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Feedback loops drive ecological succession: towards a unified conceptual framework

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ABSTRACT

The core principle shared by most theories and models of succession is that, following a major disturbance, plant–environment feedback dynamics drive a directional change in the plant community. The most commonly studied feedback loops are those in which the regrowth of the plant community causes changes to the abiotic (e.g. soil nutrients) or biotic (e.g. dispersers) 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.

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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, which 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 new 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, species availability, species 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 conceptualise studies, and to 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 specific fields and to find ways to examine the importance of and interactions among alternative causal pathways of succession. To further this aim, we argue for integrating long-term studies across environmental and anthropogenic gradients, combined with controlled experiments and dynamic modelling.

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

CONTENTS

I. 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 has been 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, a multitude of theories and models of succession have been proposed since the emergence of the field, representing equally diverse perspectives on succession [see Poorter *et al.* (2023) for a recent overview]. There are several reasons for this. Causes and mechanisms of succession are manifold, complex and vary across ecosystems (Arroyo-Rodríguez *et al.*, 2017). Also, 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). We therefore need a comprehensive framework that is general enough to account for the bewildering variability in causes and mechanisms within and across ecosystems, but specific enough to guide the generation of site-specific models and testable hypotheses.

Here we recognise that there is one core principle common to most theories and models of ecological succession: feedback dynamics between plants and their environment (Gutierrez & Fey, 1975; 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 both local and landscape scales. 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, 1987*a*). 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 cessation of disturbance in the case of human 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 (Chase & Myers, 2011; Dini-Andreote *et al.*, 2015; Estrada-Villegas *et al.*, 2020). However, 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 environmental variables is unrelated to vegetation change. In these cases environmental variables will not be part of a feedback loop, but instead externally influence the successional feedback dynamics, thereby driving 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*a*; e.g. Richter-Heitmann *et al.*, 2020). Finally, the feedback dynamics themselves may cause contingency when spatial variation in causal factors or stochastic processes leads to different species dominating the plant communities (van de Voorde, van der Putten & Bezemer, 2011).

Here, we present a conceptual framework that builds on the idea of general causes of succession developed by Pickett *et al.* (1987*a*, 2011) and structured around the idea of multiple plant–environment feedback loops as the principal drivers of spatial and temporal variation in successional plant communities. In this framework, we define 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 presents a general explanation of succession and can aid broad comparative studies that synthesise causal pathways of succession across different study systems. In the context of local sites, specific variables and processes can be substituted for the general causes described in this framework, helping to define and examine more specific 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. Next, 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 III). Finally, we go beyond discussing the conceptual framework as an explanation of succession, and explore how it can be used to guide the design or evaluation of research projects on ecological succession. Specifically, we use a case study to illustrate the use of this framework to identify, synthesise and compare the main causal pathways underpinning succession, both in terms of theoretical ideas and empirical relationships, where this framework can help us to identify key factors and relationships operating at the site level and make critical decisions about data collection and study design (Section IV).

II. 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 the landscape context, in disturbance and land use, and in biotic factors or abiotic factors (Fig. 1, 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 (the availability of seeds) or in terms of species performance, i.e. the germination, establishment, growth, survival, and reproduction of plants (Fig. 1, ⑤ and 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, 1987*b*; 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;

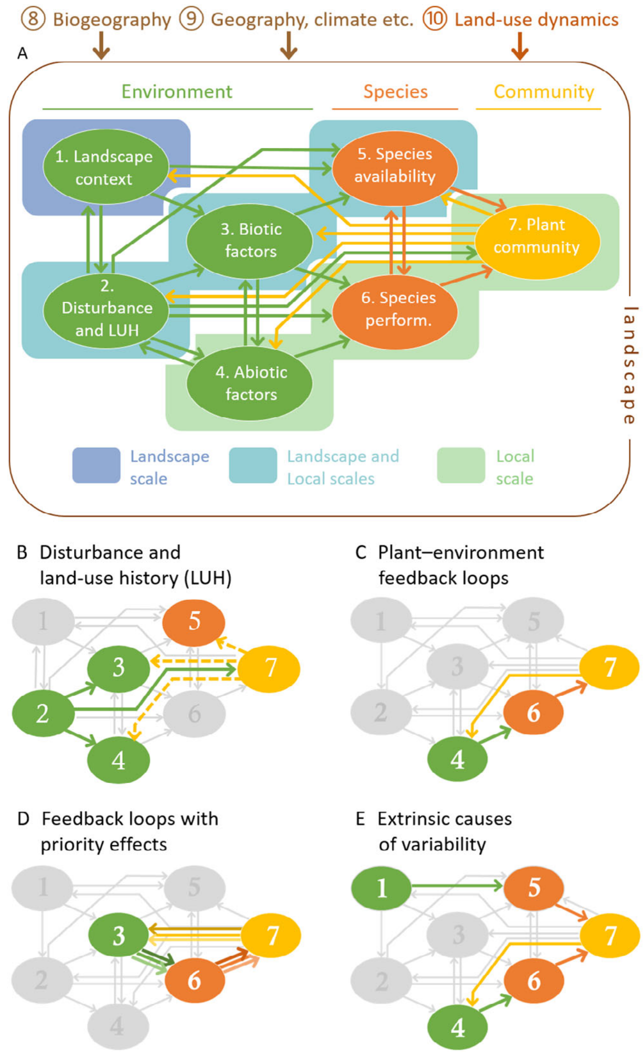

Fig. 1. A conceptual framework of succession. (A) Graphical representation of the conceptual framework. Our framework consists of four categories of causal factors that represent different aspects of the environment (green circles, ①–④), at the landscape scale (blue background), the local scale (green background), or both (purple background). 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 history (LUH) or a disturbance event modifies 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 model in C, 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 neighbourhoods 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 result 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.

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 neighbourhood or larger surroundings on the environment (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 not explicitly recognised 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), although only a few dominate the literature. 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 II.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. The environment–species availability (ESA) feedback loop (discussed in Section II.2) describes how changes in the plant community can be driven by the interaction between species availability and the biotic environment and/or the landscape. For example, the interaction between plant communities and pollinators and seed dispersers at the landscape scale drives the availability of viable seeds, thus shaping the regeneration of the plant community (Verheyen & Hermy, 2001; Piotto *et al.*, 2019; Dent & Estrada-Villegas, 2021). At a basic level, one can define three simple mechanisms of species replacement over succession, each of which can be driven by the ESP, ESA and other plant–environment feedback dynamics (discussed in Section II.3). The disturbance-mediated (DM) feedback loop involves successional interactions between recurring disturbances, local environment and species performance and availability. When recurrent 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 positive feedback loops and arrested succession (Section II.4). Overall, more complex models of succession can integrate multiple causal factors and interactions between the different feedback loops (Section II.5).

(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 ESP feedback loop (Fig. 2). This feedback loop applies when species colonise 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 colonising species and/or more habitable for other species with different environmental requirements and life-history traits. The best-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 limits the recruitment of light-demanding species and favours the recruitment of more shade-tolerant species (van Breugel, Martínez-Ramos & Bongers, 2006; van Breugel *et al.*, 2013; 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).

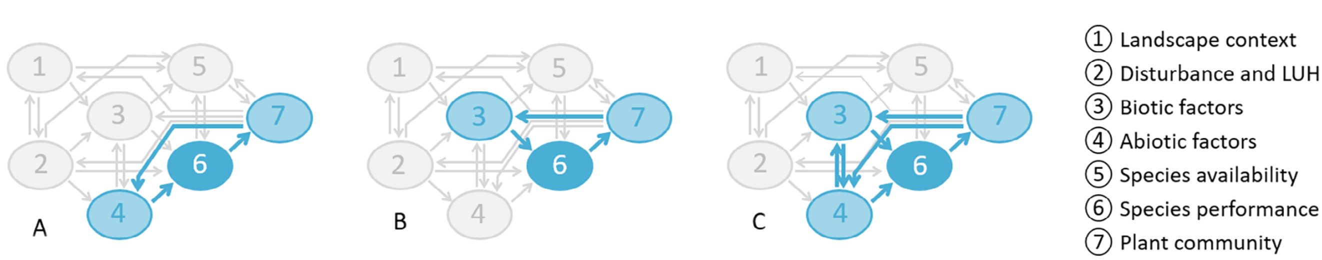

Fig. 2. Examples of environment–species performance (ESP) feedback loops. Changes in the plant community drive shifts in (A) abiotic factors, (B) biotic factors or (C) both, including their interactions, which differentially affects plant species performance and hence drives changes in the plant community. A and B are the single ESP feedback loops that can be identified within the overall framework, while C integrates four feedback loops: ⑦ → ④ → ⑥ → ⑦; ⑦ → ③ → ⑥ → ⑦; ⑦ → ③ → ④ → ⑥ → ⑦; and ⑦ → ④ → ③ → ⑥ → ⑦.

Soil properties then differentially influence the success of colonising 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-colonising shrub species *Erica tetralix* produces poor-quality litter that leads to organic matter build up and release of mineral nitrogen, favouring competitive replacement by the grass species *Molinia caerulea* (Berendse, 1998).

Among the most important plant–soil feedback loops is the one between plants and soil microbes (i.e. fungi, bacteria, archaea, protists, and viruses), which can involve either positive or negative impacts on subsets of plant species, and both can drive species replacement (van der Putten *et al.*, 2013). For example, the build up of species-specific microbial pathogens in the rhizosphere of early-colonising plants can exclude other 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 defences 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 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 coal mine (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 (both Fig. 2A; Pinho *et al.*, 2018; Caplan *et al.*, 2019; Hogan *et al.*, 2020). In arid systems, characterised 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 an example from Mount St Helens, USA, multiple interacting feedback loops define primary succession on volcanic substrates (Fig. 2C) (Fagan, Bishop & Schade, 2004; del Moral & Rozzell, 2005). First, the nitrogen-fixing forb *Lupinus lepidus* colonises 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) 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.*, 2004*a*,*b*; Schupp, Jordano & Gómez, 2010)], 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 ESA feedback loop (Fig. 3). The

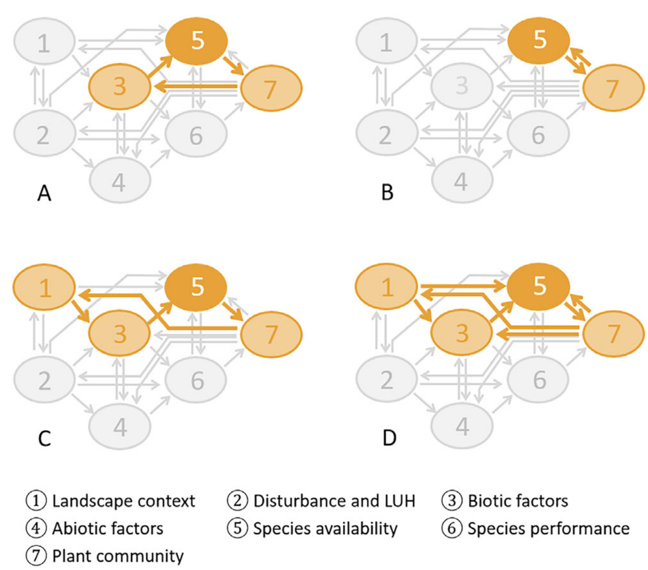

Fig. 3. Examples of environment–species availability (ESA) feedback loops. Changes in the plant community drive shifts in (A) biotic factors, (B) local seed production, (C) landscape context, or (D) all combined, which differentially affects plant species availability and hence drives changes in the plant community.

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, as well as depauperate communities of pollinators and dispersers whose abundance and movement is limited by an inhospitable landscape matrix (Fig. 3A) (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), underlying processes such as pollination or propagule dispersal are still relatively overlooked (Dent & Estrada-Villegas, 2021).

At the patch scale, dispersal could drive successional feedback loops *via* shifts in the 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 (Cubiña & 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. 3A) (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. 3B) (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 provide wildlife habitat and improve landscape connectivity (Fig. 3C), exerting a positive influence on the abundance, diversity and movement of animal pollinators and dispersers (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 multiple feedback loops where the changing composition of plant communities drives changes in the abundance and composition of the seed disperser and pollinator communities and *vice versa* (Fig. 3D) (Fiedler, Landis & Arduser, 2012; Dent & Estrada-Villegas, 2021).

(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. 4). 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 classical 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 refrain from a direct comparison (for a critical comparison of species replacement concepts, see Pickett *et al.*, 1987*b*). For the first mechanism, we assume favourable 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. 4A). 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 colonisers 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. 4B). This process may be especially important in ecosystems with strong biotic and abiotic stressors, such as many dry 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 a third mechanism, species replacement may be driven by life-history trade-offs, 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

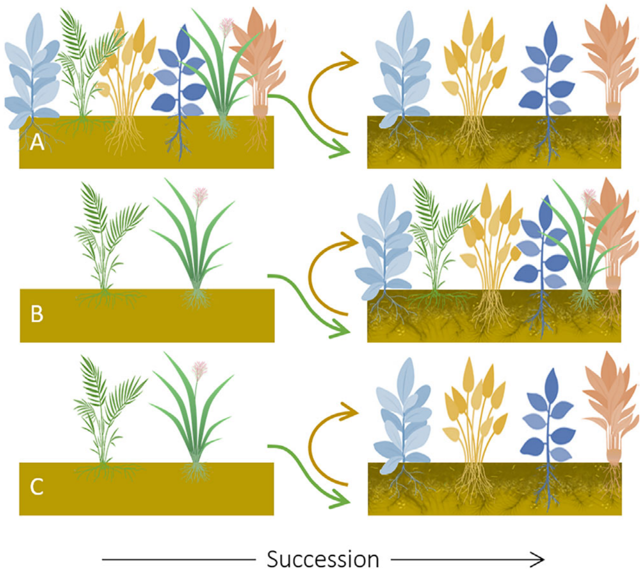

Fig. 4. The three simplest mechanisms of successional species replacement in which plants affect their environment (for example, edaphic conditions; green arrows) and these changes in their environment, in turn, benefit or adversely affect the performance of a subset of species relative to that of the 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) Life-history trade-offs 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 II.3 for further details.

community composition will reflect those trade-offs (Fig. 4C). The most widely studied life-history trade-offs are those between stress tolerance, resource conservation and high survival on the one hand and resource capture and rapid growth (Wright *et al.*, 2004) and/or early and high fecundity (Muller-Landau, 2010) on the other (Díaz *et al.*, 2016; Maynard *et al.*, 2022). Evidence for these trade-offs has been found across a wide range of vegetation types (Bruelheide *et al.*, 2018; but see Clark *et al.*, 2004*a*). Grime (2006*a*) proposed a different framework in which life-history strategies of plant species can be located in an environmental space (in contrast to a single gradient) defined by different levels of disturbance, environmental stress and competition. In his competitor–ruderal–stress tolerance (CRS) framework, ruderals are adapted to productive disturbed environments, competitors to productive undisturbed environments, and stress-tolerant species to unproductive, undisturbed environments. 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 (global and various biomes; 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; Grime, 2006*b*; Chave *et al.*, 2009; Reich, 2014). In the context of succession, we could, for example, observe a contrast between early-successional species that allocate more resources to traits that promote resource acquisition, rapid growth or early and copious reproduction under favourable conditions, while late-successional species allocate more to traits that reduce mortality under resource-limited conditions caused by increasingly intense competition (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 (Fig. 4) 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. 4A), species with all trait combinations from the trait space of the local species pool can colonise 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 temperate grasslands and regrowing forests (Strandberg, Kristiansen & Tybirk, 2005; Shipley, Vile & Garnier, 2006; Hédl, Kopecký & Komárek, 2010; Lasky *et al.*, 2014). The second species-replacement mechanism ('*narrow-to-wide trait range*', Fig. 4B) illustrates an opposite trajectory, where communities characterised 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 dry tropical forest succession (Poorter *et al.*, 2019). The third species-replacement mechanism ('*trade-off*', Fig. 4C) 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 most ecosystems, we find a small proportion of the species pool has species with life-history strategies specifically adapted to take advantage of large disturbances (Turner, 2008), a major 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 conceptualised in terms of gradual shifts in species-specific arrival, establishment and survival probabilities along a successional gradient depending upon 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 the most important mechanisms may shift over succession. The same species may partake in different species-replacement mechanisms at different times along the successional gradient (Pickett *et al*., 1987*b*). Our aim here is to highlight that species-replacement mechanisms are all, ultimately, variants of the same fundamental mechanism of succession: plant–environment feedback loops.

(4) Positive feedback loops

In the previous sections we discussed negative feedback loops, in which the interaction between the plant and the environment benefits, or less strongly inhibits, the availability or performance of new species, relative to that of earlier established species, thus driving species replacement. By contrast, positive feedback dynamics occur when (a group of) early-successional species affect their environment in ways that ultimately benefit their own persistence relative to that of other species, or inhibit the establishment of other species (Weidlich *et al*., 2021). For example, studies of landslides in Puerto Rico found that initial colonisation by ferns inhibited forest succession, while early colonisation by fast-growing trees led to successional replacement by more shade-tolerant, longer-lived tree species over time (Walker *et al*., 2010*a*). Succession on these landslides thus depends on the identity of plant species that initially colonise and dominate the site, with fern colonisation leading to a positive feedback loop and a form of arrested succession (Slocum *et al*., 2004).

DM feedback loops (Fig. 5) are mostly positive feedback loops. These dynamics can keep the plant community in an early-successional state for a prolonged period of time (Thrippleton, Bugmann & Snell, 2018), especially when different positive feedback loops reinforce each other. 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. A transition to a tree-dominated plant community is thus prevented by interacting DM (Fig. 5A) and ESP feedback loops (Fig. 2A) (Styger *et al*., 2007; Saltonstall & Bonnett, 2012). Another example is the extensively studied case of bracken fern (*Pteridium aquilinum*; Fig. 6). 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

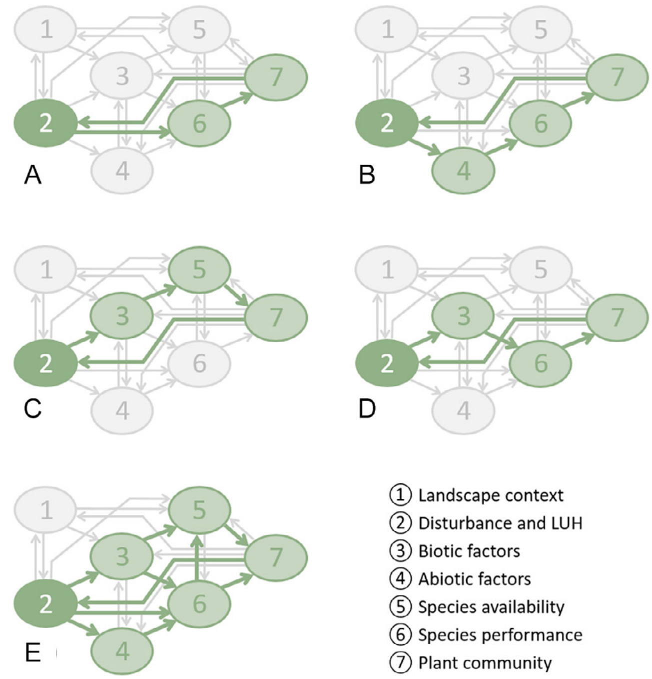

Fig. 5. Examples of disturbance-mediated feedback loops. Disturbances and land-use history (LUH) can differentially affect species performances either (A) directly or (B) through effects on the abiotic environment. Disturbances can also differentially affect species availability (C) or species performances (D) through effects on the biotic environment. In all four feedback loops, the resulting changes in the plant community in turn affect the likelihood of recurring disturbances, and/or their frequency, intensity, severity, spatial pattern or scale. (E) In reality, disturbance-mediated feedback dynamics will involve multiple interacting feedback loops, such as in this example.

mechanisms, including resource competition, as physical barriers to dispersal, by harbouring high densities of seed predators, or allelopathy (den Ouden, 2000; Marrs *et al*., 2000; Ssali, Moe & Sheil, 2018). Another example is that of poor post-disturbance regeneration of native species in many temperate forests where recurrent disturbances, such as fire or logging, favour highly competitive invasive herbaceous species, leading to strong resource competition (Fig. 2A) and higher preferential browsing pressure of ungulates on tree seedlings and saplings (Fig. 2B). Overall, this has a strong negative impact on tree regeneration (Vavra, Parks & Wisdom, 2007; Laskurain *et al*., 2013; Maxwell, Rhodes & St. Clair, 2019; Hanberry & Faison, 2023).

(5) Interacting feedback loops

Studies on plant community succession typically investigate single feedback loops (e.g. plant–light) yet, as highlighted in Section II.4, succession is influenced or shaped by multiple interacting feedback loops (Pickett *et al*., 2011). Integrating multiple feedback loops into more complex causal

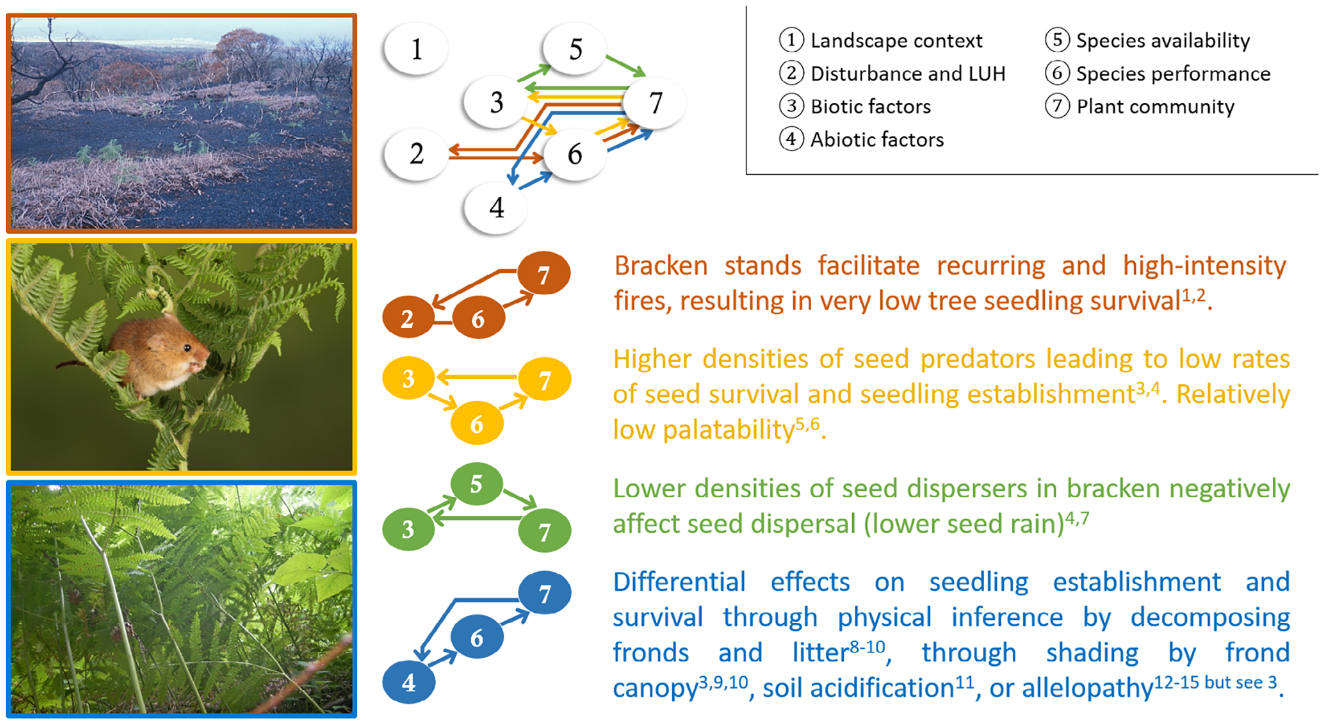

Fig. 6. Bracken fern *Pteridium aquilinum* (L.) has been hypothesised to drive positive feedback dynamics across a wide range of forest biomes. Tree regeneration in bracken fern stands seems to be affected by the simultaneous operation and interaction of multiple positive feedback loops (upper diagram), with the relative importance of each single positive feedback loop (single-colour diagrams) depending on the specifics of the particular site. Superscript numbers refer to the following references, which are examples of empirical studies that addressed the proposed feedback loops: [1]Adie *et al.* (2011); [2]Roos *et al.* (2010); [3]den Ouden (2000); [4]Ssali *et al.* (2018); [5]Vetter (2009); [6]Cooper-Driver *et al.* (1977); [7]Maya-Elizarrarás & Schondube (2015); [8]Dolling (1996); [9]Ssali *et al.* (2019); [10]Humprey & Swaine (1997); [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). Photo credits: top – Forest & Kim Starr, CC BY 3.0 https://creativecommons.org/licenses/by/3.0, via Wikimedia Commons; middle – Theclarkester, Standard Individual license, via Depositphotos.com; bottom – Danny Steaven – Own work, CC BY-SA 2.0, https://commons.wikimedia.org/w/index.php?curid=4379699, via Wikimedia.

pathways can help us to design studies that (*i*) assess their relative importance in shaping successional dynamics, and (*ii*) improve our ability to predict successional processes. One example is a causal pathway that includes both the ESA and the ESP feedback loops (Fig. 7) (Pacala & Rees, 1998; Clark *et al.*, 2004*a*,*b*). 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; ⑦ → ④ → ⑥) and species-availability processes (e.g. increasing canopy complexity attracts more dispersers; ⑦ → ③ → ⑤). 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 (③ ⇄ ④) (Turnbull *et al.*, 2004; Muller-Landau, 2010; Beckman, Bullock & Salguero-Gómez, 2018; but see Clark *et al.*, 2004*a*).

Our framework implies that succession continues as long as a change in the plant community drives a change in environmental variables and *vice versa*. In other words, when a study on succession focusses on a specific feedback loop, succession appears to have an endpoint, namely when change

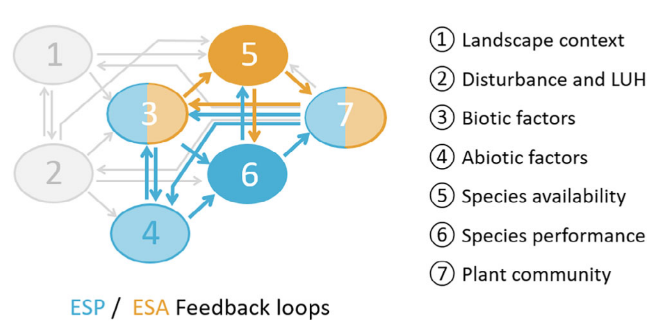

Fig. 7. Combined environment–species performance (ESP) and environment–species availability (ESA) feedback loop. Shifts in the plant community drive changes in both species performance and availability *via* impacts on abiotic and biotic factors. Both feedback loops involved are coupled through interactions between biotic and abiotic environmental factors and through trade-offs between life-history attributes that relate to both species availability and performance.

in the plant community ceases to drive a directional and continuous change in the environment. By contrast, viewing succession as a process involving multiple concurrent and interacting plant–environment feedback loops demonstrates that succession can continue long after a particular feedback loop has ended. For example, during forest succession, when 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. 2A) (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. 3C; 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.

III. 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: (*i*) what are the (dominant) feedback processes that drive similar successional trajectories among the plant communities within the meta-community (Fig. 8A, green arrow), and (*ii*) what are the causes of spatial variability in successional dynamics (Fig. 8A, 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 II). 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 (e.g. Clark *et al.*, 2004*a*; Richter-Heitmann *et al.*, 2020). Feedback loops can drive further variability if the identity of the dominant species among the early colonisers 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–environment feedback loops themselves may bring about variability in succession through '*priority effects*' (Fig. 8C) (Fukami, 2015). Because these are inherent components of feedback loops, we define them as intrinsic causes of variation and we discuss this in Sections III.1. By contrast, when environmental factors (Fig. 1, causal factors ①–④)

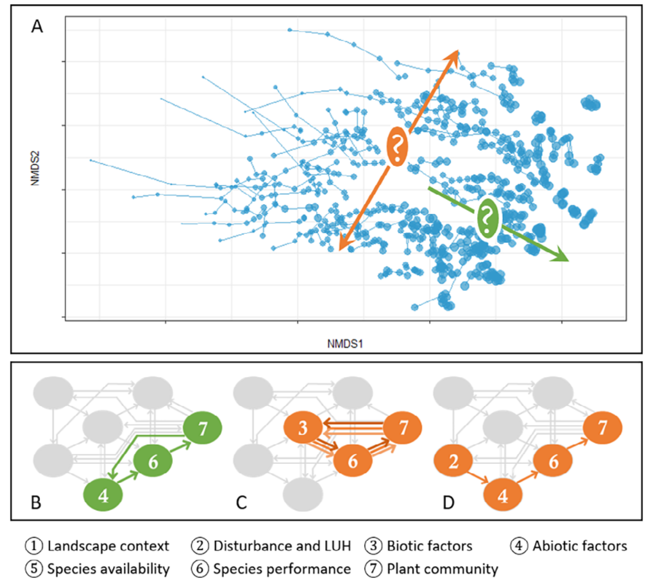

Fig. 8. Predictability and variability in successional dynamics across plant communities in a landscape. (A) A non-metric multidimensional scaling (NMDS) plot shows shifts in the species composition of 0–32-year-old secondary forests over a period of 8 years. Dots connected by a line represent the same plot at different censuses; dot size is proportional to stand basal area (M. van Breugel & J.S. Hall, unpublished data). The arrows represent 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 (B), while the drivers of variability are either plant–environment feedback loops with priority effects (C), extrinsic causal factors that themselves are not part of the feedback loop (D) or a combination of interacting extrinsic factors and feedback loops.

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 III.2) 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 promote differences in the identity and dominance of the early colonisers, which may lead to priority effects (Section III.3).

(1) Feedback loops with priority effects as drivers of variability

Variation in the composition of initial colonisers may directly influence the recruitment of other species from the local species pool and thus trigger historically contingent successional trajectories through priority effects (Fig. 8B). This is best understood when contrasted to the alternative option, where early-colonising 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 belowground biomass, leaf area index, and canopy height. Most simulation models of forest succession are primarily concerned with these stand-level environmental feedbacks and do not consider priority effects (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 II.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 colonisers 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 colonisers, 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 colonisers, 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 (Bishop, 2002; Fagan *et al*., 2004) show that not only the timing of plant species arrival, but also 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 nitrogen-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 colonisers have disappeared (Helsen, Hermy & Honnay, 2016; Pickett *et al*., 2019).

At larger scales, priority effects can also develop if early colonisers 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 II.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 when 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).

(2) 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 (Fig. 8D). Perhaps the simplest heuristic model reflecting this is that of a series of environmental 'filters' (e.g. dispersal, abiotic environment and biotic interactions) that vary across a landscape and filter out different subsets of species from a larger species pool to the local plant community (Weiher & Keddy, 1995; Kraft *et al*., 2015; Cadotte & Tucker, 2017). 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*., 2023), 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 drives different interacting ESP feedback loops, shifts 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 it is less important in benign environments or late in succession (Brooker *et al*., 2008). Likewise, the dominant competition processes can change across gradients of soil fertility, shifting from competition for belowground resources on nutrient-poor soils to aboveground competition for light on fertile soils (Putz & Canham, 1992; Wilson, 1999). Overall, 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) 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. 9, ②, e.g. use of fertiliser, 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 (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. 9) 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

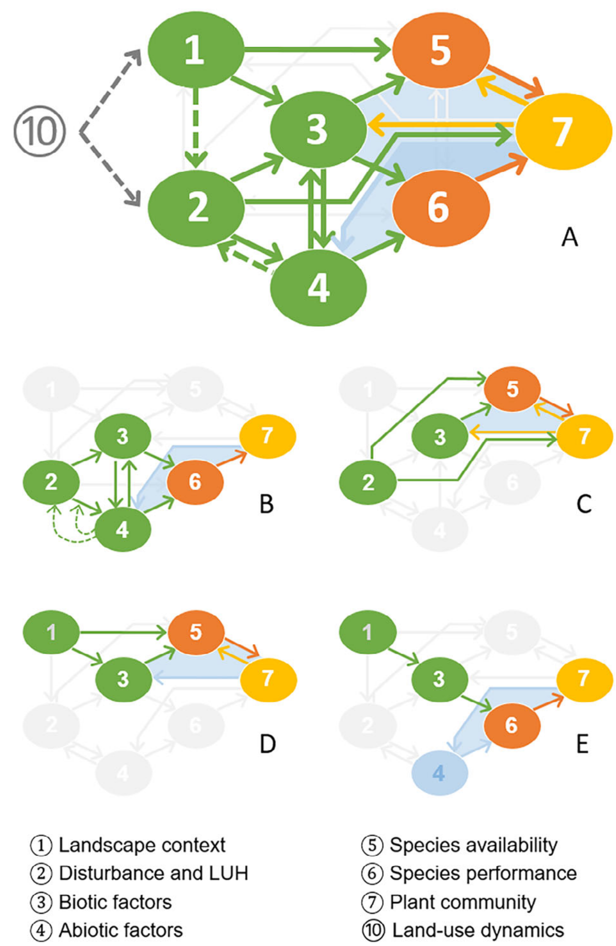

Fig. 9. Complex effects of land use on succession. (A) A complex model of land use as a driver of variability in forest succession. Variation in land-use dynamics (10) across landscapes drive spatial patterns and variation in landscape context (①) and land-use history (LUH) (②). This model can be deconstructed 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 pathway implies that land use and soil attributes are the ultimate and proximate causes of variation in species performance, conversely 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. 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.

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 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 these same 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 in 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.

IV. 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 to identify causal factors and feedback dynamics driving succession, and to understand how these may be linked. The framework is therefore a tool for defining and synthesising study-specific conceptual models, and more specifically can serve as a guide to identify explicitly the model of succession that underlies a study's research questions, or experimental design. In using this approach, one can make explicit which causal pathways and feedback loops are hypothesised 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 8A and 10; see online Supporting Information, Appendix S1).

(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, with declining light availability as the main environmental driver of the ESP feedback loop (Fig. 10A–D). In addition, spatial variability was hypothesised to be caused by heterogeneity in edaphic conditions and by variation in landscape context (Fig. 10E,F). We evaluated 12 papers and two unpublished manuscripts from the Agua Salud project, five of which were focused on the ESP feedback loop, two on both the ESP and ESA feedback loops as drivers of directional change in species composition, and two on causes of spatial variability in species dynamics. The other papers addressed changes in soil attributes over time, plant–soil interactions and soil functioning and were not specifically concerned with succession. All but two of the 14 papers are listed in the legend to Fig. 10 (the other two are cited in the text), and how they link to the conceptual models and empirical data is discussed in Sections IV.2 and IV.3.

(2) The data-driven evidence

The Agua Salud project is one of the largest studies on tropical secondary forest succession worldwide, and one of relatively few (<15 to our knowledge) that have 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.

(a) *The ESP feedback loop*

⑦ → ④: **do changes in the plant community drive changes in the local environment?** Basal area (BA) increased with forest age (Fig. 10A) and understory light levels decreased with BA (Fig. 10B). In addition, certain soil properties, including P and C pools (but not those of other nutrients), soil biochemistry and soil hydraulic conductivity changed similarly over the course of forest regrowth (Fig. 10B).

④ → ⑥: **do 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. 10C; Fig. S1). In addition, interspecific variation in sapling mortality and recruitment in response to stand basal area was moderated by interspecific trait differences (Fig. 10D), with species with acquisitive leaf trait values (associated with capacity to exploit high resource availability efficiently) performing better early in succession and species with conservative leaf trait values (associated with the capacity to survive low-resource conditions) performing better later in succession. The distribution of some of the species across the landscape was associated with soil fertility (Fig. 10E), 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

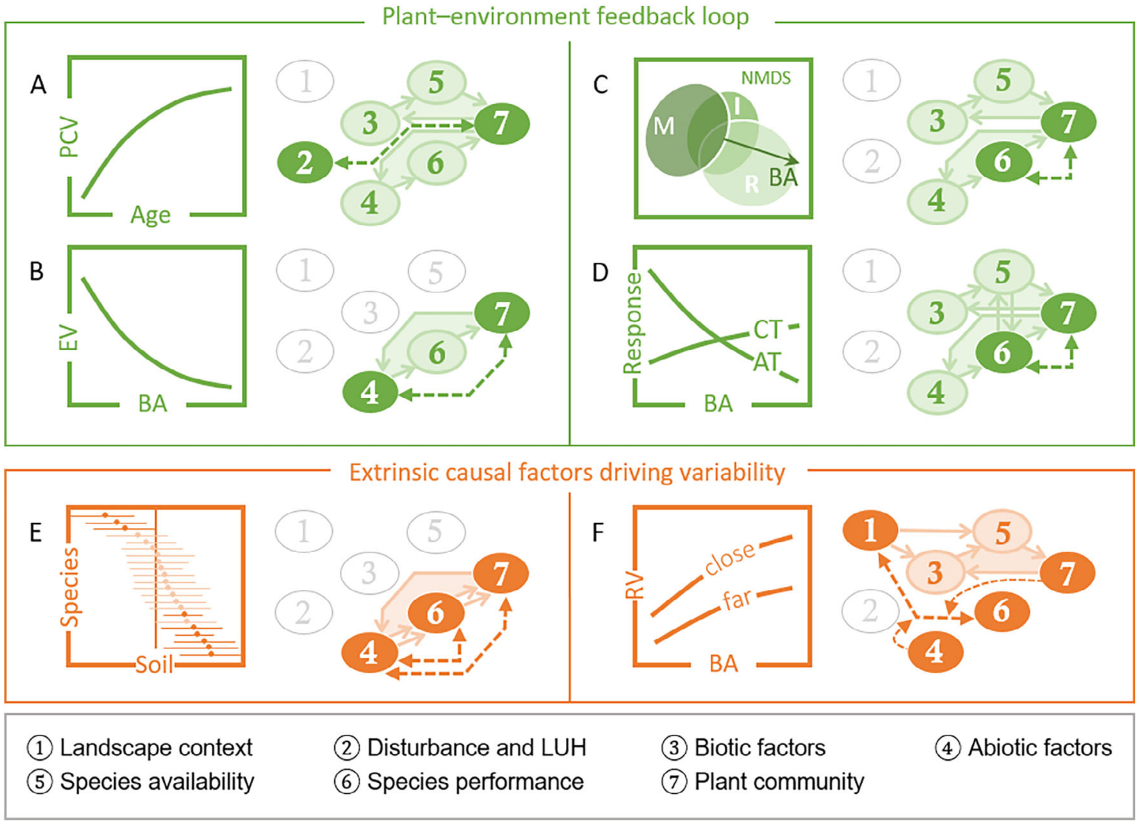

Fig. 10. Mapping field studies on a conceptual framework of ecological succession. The left-hand graphs are schematic renderings of empirical findings from the Agua Salud Secondary Forest Dynamics Project in Panama. The right-hand pathways represent the empirical results (statistical associations; darker shaded ovals and dashed arrows) and the conceptual models that underlie their interpretation (all dark- and light-shaded ovals connected by light-coloured *solid* lines and light-shaded areas representing feedback loops). Faint ovals not connected by solid lines are causal factors that do not play a direct role in the conceptual model. See Section IV 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 of the initial tree assemblage (I), the subset of trees that died (M) and the recruits (R) (⑥) *versus* BA (⑦), illustrated using non-metric multidimensional scaling (NMDS). See Fig. S1 for the original fig. (D) Sapling recruitment and mortality (⑥) as function of BA (⑦) and plant traits (⑥). CT and AT stand for conservative and acquisitive trait values, respectively and traits included maximum photosynthesis, specific leaf area and seed mass. (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). Data sources: A: van Breugel *et al.* (2013, 2019), Craven *et al.* (2015, 2018), Lai *et al.* (2018); B: van Breugel *et al.* (2013, 2019), Püspök (2019); Epihov *et al.* (2021), Neumann-Cosel *et al.* (2011), Hassler *et al.* (2011); C: van Breugel *et al.* (2013), van Breugel *et al.* (unpublished data); D: Lai *et al.* (2021), Rodriguez-Ronderos *et al.* (unpublished data); E: van Breugel *et al.* (2019); F: van Breugel *et al.* (2019), van Breugel *et al.* (unpublished data), Rodriguez-Ronderos *et al.* (unpublished data).

groups, and with changes in above- and belowground conditions and resources (Batterman *et al.*, 2013, 2018).

A 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 in the most limiting resources (e.g. soil → light and N → P). This mapping exercise thus highlights how research that goes beyond the initial conceptual model of the project can challenge ideas on the main plant–environment feedback loops in our study system and guide further work on our conceptual models.

(*b*) *ESA feedback loop*

⑦ → ③: none of the Agua Salud papers provided 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: **do changes in the disperser community affect species availability?** Although no data on seed rain were 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. 10D). 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 further from forest fragments (Fig. 10F).

The mapping exercise elucidates that, as no data on dispersers (③) or dispersal (⑤; e.g. seed rain) were collected, interpretations of the available data in terms of the ESA feedback loop requires multiple assumptions. First, the assumption that disperser limitation (Dent & Estrada-Villegas, 2021) is reduced by forest regrowth was based on previously published work from human-modified landscapes that related reduced fragmentation and increased connectivity to increased abundance and movement of dispersers (Uriarte *et al.*, 2011; de la Peña-Domene *et al.*, 2013). These studies, however, were conducted in different study systems and did not explicitly address forest succession (Dent & Estrada-Villegas, 2021). Second, inferences about dispersal limitation depended on the 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). The mapping exercise thus lays bare that, although these assumptions might be robust, actual data on the relationship between seed dispersers and species availability and its impact on successional pathways are critically needed.

(*c*) *Both ESP and ESA feedback loops.*

⑥ → ⑦ and ⑤ → ⑦: **do the ESP and ESA feedback loops drive a directional shift in species composition?** Species composition changed directionally with forest age (Fig. 10A), 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. 10A). 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.

(3) Synthesis of the mapping exercise

In Section IV.2 we illustrated how our framework can be used for a single study to compare explicitly the causal pathways representing the empirical outcomes with the pathways representing the study's conceptual model. This mapping exercise reveals that the Agua Salud project was set up to evaluate a conceptual model that predicts directional change in plant species composition driven by interacting ESP and ESA feedback loops, with declining light availability as the main environmental driver of the ESP feedback loop (Fig. 10A–D) and many of its publications interpreted the results in light of that model, with a range of assumptions made for components of the hypothesised causal pathways for which data were not collected. The strongest evidence found was for the hypothesised association between declining light availability and shifts in plant life-history strategies. Various studies further provided 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). Thus, the mapping exercise parsed out which feedback loops and causal factors are key drivers of succession, and how their relative importance shifts over the course of succession. Also, it elucidated that support for many feedback loops was largely indirect, with the lack of data on the disperser community and species availability (dispersal) constituting a considerable data gap. Finally, many of the Agua Salud papers that examined tree–soil interactions during succession strongly suggest that more complex causal pathways are needed to encapsulate the successional dynamics of these Panamanian forests than envisioned in the project's original conceptual framework.

Our intention here is not to find fault with a project but to enable researchers to assess objectively how study methods and data collection map on to their original conceptual model. We have found the framework to be particularly useful in highlighting the distinction between direct and indirect support for key causal pathways and feedback loops. Studying succession in the field is complicated, time consuming and often lacks sufficient funding. Going forwards, our hope is that this framework can help researchers to design projects more efficiently and to gather data that relate directly to their conceptual model. This exercise also highlights that diverse approaches are required to study feedback loops, such as replicated studies along larger soil gradients, long-term studies, controlled experiments and dynamic modelling (Johnson & Miyanishi, 2008; Walker *et al.*, 2010*b*; van der Putten *et al.*, 2013; Larocque *et al.*, 2016; Chang & Turner, 2019; Maréchaux *et al.*, 2021). 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).

While we illustrated the use of our framework with an in-depth analysis of a single project, this framework can also be used for systematic comparisons among study sites and along environmental gradients. One could, for example, examine (*i*) which causal pathways and feedback loops – and variables within pathways – are found to be key drivers of (variability in) succession; and (*ii*) how this varies along larger environmental, disturbance or other gradients. This framework allows for a hierarchical approach, in which studies can be compared in terms of the general feedback loops and pathways (e.g. relative importance of the performance and availability feedback loops) and, subsequently, more detailed comparisons can assess the importance of different variables within specific loops (e.g. soil *versus* light in the performance feedback loop).

V. 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 has 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 simple 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 and dispersal processes involved in successional feedback dynamics cause variability in successional dynamics of plant communities. Second, extrinsic causes of variability are independent of changes in the plant community but do differentially affect species performance or availability, thereby prompting spatial variability in succession. Finally, both these causes can generate variation in the dominant species in plant communities. Feedback loops may cause further contingency if these species differ in their impacts on the environment (priority effects).

(3) Predictability and variability are intrinsically linked features of ecological succession. This implies two fundamental questions in any study on ecological succession: (*i*) what are the (dominant) feedback processes that drive similar successional trajectories among plant communities; and (*ii*) 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. The conceptual framework defines seven general causes (landscape context, disturbance and land use, biotic factors, abiotic factors, species availability, species performance, and the plant community) that can be linked to 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 assess critically 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 conceptualise 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 scales. 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 specific fields and to examine the role and importance of alternative causal pathways of succession.

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VII. AUTHOR CONTRIBUTIONS

The idea for this study was conceived by M. v. B. and further developed during workshops attended by M. v. B., F. B., N. N., L. A., W. C., R. C., D. C., C. F., B. H., E. L.-T., M. M.-R., J. A. M., R. M., L. P., N. R., M. v. d. S. and D. H. D. M. v. B. and J. S. H. contributed data and M. v. B. analysed the data. M. v. B. wrote the manuscript with the support of D. H. D., N. N., F. B. and J. A. M., and all authors discussed the ideas and commented on previous versions. All authors approved submission of the final version. The authors declare no competing interests.

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IX. SUPPORTING INFORMATION

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

Appendix S1. Description of the Agua Salud Secondary Forest Dynamics Study.
Fig. S1. Non-metric multidimensional scaling (NMDS) plot using Růžička dissimilarity distances for species composition of secondary forests.

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