded areas indicate the most directly associated Environment-Species-Performance and Environment-Species-Availability feedback loops.

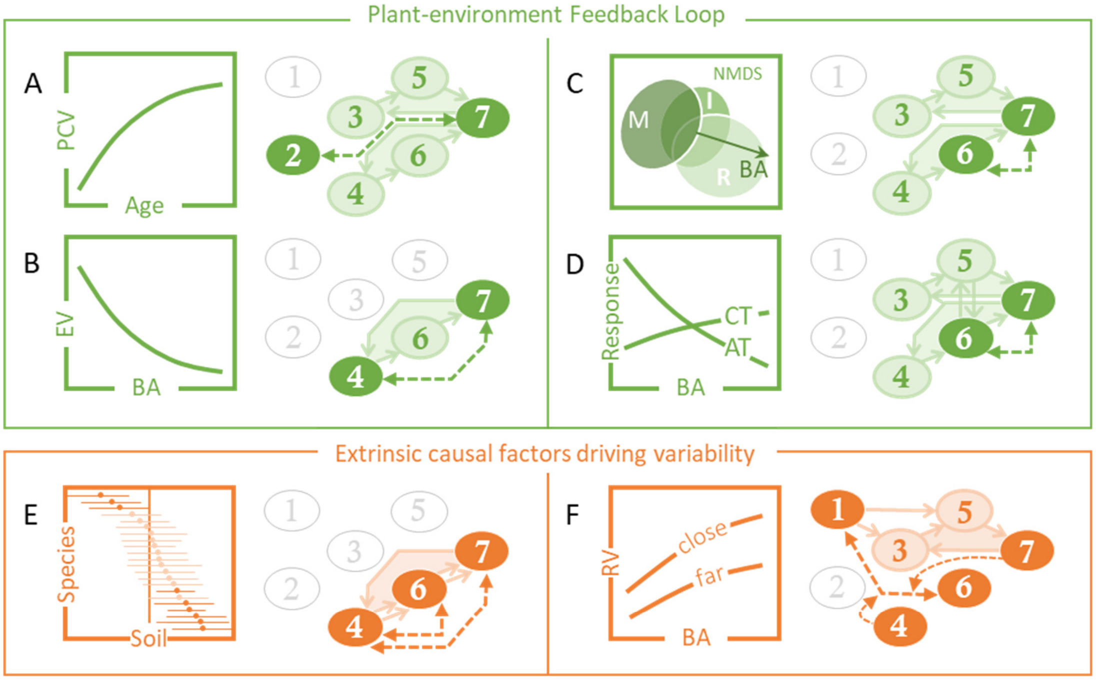
species from the regional species pool (Crouzeilles *et al.*, 2021). If these species differ in their impact on the biotic and abiotic features of the local ecosystem, this may lead to further divergence in the successional trajectories of local plant communities. In Manaus, Brazil, the canopy of 10 year old forests on abandoned pastures was dominated by *Vismia* and *Bellucia* spp., and by *Cecropia* spp. on lands that had been clear cut without subsequent use (Mesquita *et al.*, 2015). Recruitment in *Vismia*-dominated forests was dominated by seedlings and resprouts of the canopy species, while recruitment below *Cecropia* canopies was diverse, with more late-successional species and no *Cecropia* seedlings (Wieland *et al.*, 2011; Jakovac *et al.*, 2014). Thus, while land-use history explained initial differences the dominant species (*legacy effect*), interspecific differences in how these dominant species affected the availability and performance of other species caused the successional trajectories of *Vismia* and *Cecropia*-dominated forests to diverge further (*priority effect*). In sum, in many plant communities, priority effects are often the proximate cause of variability in succession, and extrinsic causal factors – outside the feedback loop – are the ultimate cause.

4. The conceptual framework as an analytical tool: an example

Fundamental research on succession and applied research on restoration ecology can be mapped onto our framework. This allows us to identify causal factors and feedback dynamics driving succession, and to understand how these may be linked. The framework can therefore be used as a tool for defining and synthesizing study-specific conceptual models, and more specifically, as a guide to explicitly identify the model of succession that underlies a study's research questions, experimental design, and inferences. In using this approach, one can make explicit which causal pathways and feedback loops are hypothesized to drive succession at a given site (initial model). We can then compare conceptual pathways with empirical data to assess how the initial model shapes the interpretation of the empirical results and, the other way around, how and to what extent those results support the initial model. To illustrate this approach, we mapped one of our own field studies – the long-term Agua Salud Secondary Forest Dynamics study in Panama – onto the framework (Figs. 4a, 7; Suppl. Info 1).

4.1. Conceptual model

The underlying conceptual model of the Agua Salud study was that directional change in plant species composition would be driven by interacting ESP and ESA feedback loops (Fig. 2g), with declining light availability as the main environmental driver of the ESP feedback loop (Fig. 7a-d). In addition, spatial variability was hypothesized to be caused by heterogeneity in edaphic conditions and by variation in landscape context (Fig. 7e, f). We evaluate 14 papers from the Agua Salud project, six of which were focused on the ESP feedback loop, and two on both the ESP and ESA feedback loops as drivers of directional change in species composition. The other six papers addressed plant-soil interactions and soil functioning, and were not specifically concerned with succession, but do contribute to our understanding of succession in this system and point to important gaps in both the conceptual model and data collected at the Agua Salud project. All 14 papers are listed in Figure 7g, and how they link to the conceptual models and empirical data is discussed in the following sections (4.2 and 4.3).



G. van Breugel et al. 2013^{ABC} , 2019^{ABE}; *in prep*^{CF}; Craven et al. 2015, 2018^A, Lai et al. 2018^A, 2021^D; Puspok 2019^B; Epihov et al. 2021^B; Rodriguez-Ronderos et al. *in prep*^{DF}; Batterman et al, 2013, 2018^D Nuemann-Cosel et al.,2011^B, Hassler et al. 2011^B.

① Landscape Context ② Disturbance / Land use history ③ Biotic Factors ④ Abiotic Factors
⑤ Species Availability ⑥ Species Performance ⑦ Plant Community

Figure 7. Mapping field studies on a conceptual framework of ecological succession. The left-hand graphs are schematic renderings of empirical findings from the Agua Salud Secondary Forest Dynamics Project in Panama (Figure 4a). The right-hand pathways represent the empirical results (statistical associations; darker shaded ovals and dashed arrows) and the conceptual models that underlie their interpretation (all dark and light shaded ovals connected by light-colored *solid* lines and light shaded areas representing feedback loops). Ovals not connected by solid lines are causal factors that do not play a direct role in the conceptual model. See section 4 for a more detailed description of the empirical relationships and underlying conceptual causal pathways. **A**) Relationships between forest age (②) and plant community variables (PCV), such as basal area (BA), diversity and composition (⑦). **B**) Relationship between BA or N_2-fixer density (⑦) and environmental variables (EV: understory light and various soil properties; ④). **C**) Species dissimilarities between the initial tree assemblage (I), of the subset of trees that died (M) and of the recruits (R)(⑥) versus BA (⑦). See Suppl. Info 2 for the original figure. **D**) Sapling recruitment and mortality (⑥) as function of BA (⑦) and plant traits (⑥). CT and AT: conservative and acquisitive trait values, respectively. Or species-specific levels of nodulation, N_2-fixation and root phosphatase (⑥) as a function of BA. **E**) Species abundances (⑥) and composition (⑦) as function of soil nutrients (④) in interaction with BA (⑦). **F**) Recruitment variables (RV) such as species diversities, community-weighted seed mass, and compositional similarity with the adjacent older forest fragment (⑥) as function of proximity to the forest fragment (①), in interaction with BA (⑦) or soil resources (④). **G**) The publications on which the graphs of A-F are based, with superscripts referring to the panels.

4.2 The data-driven evidence

The Agua Salud study is one of the largest studies on tropical secondary forest succession worldwide, and one of relatively few (<15 to our knowledge) studies that has monitored successional dynamics over multiple years. To understand how much empirical support was found for the ESP and ESA feedback loops in this particular study system, we first evaluate systematically the direct and indirect evidence for each of the pathways underlying the ESP and ESA feedback loops; we then discuss insights from this mapping exercise.

The ESP feedback loop:

⑦→④: **Did changes in the plant community drive changes in the local environment?** Forest basal area (BA) increased with forest age (Fig. 7a) and understory light levels decreased with BA (Fig. 7b). In addition, certain soil properties, including phosphorus and carbon pools (but not those of other nutrients), soil biochemistry and soil hydraulic conductivity changed over the course of forest regrowth (Fig. 7b).

④→⑥: **Did changes in the local environment differentially affect species performance?** Several papers reported that species with high recruitment and survival rates early in succession were distinct from species with high recruitment and survival rates later in succession (Fig. 7c; Suppl. Info 2). In addition, interspecific variation in sapling mortality and recruitment in response to stand basal area was moderated by interspecific trait differences (Fig. 7d), with species with acquisitive leaf trait values performing better early in succession and species with conservative leaf trait values performing better later in succession. The distribution of some of the species across the landscape was associated with soil fertility (Fig. 7e), and this association was strongest early in succession. Finally, how trees responded to and affected soil biochemical processes, through facultative symbiotic nitrogen-fixation and phosphatase activity, varied across the studied species and functional groups, and with changes in above and below ground conditions and resources (Fig. 7d).

The role of the ESP feedback loop was inferred; none of these results involved a direct analysis of the ESP pathway. The interpretation that decreasing light availability drives succession was based on the observed associations between BA and light, and on broader previously published ecological and ecophysiological work on relationships between light availability and functional traits (Sterck, Poorter & Schieving, 2006; Poorter & Bongers, 2006; Lusk & Jorgensen, 2013). Some of the Agua Salud results suggest successional shifts in resource acquisition strategies in response to shifts the resources that are the most limiting (e.g., soil → light and N → P), but these inferences are based on analyses that were not set up to test the ESP feedback loop. Direct evaluations of such feedback loops need replicated studies along larger soil gradients, controlled experiments, or dynamic simulation modeling that tests specific feedback loops. In the tropics the former two are scarce, but advances in the development of dynamic simulation models combined with long-term monitoring data and large trait databases represent an important toolkit to test the importance of the different feedback loops (Rüger *et al.*, 2020; Cusack *et al.*, 2021; Maréchaux *et al.*, 2021).

ESA feedback loop

⑦→③: None of the Agua Salud papers presented data on the abundance, composition or movement of dispersers in association with successional changes in the structure, diversity or composition of the plant community.

③→⑤: **Did changes in the disperser community affect species availability?** Although no data on seed rain was collected, data analysis based on sapling recruitment (diameter ≥ 1 cm) provided key insights about compositional changes driven by dispersers. The proportion of larger-seeded species among recruits increased over succession (Fig. 7d). In addition, recruitment in sites closer to forest fragments (i) was more diverse, (ii) was composed of a higher proportion of less-common, larger-seeded plant species, and (iii) showed higher floristic similarity with nearby older forest fragments compared to sites farther from forest fragments (Fig. 7f).

As no data on dispersers (③) or dispersal (⑤; e.g. seed rain) was collected, interpretations of the available data in terms of the ESA feedback loop depend on multiple assumptions. First, the assumption that ***disperser*** limitation (Dent & Estrada-Villegas, 2021) is weakened by forest regrowth was based on previously published work from human-modified landscapes that relates reduced fragmentation and increased connectivity to increased abundance and movement of dispersers (Uriarte *et al.*, 2011; de la Peña-Domene *et al.*, 2013). However, most of these studies were conducted in different study systems and did not explicitly address forest succession (Dent & Estrada-Villegas, 2021). Second, inferences about dispersal limitation depended on a assumed correlation between seed mass and dispersal limitation, which is supported by many studies (Muller-Landau, 2010; Beckman *et al.*, 2018). Finally, the use of recruitment data instead of seed arrival data means that interpretations hinge on the assumption that the signal of dispersal limitation persists beyond establishment, growth and survival filters (Kraft *et al.*, 2015). Overall, although these assumptions might be robust, actual data on the relationship between seed dispersers and species availability and its impact on successional pathways is critically needed.

ESP and ESA feedback loops

⑥→⑦ & ⑤→⑦: **Did the ESP and ESA feedback loops drive a directional shift in species composition?** Species composition changed directionally with forest age (Fig. 7a), and community-weighted mean (CWM) functional trait values changed with BA, reflecting a shift from acquisitive to conservative trait values over the course of succession. Moreover, CWM seed mass increased and the proportion of species that were found only in a few plots across the landscape increased with BA, reflecting that more dispersal-limited species became increasingly common over the course of succession (Fig. 7a). These results illustrate successional patterns that are predicted by the ESP and the ESA feedback loops, but do not provide insight into the underlying processes and which feedback loops are the strongest drivers of succession in our system.

4.3 Synthesis of the mapping exercise

The results of the mapping exercise (Fig 7) illustrate that the pathways representing the empirical outcomes and the study's conceptual model are not identical. Fundamentally, the Agua Salud project was set up to evaluate the study's initial conceptual model (section 4.1) and many of its publications interpreted the results in light of that same model, with a range of assumptions filling in for the parts of the hypothesized causal pathways where data were not collected. The strongest evidence found was for the hypothesized association between declining light availability and shifts in plant life history strategies. However, support for the idea that succession is driven by a coupled ESP-ESA feedback loop with life history trade-offs between species availability (fecundity, dispersal) and performance (shade tolerance) was largely indirect, with the lack of data on the disperser community and species availability (dispersal) constituting a considerable data gap. Several of the Agua Salud papers examined tree-soil interactions during succession but none explicitly examined the relative importance of alternative ESP feedback loops in shaping successional trajectories. These observations imply that, while the combined results of the Agua Salud papers demonstrate greater complexity than envisioned in the project's original conceptual framework, they do not yet provide a complete analysis of how the relative importance of multiple interacting causal pathways shift over succession. This exercise also highlights the need for approaches that test feedback loops through combinations of long-term studies, controlled experiments and dynamic modeling (Johnson & Miyanishi, 2008; Walker *et al.*, 2010b; van der Putten *et al.*, 2013; Larocque *et al.*, 2016; Chang & Turner, 2019; Maréchaux *et al.*, 2021). This picture is not unique to the Agua Salud study. Many studies of tropical forest succession build on similar conceptual ideas, use similar study designs and choice of variables and measurements, and fill in similar data gaps with assumptions based on theoretical or empirical findings from other studies. Collectively, most successional studies thus tend to reinforce the dominant a-priori assumptions and provide little or none of the data needed to examine the relative importance of- and interactions among alternative causal pathways and how their relative importance may shift with succession.

5. Conclusions

(1) Ecological succession is a process that is defined by one or multiple interacting plant-environment feedback loops that lead to directional changes in the plant community after a major disturbance removed some or all of the original vegetation. These feedback loops involve vegetation-driven changes in the plant community's environment, which benefits or hinders the availability or performance of a subset of species relative to other species in the local species pool. The three most commonly studied feedback loops are those between environment and species performance, between environment and species availability, and disturbance-mediated feedback loops, but there are many other feedback loops that could drive succession. Feedback loops can be thought of as models of succession, with more complex models of succession including multiple feedback loops.

(2) Succession is generally observed to be highly variable within a single landscape, and more so across larger environmental gradients. There are three main causes of variability. First, the probabilistic nature of the demographic processes involved in successional feedback dynamics, such as mortality and dispersal, cause variability in successional dynamics of plant communities. Second, extrinsic causes of variability are not affected by changes in the plant community but do differentially affect species performance or availability, thus causing spatial variability in succession. Finally, both these causes can generate variation in the dominant species in plant communities. Feedback loops cause further contingency if these species differ in their impacts on the environment (priority effects).

(3) Predictability and variability are thus intrinsically linked features of ecological succession. This implies two fundamental questions in any study on ecological succession: (1) What are the (dominant) feedback processes that drive similar successional trajectories among plant communities? (2) What are the causes of spatial variability in successional dynamics?

(4) We present a novel conceptual framework of ecological succession that integrates the concepts listed above and is built on the idea of a hierarchy of causes (Pickett et al., 1987a). It defines seven general causes (landscape context, disturbance and land-use, biotic factors, abiotic factors, differential species availability and performance, and the plant community) that can be linked in multiple different causal pathways with feedback loops and extrinsic causes of variability.

(5) To illustrate the applicability of this framework, we mapped one of our own field studies onto the framework to critically assess how the study's conceptual model shaped the interpretation of the empirical results and, the other way around, how and the extent to which those results supported the conceptual model.

(6) Going forward, this framework could be used for systematic comparisons among study sites and along environmental gradients, to conceptualize studies, refine research questions, and to design field studies and fine-tune data collection. From a restoration perspective, this framework can be used to identify causal pathways that are important in the local context and that can feasibly be targeted with specific restoration measures (e.g., Jones & Davidson, 2016).

(7) Our hope is that this framework will enable a more integrated understanding of ecological succession at the local and landscape scale. Specifically, we foresee that by structuring future work around this framework, as a community of researchers, we will be better able to move beyond the conceptual models that currently dominate in our specific fields and to examine the role and importance of alternative causal pathways of succession.

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Statement of authorship

The idea for this study was conceived by MvB and further developed during workshops attended by MvB, FB, NN, LA, WC, RC, DC, CF, BH, ELT, MMR, JM, RM, LP, NR, MS and DD. MvB and JH contributed data and MvB analyzed the data. MvB wrote the manuscript with support of DD, NN, FB and JM, and all authors discussed the ideas and commented on previous versions of the manuscript. All authors approved submission of the manuscript. Competing interests: The authors declare no competing interests.

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Supplementary Information

Supplementary Information 1 | Description of the Agua Salud Secondary Forest Dynamics Project

The Agua Salud Secondary Forest Dynamics Study is a long-term study on secondary forest succession, conducted in a 15 km^2 area in the central Panama Canal watershed (9°13' N, 79°47’ W, 330 m asl). The study area is adjacent to the Soberanía National Park, which is a mix of old growth and older (> 80 y) secondary forests. Annual precipitation averages 2700 mm per year, with a dry season from mid-December to early May (Ogden *et al.*, 2013). The area is characterized by an undulating topography, with short, steep slopes intersected by a dense network of narrow streams (Hassler *et al.*, 2011). Soils are classified as Oxisols and Inceptisols, and are strongly weathered, infertile, and well drained. Topsoil texture (silty clays to clays) and soil nutrient concentrations vary little across the landscape (Neumann-Cosel *et al.*, 2011; Breugel *et al.*, 2019). On a local scale, however, soil fertility and dry season soil water tend to be higher at downslope locations than at locations towards the top of the hill slopes, although this varies strongly across sites. The landscape is dominated by active and abandoned cattle pastures and secondary forest of different ages (van Breugel *et al.*, 2013). Over the last 40 years (age of oldest plot in this study at the end of the study), active pastures usually include or border narrow strips of secondary forests fragments alongside streams that cover on average 14.3% (± 6.6 sd) of the pasture areas (M. van Breugel & J.S. Hall, unpublished data).

In 2009, 54 sites were randomly selected within the study area and information on land-use history and time since abandonment was acquired from interviews with former landowners and local residents. Sites were defined as a single slope within a secondary forest on an abandoned pasture. All sites bordered a small stream with on both sides a strip of secondary forest of unknown age but in all cases older than the secondary forest on the selected hill slope (henceforth ‘stream-side vegetation’). The study was set up as a paired-plot design nested in a chronosequence, with one 20×50m plot near the bottom of the slope adjacent to the stream-side vegetation and another near the top of the slope. Distance between plots within a site ranged between 23 m and 149 m (mean ± sd: 83 ± 25 m). The initial age of the five oldest sites (at least 50 years) was not known and these were therefore excluded from all analyses referred to in figure 7 of the main text. Initial forest age of the other plots varied from one to 32 years, with sites fairly well distributed along this age range.

In each plot, all stems of trees, shrubs, and palms with a diameter-at-breast-height (DBH) ≥ 5 cm and all stems of woody climbing plants with a diameter ≥ 1 cm were tagged, identified and their DBH was measured. In one-half of each plot, stems of trees, shrubs, and palms with a DBH of [1 — 4.99] cm were also included (van Breugel *et al.*, 2011, 2013). From 2009 until 2017, the growth and mortality of established plants and the recruitment of new plants was monitored annually, with the exception of 2013 (Lai *et al.*, 2017, 2018, 2021).

In 2010, an inventory of trees ≥ 20 cm DBH was done in 2-m wide transects perpendicular to the stream (mean length 12 m), from the waterside to the border of the streamside vegetation, at 5 m intervals over a total distance of 150 m, alternately at either side of the stream (M. van Breugel & J.S. Hall, unpublished data).

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Supplementary Information 2 | Dissimilarities between demographic groups

Růžička dissimilarities between species composition of the initial community of trees (blue), and the subset of trees that died (yellow) and the trees that recruited (red) over an eight-year period of the Agua Salud Secondary Forest Dynamics Project. Each dot represents one plot (N = 45 plots), with dot size being proportional to plot basal area, and the color represents the demographic community of these plots (initial community, deaths, recruits). See Supplementary Info 1 for information about the study site and study set up.