Successional theories

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ABSTRACT

Succession is a fundamental concept in ecology because it indicates how species populations, communities, and ecosystems change over time on new substrate or after a disturbance. A mechanistic understanding of succession is needed to predict how ecosystems will respond to land-use change and to design effective ecosystem restoration strategies. Yet, despite a century of conceptual advances a comprehensive successional theory is lacking. Here we provide an overview of 19 successional theories ('models') and their key points, group them based on conceptual similarity, explain conceptual development in successional ideas and provide suggestions how to move forward.

Four groups of models can be recognised. The first group (*patch & plants*) focuses on plants at the patch level and consists of three subgroups that originated in the early 20th century. One subgroup focuses on the processes (dispersal, establishment, and performance) that operate sequentially during succession. Another subgroup emphasises individualistic species responses during succession, and how this is driven by species traits. A last subgroup focuses on how vegetation structure and underlying demographic processes change during succession. A second group of models (*ecosystems*) provides a more holistic view of succession by considering the ecosystem, its biota, interactions, diversity, and ecosystem structure and processes. The third group (*landscape*) considers a larger spatial scale and includes the effect of the surrounding landscape matrix on succession as the distance to neighbouring vegetation patches determines the potential for seed dispersal, and the quality of the neighbouring patches determines the abundance and composition of seed sources and biotic dispersal vectors. A fourth group (*socio-ecological systems*) includes the human component by focusing on socio-ecological systems where management practices have long-lasting legacies on successional pathways and where regrowing vegetations deliver a range of ecosystem services to local and global stakeholders.

The four groups of models differ in spatial scale (patch, landscape) or organisational level (plant species, ecosystem, socio-ecological system), increase in scale and scope, and reflect the increasingly broader perspective on succession over time. They coincide approximately with four periods that reflect the prevailing view of succession of that time, although all views still coexist. The four successional views are: *succession of plants* (from 1910 onwards) where succession was seen through the lens of species replacement; *succession of communities and ecosystems* (from 1965 onwards) when there was a more holistic view of succession; *succession in landscapes* (from 2000 onwards) when it was realised that the structure and composition of landscapes strongly impact successional pathways, and increased remote-sensing technology allowed for a better quantification of the landscape context; and *succession with people* (from 2015 onwards) when it was realised that people and societal drivers have strong effects on successional pathways, that ecosystem processes and services are important for human well-being, and that restoration is most successful when it is done by and for local people.

Our review suggests that the hierarchical successional framework of Pickett is the best starting point to move forward as this framework already includes several factors, and because it is flexible, enabling application to different systems. The framework focuses mainly on species replacement and could be improved by focusing on succession occurring at

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different hierarchical scales (population, community, ecosystem, socio-ecological system), and by integrating it with more recent developments and other successional models: by considering different spatial scales (landscape, region), temporal scales (ecosystem processes occurring over centuries, and evolution), and by taking the effects of the surrounding landscape (landscape integrity and composition, the disperser community) and societal factors (previous and current land-use intensity) into account. Such a new, comprehensive framework could be tested using a combination of empirical research, experiments, process-based modelling and novel tools. Applying the framework to seres across broadscale environmental and disturbance gradients allows a better insight into what successional processes matter and under what conditions.

Key words: assembly, community, dispersers, ecosystem, landscape, secondary, socio-ecological system, species, succession, vegetation.

CONTENTS

I. INTRODUCTION

Succession is a fundamental concept in ecology because it indicates how populations, species, communities, and ecosystems change over time after disturbance has created a new substrate [i.e. primary succession (Miles & Walton, 1993; Walker & Del Moral, 2003)] or has removed part of the vegetation (i.e. secondary succession). Succession is one of the most widely used concepts in ecology because it integrates different ecological fields and is globally applicable (Pickett, Meiners & Cadenasso, 2011). In addition, succession has attracted much attention in the Anthropocene because global change (i.e. land-use change and climate change) is creating disturbance regimes of increasing frequency and

intensity that cause severe losses in biodiversity, ecosystem functioning and contributions of nature to people. It is an open question whether succession can recover such losses. Therefore, a mechanistic understanding of succession is urgently needed, to understand and predict how species and ecosystems respond to global change and to design and implement effective ecosystem restoration strategies. This last aspect is vitally important to support global ambitions to restore 3.5 million km^2 of degraded land by 2030 (Holl, 2017) and to support global initiatives such as the UN Decade on Ecosystem Restoration (UNEA, 2019). Successional theories can provide the mechanistic basis to underpin such predictions and designs (but see Rapson, 2023).

There are several excellent reviews on succession that summarise successional patterns, processes, and ideas by focusing respectively on succession in general (Miles, 1987; Burrows & Burrows, 1990; Glenn-Lewin, Peet & Veblen, 1992), primary succession (Miles & Walton, 1993; Walker & Del Moral, 2003), different disturbance types (Clements, 1916; Prach & Walker, 2020), different study systems such as temperate old fields (Meiners, Pickett & Cadenasso, 2015), tropical pastures (Peterson & Carson, 2008), and tropical forests (Chazdon, 2014), conceptual advances (Pulsford, Lindenmayer & Driscoll, 2016), empirical evidence (Drury & Nisbet, 1973; Connell & Slatyer, 1977), new tools and approaches (Connell & Slatyer, 1977; Meiners *et al.*, 2015), and the implications for restoration (Temperton *et al.*, 2004; Walker, 2007). Despite numerous conceptual advances made over the past century, a comprehensive successional theory is currently lacking (Peterson & Carson, 2008; Meiners *et al.*, 2015). This is partly because of the heterogeneous nature of succession, where a bewildering array of different successional pathways is observed across different study systems (Clements, 1916), and even within single sites (Vandermeer *et al.*, 2004; Norden *et al.*, 2015). Perhaps this bewildering number of successional pathways has led to an equally bewildering number of successional theories and explains why there is not yet a comprehensive theory available (Meiners *et al.*, 2015). A comprehensive theory is also lacking because scholars have focused on different components of the successional process, on different ecosystems, have used different terminology, and hold fundamentally different views on succession (Pickett *et al.*, 1987*b*; Pickett *et al.*, 2011). A few studies have reviewed successional theories, but they either evaluated a limited number of theories (Pulsford *et al.*, 2016) or presented them in the form of a rather succinct narrative on theory development (Walker & Del Moral, 2003; Peterson & Carson, 2008; Meiners *et al.*, 2015). A full appreciation of the wealth of available theories, their conceptual details and their conceptual differences and generalities still remains elusive. To advance successional theory further, we (*i*) provide an overview of successional models and their key points in a standardised way, (*ii*) group successional models based on similarities in concepts and approaches, (*iii*) build a timeline of models to explain the conceptual development in the ideas about succession, and (*iv*) provide suggestions on how to move forward. By summarising the most influential, but sometimes forgotten, successional models we hope to motivate researchers to test and expand existing models, thus contributing towards the development of a comprehensive successional theory.

(1) Concepts and definitions

For the development and use of any theory, it is important to define its elements and concepts clearly from the start. This increases clarity and understanding, facilitates communication, and prevents misunderstanding, as scholars may have different ideas in mind when using the same terms or when using different terms referring to the same ideas.

Succession is defined here as the changes displayed by an ecosystem over time following a disturbance. These changes occur in a range of ecosystem attributes, such as species diversity and composition, vegetation structure, ecosystem processes and soils (Poorter *et al.*, 2021). Most successional theories have focused on plants, probably because the field was developed by plant ecologists, because plants are sedentary and can easily be identified, and because they are primary producers that account for most of the ecosystem structure and processes and have cascading effects on other trophic levels (Connell & Slatyer, 1977). Therefore, most successional concepts and definitions we present here are related to plant succession.

A *successional pathway* is a temporal change in state variables displayed by a successional system (Lebrija-Trejos *et al.*, 2010). It can encompass changes in community types, system states, or species composition and abundance (Pickett, Collins & Armesto, 1987*a*). Successional pathways can be highly variable, as they may vary across vegetation types, within a vegetation type, and even within a site (e.g. Vandermeer *et al.*, 2004; Norden *et al.*, 2015).

A *successional mechanism* is a factor (e.g. seed availability) or process (e.g. facilitation, competition) that causes successional change. Mechanisms can operate at different organisational levels, such as the species level or community level (Pickett *et al.*, 1987*a*).

A *successional model* is a conceptual representation of how successional change works. It specifies the relationship between the various stages of the successional pathway and the successional mechanisms that cause the change from one stage to the next. Such a model can be verbal, diagrammatic, or quantitative (Pickett *et al.*, 1987*a*).

A *successional theory* is more comprehensive than a successional model. It is not only a conceptual representation of the whole successional process and its underlying mechanisms, but it should also clearly state and explain the (*i*) definitions, (*ii*) assumptions, and (*iii*) relationships amongst all components of the successional model, ideally using a conceptual diagram. It provides (*iv*) predictions about the direction of general successional patterns, and (*v*) (testable) hypotheses for the underlying mechanisms (Pickett *et al.*, 1987*b*). Ideally, such a theory is sufficiently general to be globally applicable across biomes, but also sufficiently

flexible and detailed to be context dependent and locally relevant and realistic.

The formulation of a global, comprehensive successional theory is clearly a daunting task, which explains why, despite various attempts, it has not been developed yet. Given the diversity, complexity and heterogeneity of succession, a single 'final' comprehensive theory may be elusive, but striving towards it will increase our understanding and generalisation. Here we contribute towards the development of such a comprehensive theory by reviewing foundational papers in the field of succession that have provided different successional models or mechanisms. Henceforth, we will refer to them as successional models, rather than as successional theories, because few of them comply with the stricter definition of theory as presented above. We discuss general successional models, and pay special attention to forest succession because it includes most life forms (from lichens, mosses, herbs, grasses to shrubs and trees), and presents therefore the longest and fullest successional gradient. We also include models that can explain tropical forest succession, because they have been less absorbed by the mainstream literature. Tropical forest succession provides an acid test for successional models, as it is more complex because of (*i*) the large number of species, life forms and functional guilds involved, (*ii*) the strong co-evolution between plant and animal species, and (*iii*) the highly complex forest structure.

This review is organised in four sections. First, we briefly summarise 19 successional models and explain their key ideas, assumptions, strengths and limitations using a standardised format (see Section III), so that it is easier to compare successional models directly. Second, we identify main groups of successional models based on similarities in concepts and approaches. Third, we build a timeline of models and explain the development in successional thinking. Fourth, we provide suggestions how to integrate current models and move forward.

II. METHODS

(1) Study selection

Selecting papers to include in a review is always challenging, as the difference between a foundational paper, a paper that presents a theory, and those that provide hypotheses or empirical findings is often implicit and gradual. As a starting point, we focused on successional models that are generally applicable to different ecosystems around the globe. We enriched this with more recent studies published over the last 15 years, and with studies on forest succession because it is one of the focal points of this review. To cover multiple ecosystems we include successional models from both temperate and tropical zones, as for historical and geographical reasons

tropical successional models have been less easily absorbed by the mainstream literature.

(2) Terminology

Because the study of succession is nearly as old as the field of ecology (Cowles, 1899; Clements, 1916), over the past century the use and meaning of successional terminology underwent substantial changes. To facilitate comparison and increase readability, throughout this review we use current terminology. To be explicit about these changes, and to ensure that the original meaning is not lost in translation, we also present at first use the original terminology in italics.

(3) Conceptual diagrams

For each model we made a graphical conceptual diagram (or adapted the original diagram) to summarise the key ideas of the model. To facilitate comparisons amongst conceptual diagrams, we use colour-coded boxes that refer to similar concepts: disturbance is shown in white; factors or processes that operate at a larger scale than the patch are shown in dark green; succession at the patch level in light green; environmental factors in blue; and socio-ecological factors in orange.

(4) Classification of models and timeline of development

To provide a synthetic overview of the overwhelming quantity of successional models, we group them based on similarities in concepts and approaches. This grouping allows us to understand their essence, identify common points, and highlight differences. Finally, to explain the development in successional thinking, we place the four main groups of models along a timeline.

III. REVIEW OF SUCCESSIONAL MODELS

In this section, we briefly present each model and (*i*) explain the key ideas and summarise these in a graphical conceptual diagram to make the line of thought explicit; (*ii*) identify the main assumptions as this may indicate whether the model is reasonable and under what set of conditions it applies; (*iii*) evaluate two main strengths and limitations; (*iv*) explain the development in successional thinking, and how it builds further on earlier models; (*v*) provide additional remarks on how the model has been used and tested, or under what successional conditions it applies. Using this standardised format allows us to understand and appreciate each model, and to compare them more directly. We present the models mostly in chronological order, as this clarifies the development in successional thinking. When models focused on the same topic or when they are conceptually very similar, we present and discuss them together.

(1) Relay floristics (Clements, 1916)

Key ideas: according to Clements (1916), succession is driven by six consecutive processes that operate during different stages of vegetation development (Fig. 1): (*i*) a disturbance creates an open site that is available for colonisation (*nudation*, in his terminology); (*ii*) seed dispersal to the new site (*migration*); (*iii*) species performance, i.e. seed germination, plant establishment and growth (*ecesis*); (*iv*) plants compete for the same limiting resources (*competition*); (*v*) plants modify the abiotic and biotic environment in terms of microclimate, soils, and resources (*reaction*); and (*vi*) succession progresses until environmental conditions and species composition change little and a final stable endpoint is reached (*stabilisation*). Although Clements considered succession to be continuous, he distinguished marked successional stages based on a dominant life form or species. He identified a common terrestrial successional sequence starting with lichens, transitioning into mosses, herbs, grasses, shrubs, and finally trees.

Assumptions: Clements made an analogy between the development of a plant community and the development of a plant organism that is born, grows, matures, reproduces and dies. Although Clements acknowledged that there can be different successional pathways, he assumed, based on this analogy, that vegetation in the same macroclimatic region should follow (in general) the same successional pathway (a series of *seres*) leading to the same climax vegetation.

Strengths: Clements (1916) summarised the existing successional knowledge from temperate North America. This allowed him to develop a general, coherent, and highly structured model about the main mechanisms underlying vegetation succession that can be applied to different situations while using many examples to clarify his ideas. As such, Clements (1916) provided much of the theoretical foundation for succession that we still use today.

Limitations: the analogy between vegetation succession and the development of an organism is interesting, but of course a plant community is not a single entity or an organism. The main limitation of Clements' model is, therefore, that he postulates the existence of a single, predictable successional pathway whereas in reality there are many different pathways and multiple potentially stable endpoints, even within the same climatic zone and within the same site.

Additional remarks: Egler (1954, p. 414) coined Clements' theory 'Relay floristics' because 'the torch of predominance is relayed along from one floristic group to another'.

(2) Individualistic model (Gleason, 1926)

Key ideas: the individualistic model postulates that plant associations and successional stages (e.g. grassland, shrubland, and forest) are the result of individual plant and species responses (Gleason, 1926). This model (Fig. 2) identifies two main causes of succession: (*i*) species dispersal (*migration*), and (*ii*) environmental selection. Seed availability in the surrounding landscape and proximity to adjacent vegetation determine the patterns of species dispersal and hence, successional pathways. Successional pathways are highly variable and unpredictable simply because they depend on which species disperse into the site. After establishment, environmental selection occurs in which species performance or abundance declines when the average environmental conditions are further away from their optimum. At the same time, plants respond to and can modify their environment.

Assumptions: apart from dispersal, successional shifts in species composition may only occur when environmental conditions change during succession.

Strengths: this model provides a simple mechanism for succession (immigration and species environmental requirements and tolerances), which is applicable to all vegetation types and can be tested (see Section VI). It recognises dispersal limitation (*migration*) as a key determinant of succession, that pioneers are characterised by high mobility, and explains why the order of arrival (priority effects) matters for succession.
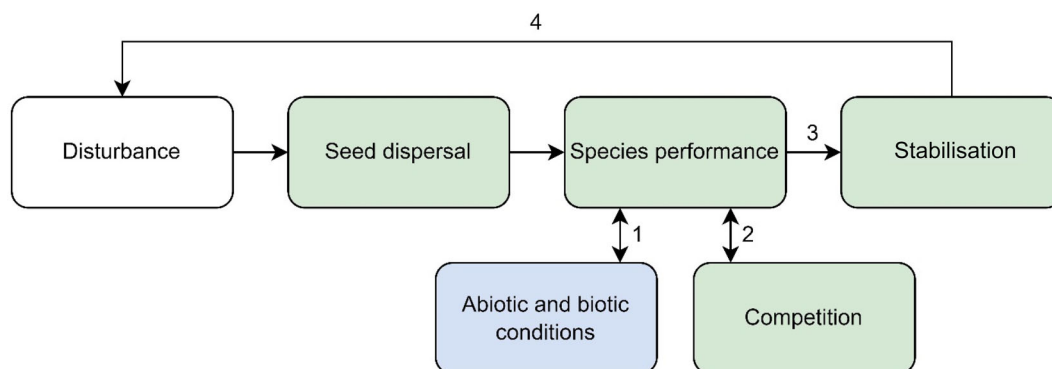
Fig. 1. Relay floristics (Clements, 1916). Species succession (light green boxes) is driven by a series of consecutive processes; a disturbance (white box) creates a new site. Seed dispersal to the new site leads to differential species performance (germination, establishment, growth), which is modified by changes in abiotic and biotic conditions (1, blue box) and competition (2). Over time, the rate of successional change will decline (3), leading to stabilisation of the community into a climax vegetation, until a new disturbance creates an open site (4), resetting succession to an earlier successional stage.

Fig. 2. Individualistic model (Gleason, 1926). Species composition of a patch is the result of the presence of individual species (7). Disturbance creates an open site (1) that is available for colonisation by species and modifies environmental conditions (2). The surrounding landscape (proximity to the nearest vegetation and its species composition, dark green box) determines (3) seed dispersal (light green), and hence, species availability (4). Species-specifi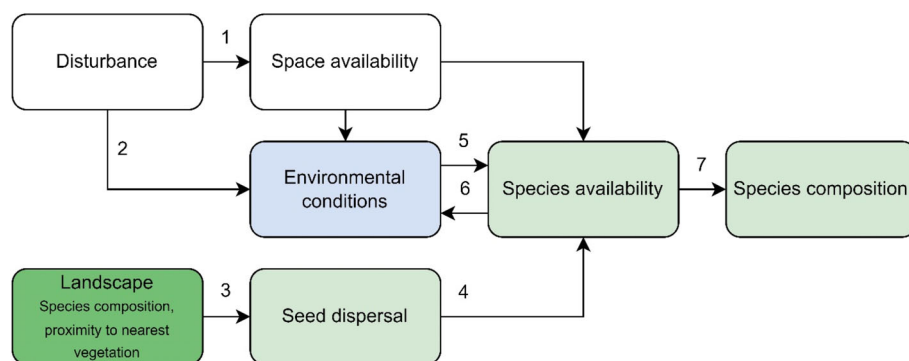c responses to the environmental conditions (blue) then determine if the species is filtered by the environment (5) and can establish and become abundant in the patch. Species can also modify the environmental conditions (6).

Limitations: it does not consider other mechanisms beyond migration and environmental selection, and focusses on the individual plant and species level, hence to understand succession you must know and understand what each individual species does, which is labour intensive and makes it difficult to generalise across regions.

Additional remarks: Gleason was visionary; his ideas are very similar to current community assembly theory, which states that species are filtered from the regional species pool based on species traits, dispersal filters, and environmental filters. He presents many ideas currently still used in ecology (community assembly, the role of the regional species pool, landscape, the important role of dispersal limitation, ecophysiological responses to environmental conditions, chance and unpredictability). His emphasis on species-specific responses also explains why succession in species-rich systems is so unpredictable.

(3) Initial floristic composition (Egler, 1954)

Key ideas: Egler (1954) focuses on succession (*vegetation development*) on abandoned agricultural pasture or crop fields ('*old fields*') and discusses two contrasting successional models based on the timing of species arrival; relay floristics (RF; Clements, 1916), and initial floristic composition (IFC). RF refers to the successive appearance and disappearance of species groups. Each group establishes (*invades*) at the site at a certain stage of its development, and soon makes conditions unsuitable for themselves but suitable for colonisation by the next group. As a result, dominance is relayed from one floristic group to another (Section III.1). By contrast, in the IFC model (Fig. 3) all species are present at land abandonment, and no additional immigration occurs. Over time, different groups of species become dominant and replace each other based on differential competitive abilities. RF and IFC represent the

conceptual extremes of a continuum; actual succession depends on both factors and is somewhere in between.

Assumptions: the IFC model assumes that all species are (*i*) spatially widely distributed (i.e. through a high abundance or an effective dispersal mechanism), (*ii*) present as seeds or seedlings during the agricultural phase (which should be long enough for species accumulation to occur), (*iii*) able to create a seed bank (most applicable to temperate or early-successional species).

Strengths: the IFC provides a simple contrast to the RF model, only based on timing of species arrival and establishment. The original article contains a nice diagrammatic visualisation of the salient differences, which can be tested with longitudinal data.

Limitations: the IFC model only considers internal, autogenic causes for succession, but no external, allogenic causes. It does not explain the mechanisms that drive successional turnover of life forms or species, why species groups become dominant (fast growth?), drop out (maximum longevity attained? outcompeted?) or cannot regenerate below their own canopy. In addition, this model does not consider additional immigration over time, which normally occurs in diverse vegetation types such as tropical forests.

(4) Life form replacement (Clements, 1916; Budowski, 1965; Gómez-Pompa & Vázquez-Yanes, 1981)

Key ideas: life form (sometimes referred to as growth form) is determined by the size, morphology, woodiness and lifespan of a plant. One of the most general successional patterns is the replacement of small short-lived life forms (LFs) by tall long-lived LFs (Clements, 1916; Budowski, 1965; Gómez-Pompa & Vázquez-Yanes, 1981) (Fig. 4). This replacement is probably caused by a trade-off between rapid colonisation ability of small LFs *versus* strong
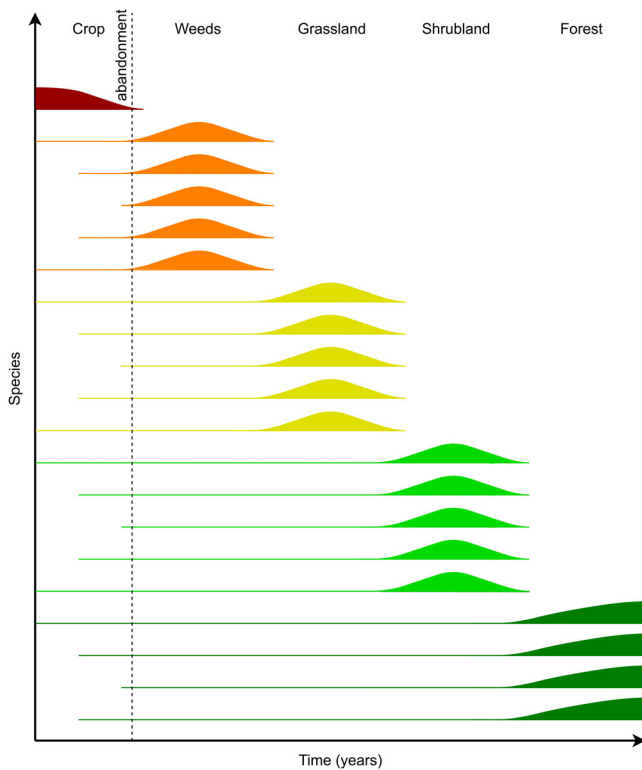
Fig. 3. Initial floristic composition model (Egler, 1954), in which all species are present at the time of agricultural abandonment as propagules or seedlings, and different species groups (weeds, grasses, shrubs, trees, as indicated by different colours) either establish and/or become dominant at different points in time. Each line represents a different species.

competitive ability for light by tall LFs (*colonisation–competition trade-off*; Tilman, 1994). Therefore, a successional pathway includes several LFs, often in the following order of arrival (although not each LF is present in each sere and their position in the sequence may change): lichens and mosses (mostly in the temperate zone), annual-, bi-annual- and perennial herbs, grasses, ferns (which may occur at any time, because of easy dispersal by spores), scramblers, herbaceous vines, shrubs, woody lianas (mostly in the tropics) and finally palms (in the tropics) and trees.

Assumptions: the predicted order of LF replacement implicitly assumes a trade-off between colonisation and (light) competition.

Strengths: LF replacement is the most ubiquitous successional phenomenon for different types of succession (primary, secondary, cyclic) across the globe. Species are easily classified into LFs and this can be done in a consistent way across biomes, enhancing comparability and generalisation.

Limitations: each LF contains many species that may differ strongly in their traits and successional position (Wright *et al.*, 2005). Hence, LF replacement provides a physiognomic description of succession, and can therefore explain the mechanisms underlying species replacement only to a limited extent.

Additional remarks: LF replacement is clearest in primary succession on newly formed bare substrate, as it depends on species arrival, environmental modification, and species interactions. In general, LF replacement in primary succession may follow the following order: mosses may arrive first through their ubiquitous, light spores, and together with microbial crusts they can capture, bind, and stabilise soil particles leading to soil development. Then lichens build up the organic nitrogen pool through atmospheric nitrogen fixation and induce weathering and substrate formation. They are replaced by herbaceous and woody nitrogen fixers that can establish in the accumulated substrate with increased water-holding capacity, and are in turn replaced by increasingly taller LFs when the vegetation builds up (Miles & Walton, 1993). By contrast, secondary succession is characterised by many legacies, such as well-developed soils and abundant propagules (seed bank, resprouts, and advanced regeneration). As a result, at the onset of succession there may be many LFs (e.g. in swidden agriculture), dominance of one LF (e.g. in pastures) (Egler, 1954), or dominance of shade-tolerant longer-lived LFs (in the case of cyclic forest succession). It should be noted that primary and secondary succession provide categorical descriptions for succession following different types of disturbances. Yet, different types of disturbance result in a continuum of initial site conditions and legacies. As a result, primary and secondary succession may overlap to some extent (Miles & Walton, 1993; Walker & Del Moral, 2003), and may have less effect on succession compared to climate or the surrounding landscape (Vítovcová *et al.*, 2021).
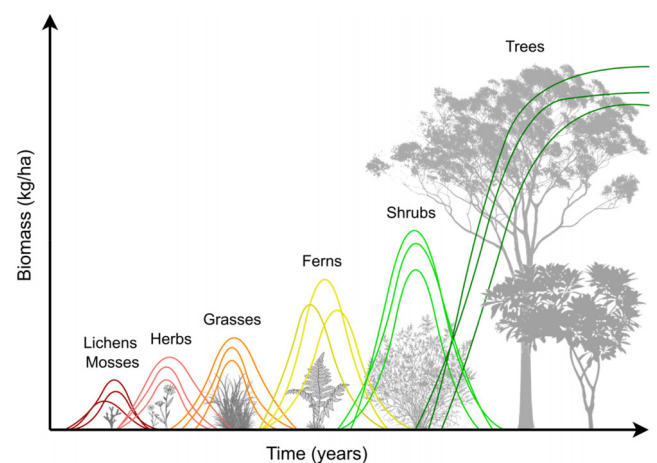
Fig. 4. Life form (LF) replacement where small, short-lived LFs are replaced by taller, longer-lived LFs. Each LF is indicated by a different colour. Several species of the same LF that differ in abundance co-occur at the same time (indicated by the multiple lines for each colour) and LFs gradually replace each other (as indicated by the overlapping lines for different LFs). In general, LF replacement may follow the order indicated in this diagram, although not each LF is present in each sere and their position in the sequence may change.

(5) Forest stand development (Watt, 1947; Whitmore, 1975; Oliver, 1980)

Key ideas: many vegetation types consist of a shifting mosaic of patches in different successional phases (Watt, 1947), also known as cyclic succession. After disturbance, patch development consists of an aggrading phase when vegetation builds up, and a degrading phase when the dominant plants become senescent and die (Watt, 1947). Cyclic succession is typical of forests where a small-scale disturbance such as a treefall creates a canopy gap, thus initiating patch development (Fig. 5). Van Steenis (1958) was one of the first to recognise that old-growth tropical forests consist of a shifting mosaic of patches in different phases of successional development. Patch development is initiated by the formation of a canopy gap that may be closed in due time due to rapid vertical regrowth of regenerating plants. Patch development is characterised by four different phases (*gap, building, mature,* and *degenerate*) (Whitmore, 1975; Oldeman, 1990), which together form the forest growth cycle. Another disturbance may take place at any time. Larger stand-replacing disturbances (such as crown fires) lead to comparable successional patterns in temperate forests, where four successional phases can be distinguished based on development in stand structure and its underlying processes (Oliver, 1980; Peet & Christensen, 1980; Oliver & Larson, 1996). The *stand-initiation stage* is characterised by rapid germination, establishment and growth. Plants can establish or regrow at a site through advanced regeneration (i.e. plants that have already established before disturbance), resprouting from damaged stems or roots, or through germination from the seed bank or seed rain, while high light conditions result in rapid height growth. The *stem-exclusion stage* is characterised by canopy closure and light limitation, followed by high mortality and vertical stratification. Stems are excluded because new plants cannot establish in the shade and pioneers die because of light competition and thinning. Vertical stratification (i.e. layering) occurs as some trees dominate the canopy (the pioneers) while others are suppressed, stay behind, and form a second layer. The *understorey-reinitiation stage* is characterised by canopy tree mortality and gap formation. It starts when the canopy opens up when some canopy trees die, or when the understorey environment is favourable for the regeneration of herbs and shade-tolerant trees. In the *old-growth stage* senescence, disease, and disturbances cause trees to die and disintegrate alone or in groups, which releases understorey plants and results in tree stems in all size classes.

Strengths: a simple successional model based on development of patch structure and underlying demographic processes. It can be applied to small- and large-scale disturbances (Chazdon, 2014).

Limitations: it does not make a clear prediction of what species will dominate when in succession and in what canopy layer.

Development: the stand development model emphasises the three-dimensional *structural* development of the vegetation and its associated demographic processes, whereas the LF replacement model (Section III.4) emphasises more the *physiognomic* development of the vegetation, and how it is caused by the life-history traits of these LFs. Ideas derived from the stand development model have also been implemented in mathematical models of forest succession, such as forest gap models (Shugart Jr & West, 1980).

Additional remarks: in the tropics, stand development after agriculture is faster because of productive growing conditions, regeneration is continuous throughout stand development because of later arrival of mammal-dispersed species and larger shade tolerance, and canopy structure is therefore
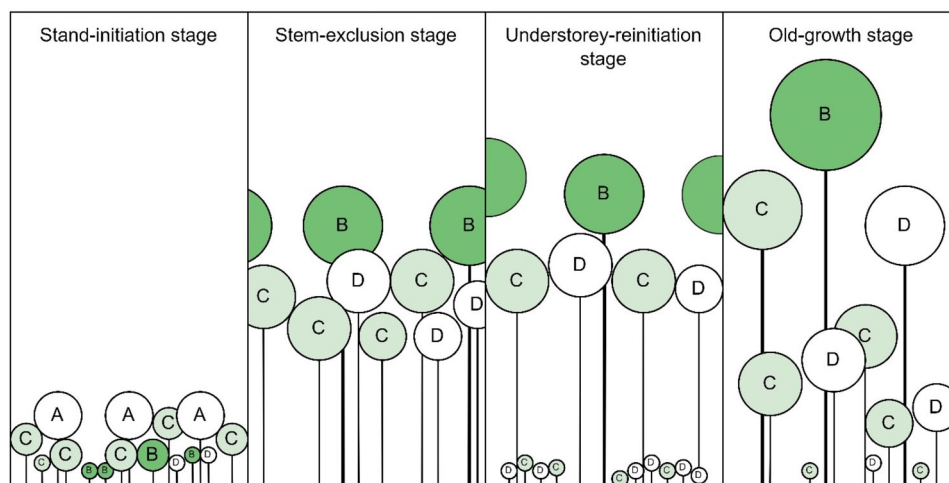
Fig. 5. Forest stand development (Oliver, 1980). Four stand-development phases following a large disturbance. In the stand-initiation stage plants establish through advanced regeneration, resprouts or germination. The stem-exclusion stage is characterised by canopy closure, which results in thinning and vertical stratification. The understorey-reinitiation stage starts with gap formation, which allows for the regeneration of new shade-tolerant trees. The old-growth stage is characterised by senescence of some canopy trees and trees in all size classes. Different species are indicated by different crown colours and letters.

more heterogenous and complex, and less clearly layered (Budowski, 1965; Chazdon, 2008).

(6) Tree functional groups (van Steenis, 1958; Budowski, 1965; Finegan, 1996)

Key ideas: the herbaceous and shrub-dominated phase in forest succession lasts only a few years to decades, whereas the tree-dominated phase lasts one to several centuries. Life form (LF) replacement explains, therefore, only a small part of forest succession (<5 years in the tropics), with the remainder explained by the large variation in tree strategies (Budowski, 1965; Finegan 1996). This is especially the case for species-rich tropical forests where tens to hundreds of tree species coexist. Tropical ecologists have classified tree species in 3–6 successional groups, ranging from early-, to mid-, to late-successional species.

Pioneers (*nomads*) are the first species to establish in a gap and need to grow and reproduce before the gap closes and they die (van Steenis, 1958). Van Steenis (1958) termed pioneers 'nomads', as they have to move around and disperse their seeds in space or time in order to colonise a new gap somewhere else. He recognised three groups: short-lived pioneers (SLPs <10 years), long-lived pioneers (LLPs, *ca.* 100 years) that establish after large disturbances and may form even-aged stands, and shade-tolerant species (*dryads* – or forest nymphs) that establish in the shade and grow up to different maximum sizes in different forest strata.

Budowski (1965) focused on succession after larger-scale disturbances, by evaluating succession on abandoned agricultural fields. He recognised four successional stages (Fig. 6), each with its corresponding dominant functional group and life-history traits. *Pioneers* and *early successional* species are not only light demanding, but also drought tolerant because they experience atmospheric drought in their hot early successional environment. *Late-successional* species are tall, deciduous, and often also part of the dry forest climax. *Climax* species are later successional, old-growth species and shade tolerant.

Finegan (1996) recognised four successional phases based on LFs and the longevity of the dominant trees (Fig. 6). The first phase (<5 years) is dominated by herbs, shrubs and climbers, during which SLP trees establish. The second phase (10–30 years) is dominated by SLPs that form a dense, even-aged stand, under which shade the species of the first phase disappear. The third phase (75–150 years) is dominated by LLPs that establish early in succession and form dense, even-aged stands. Both phases last as long as the lifespan of the dominants. The fourth phase is dominated by shade-tolerant (ST) species that recruit continuously during succession.

Assumptions: trees belong to distinct functional groups rather than showing a continuum in strategies.

Strengths: species classification into a few successional groups is relatively easy, especially when they are tied to a specific forest development stage (see Budowski, 1965). As with life forms, the use of successional groups facilitates

communication amongst researchers and comparisons across regions.

Limitations: functional groups may represent the (arbitrary) extremes or landmarks along a continuum, as tree species show a continuum in their traits, performance, shade tolerance (Poorter & Bongers, 2006), lifespan (Condit, 2022), and successional position.

Development: whereas the LF replacement model (Section III.4) considers trees to belong to one single functional group, the tree functional group model explains how succession is driven by plant strategy variation within the tree group. Although forest structure and tree functional groups mutually affect each other during succession, the stand development model (Section III.5) focusses on changes in forest structure and how it affects light conditions, demographic processes and, hence, tree functional group replacement, whereas the tree functional group model focuses on the successional replacement of functional tree groups, with changes in forest structure as an emergent property.

Additional remarks: a recent demographic modelling study (Rüger *et al.*, 2023) shows that LLPs increase during tropical forest succession but that there is little successional replacement, and as a result they form a dominant, stable component of old-growth forests, partly in line with Budowksi's (1965) ideas.

(7) Ecosystem development (Odum, 1969)

Key ideas: during succession, ecosystems develop in a predictable way over time because communities modify the environment, resulting in a stable ecosystem with maximum biomass in homeostasis with the environment (Odum, 1969). Odum (1969) discusses the successional development of six groups
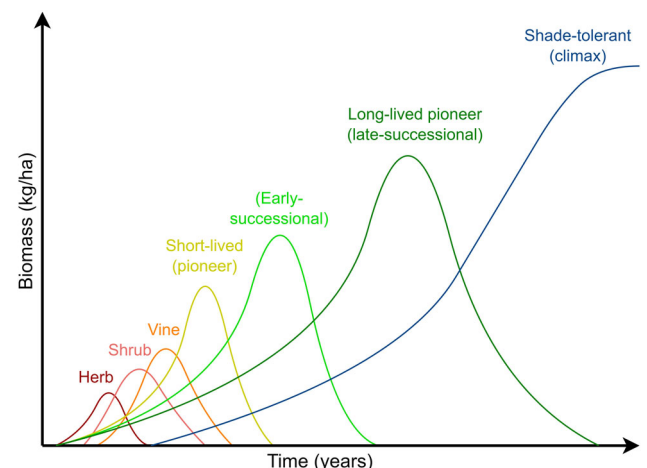
Fig. 6. Tree functional groups. During the first 5 years of tropical forest succession, herbaceous life forms (herb, shrub, vine) establish and are replaced by short-lived pioneer trees. They are followed by long-lived pioneers and shade-tolerant species (Finegan, 1996). The corresponding terminology of Budowski (1965) is shown in parentheses.
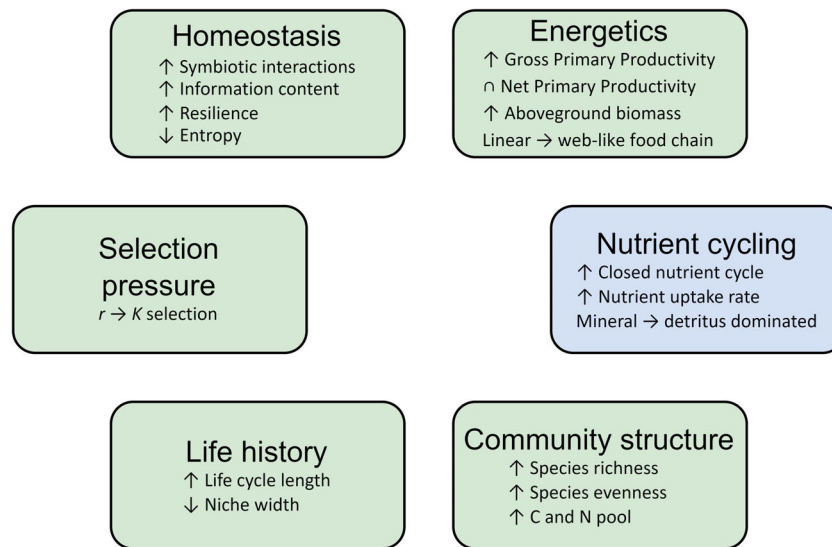
Homeostasis	Energetics
↑ Symbiotic interactions ↑ Information content ↑ Resilience ↓ Entropy	↑ Gross Primary Productivity ∩ Net Primary Productivity ↑ Aboveground biomass Linear → web-like food chain

Selection pressure	Nutrient cycling
$r \to K$ selection	↑ Closed nutrient cycle ↑ Nutrient uptake rate Mineral → detritus dominated

Life history	Community structure
↑ Life cycle length ↓ Niche width	↑ Species richness ↑ Species evenness ↑ C and N pool

Fig. 7. Ecosystem development (Odum, 1969). During succession, six groups of ecosystem attributes (related to energetics, nutrient cycling, community structure, life history, selection pressure, and homeostasis) develop over time. For each attribute it is predicted whether they increase (↑), decrease (↓) or show an optimum (∩) over time.

of 24 ecosystem attributes related to energetics (i.e. carbon stock and sequestration), structure, life history, nutrient cycling, selection pressure, and homeostasis (Fig. 7).

Energetics: gross primary productivity increases over time due to build up of vegetation, but because of increased maintenance costs respiration catches up, leading to a mid-successional peak in net primary productivity and an asymptotic increase in aboveground biomass over time. The food chain changes from linear, grazing-dominated plant–herbivore–carnivore chains in open herbaceous vegetations, to complex web-like food chains dominated by detritivores in closed forest vegetations.

Community structure: species richness increases due to the arrival of new species, species evenness increases because dominant pioneer species decline in abundance, and there is an increase in vertical stratification and spatial heterogeneity. The carbon and nitrogen pool size increase due to autotrophic assimilation, nutrient uptake, and biological nitrogen fixation, and an increasing part of the nutrients is moved from the soil and locked up in biomass.

Nutrient cycling: nutrient cycles become more closed as mature systems have greater capacity to entrap and hold nutrients with denser and deeper root systems. Nutrient uptake rate from the soil is initially fast because of rapid plant growth but decreases over time when plant growth slows down. With the accumulation of biomass, detritus becomes more important for nutrient cycling.

Life history: during succession, species niches become narrower because of increased species packing and competition. Organisms and species become taller, and consequently, life cycles become longer and more complex.

Selection pressure: selection shifts from *r*-selection (favouring rapid growth and reproduction) in early-successional environments, where the availability of some resources is high, to *K*-selection (favouring slow growth, high survival, delayed reproduction and high parental care) in later successional environments where the availability of some resources is low and, as a result, there is more competition.

Homeostasis: homeostasis refers to the ability of an organism or a system to keep the internal conditions unchanged, so that the system remains in a stable state. During succession, symbiosis increases (i.e. biological interactions between organisms such as mutualism, parasitism, predation, and commensalism) leading to biotic control and stability, increased resilience ('*resistance to external perturbations*') and information content, and as a result a decrease in entropy (i.e. randomness or chaos; see Margalef, 1963).

Strengths: this model provides a holistic, ecosystem-level perspective on succession, by focussing on six complementary groups of ecosystem attributes and by considering the whole biotic community (i.e. not only plants but all organisms). It makes clear predictions of how attributes should change during succession, and is therefore testable. Succession is described in terms of energy flows in the system, which facilitates comparisons amongst different ecosystems.

Limitations: although clear predictions are made about how ecosystem attributes should change during succession, sometimes the mechanisms are not clear.

Development: both Clements (1916) and Odum (1969) assumed that succession is mostly autogenic, orderly and predictable; Clements from a taxonomic point of view, and Odum from an ecosystem point of view. Clements compared vegetation development with the development of an organism, whereas Odum compared ecosystem development with the long-term evolutionary development of the biosphere to attain homeostasis. Most prior successional models had only focused on species replacement. Odum (1969) was the first to discuss changes in species richness, evenness and ecosystem

development, probably because it coincided with the emergence of systems ecology and ecosystem approaches in the 1960s.

Additional remarks: Odum pointed out that humans are mostly interested in maximising the production services of ecosystems by keeping them in an early-successional state. By contrast, other important regulating and cultural services are provided by later successional ecosystems. Because of this trade-off, he proposed multifunctional landscapes based on land sparing (productive early-successional systems and late-successional conservation areas) and land sharing (combining production and conservation).

(8) Nucleation (Yarranton & Morrison, 1974)

Key ideas: plant species such as shrubs and trees can act as nuclei of regeneration (Fig. 8), as other species can regenerate below their crown because of more benign microclimatic conditions (less solar radiation, cooler, and more humid), trapping of organic material, and improved soil conditions (Yarranton & Morrison, 1974). This results in a landscape mosaic of different regeneration patches that increase in size over time and eventually coalesce, resulting in a uniform vegetation. This process is called nucleation, in analogy to nucleation in physics where it is a first step in the formation of a new structure due to self-assembly. Hence, depending on the successional starting point, vegetation mosaics can be the result of open patches in a closed vegetation matrix (van Steenis, 1958) or of vegetation patches in an open landscape matrix (nucleation).

Strengths: it explains why early succession can be heterogeneous, resulting in mosaic-like landscapes, and highlights the key role of (remnant) nurse trees.

Limitations: the nucleation model focused initially on only one successional mechanism (facilitation) although later other mechanisms were included as well (see *Additional remarks*). *Development*: the model builds on the ideas of Clements (1916) by focusing on facilitation and life form replacement. Its spatial focus coincides with the development of statistical tools for pattern analysis in the 1950s and 1960s, and with the emergence of spatial ecology as a research field.

Additional remarks: nucleation is important during primary succession where microclimatic conditions are harsh, the substrate is less developed, and facilitation and soil development are key. Nucleation is also important during secondary succession, for example in rangelands where nurse shrubs may protect regeneration from animal browsing (Olff *et al.*, 1999; Smit *et al.*, 2007). In abandoned fields, remnant trees may act as a food source and perching site for birds and mammals. This increases seed input and speeds up succession, especially of later successional, animal-dispersed tree species that otherwise would take a long time to arrive (Guevara, Purata & Van der Maarel, 1986; Holl *et al.*, 2020) (although in some successions endozoochorous-dispersed tree species are the first colonisers).

(9) Facilitation, tolerance, and inhibition (Connell & Slatyer, 1977)

Key ideas: successional species replacement is the result of three types of species interactions ('*models*'), in which pioneer species can have a positive (facilitation), neutral (tolerance) or negative (inhibition) effect on later successional species (Connell & Slatyer, 1977) (Fig. 9). In facilitation, pioneers modify the environment so that it becomes more suitable for later successional species to establish and grow to maturity. Facilitation is most likely to occur during heterotrophic degradative succession, primary succession (with no prior soil development), early in secondary succession, and under harsh environmental conditions. In tolerance, changes in environmental conditions have neutral effects on the recruitment and growth to
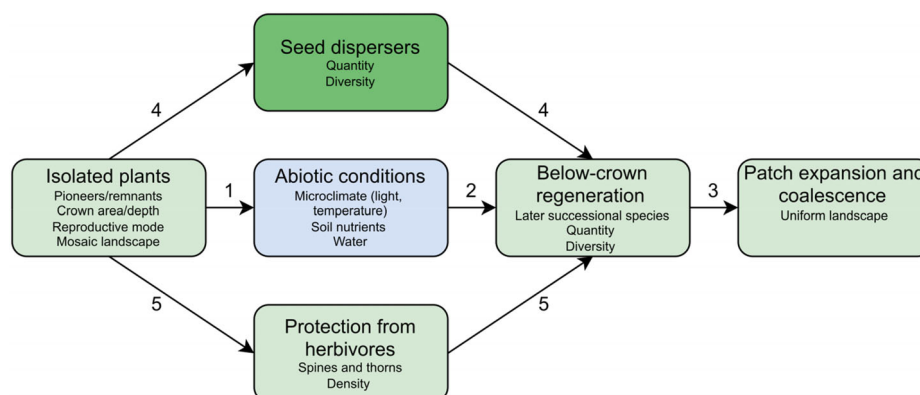

Fig. 8. Nucleation (Yarranton & Morrison, 1974). When isolated pioneer plants become established, the abiotic conditions below their crown improve (1) which facilitates the regeneration of later successional species below the crown (2). Lateral patch expansion leads to patch coalescence and a more uniform landscape (3). Later studies highlighted the role of these isolated, and sometimes remnant trees to attract seed dispersers, which defecate their seeds, leading to a high quantity and diversity of later successional species (4; Guevara *et al.*, 1986). Additionally, in herbivore-dominated landscapes, isolated plants provide safe regeneration sites by protecting seedlings from herbivores (5; Smit *et al.*, 2007).
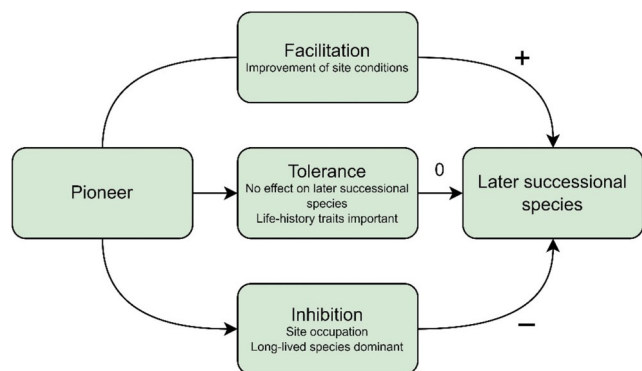
Fig. 9. Facilitation, tolerance, and inhibition (Connell & Slatyer, 1977). Pioneers can affect succession by later successional species in three ways. Pioneers can have a positive effect (facilitation) by improving site conditions, a neutral effect (tolerance) because later successional species are tolerant to changed environmental conditions, or a negative effect (inhibition) by occupying the site and preventing the establishment of other species.

maturity of later successional species. Successional replacement is solely driven by life-history characteristics because pioneers arrive quickly and have short life cycles, and later successional species arrive more slowly, live longer, and can tolerate low-resource conditions. In inhibition, pioneers inhibit establishment ('*invasion*') by pre-empting the space or by reducing the growth of later successional species. Once the pioneer dies because of disturbance, pathogens, or senescence, it can be replaced by another pioneer or by a later successional species. Because pioneers are short lived, they will be replaced more often than long-lived later successional species. As a result, pioneers will decline and long-lived species will increase in abundance during succession. Successional patterns in community composition can, therefore, be explained by species longevity alone.

Assumptions: because pairwise species interactions are thought to drive succession, it seems that Connell & Slater (1977) only consider successional seres that involve a few dominant pioneer and late-successional species, rather than many species within each group that all differ in their life-history traits, and thereby in their effects and responses.

Strengths: this is a simple classification of species interactions based on positive (facilitation), neutral (tolerance) and negative (inhibition) effects. It emphasises the additional role of biotic interactions such as herbivores, predators, and pathogens in succession (although this is not really included in their three models), and predicts how the successional pathway changes with disturbance size and intensity (see Bazzaz, 1984).

Limitations: all three postulated mechanisms operate often at the same time during succession for some species pairs, and therefore it is not clear how this will steer the overall successional pathway (Finegan, 1984). The difference between tolerance and inhibition also is not clear; the tolerance mechanism assumes that pioneers have neutral effects on 'tolerant'

species, although pioneers often reduce the recruitment, growth, and survival of later successional species which is, in fact, 'inhibition' (Finegan, 1984).

Development: most successional models thus far were developed by plant ecologists and most of the focus was therefore on plant competition for resources driving succession. Similarly, at that time community structure theory was nearly entirely focused on competition (Hutchinson, 1957; MacArthur, 1984). Connell & Slatyer (1977) advanced successional theory by presenting two new successional mechanisms: tolerance and inhibition.

(10) Competitor, stress-tolerator and ruderal (CSR) plant strategies (Grime, 1979, 2006)

Key ideas: three groups of plant strategies (Fig. 10) determine the dominance of species during different types of succession. *Ruderals* (R) are adapted to productive and disturbed habitats; they rapidly colonise an area following disturbance, grow fast, reproduce rapidly, have a short lifespan, and comprise a narrow range of life forms (LFs, annual and perennial herbs). *Competitors* (C) are adapted to productive, little-disturbed habitats; they rapidly acquire limiting resources through fast horizontal or vertical expansion and growth, and consist of a wide range of LFs (perennial herbs, shrubs, trees). *Stress-tolerators* (S) are adapted to unproductive (i.e. stressful) habitats with little disturbance: they increase persistence through slow growth and conservative resource use, and consist for example of lichens, mosses, and perennial plants. The strategies are visualised using a triangle, where each strategy occupies a different corner of the triangle (Fig. 10) and different LFs occupy different areas of the triangle (Fig. 10). The three sides of the triangle reflect a spectrum of intermediate strategies (SR, CR, CS). Different types of succession are predicted to show different successional pathways through CSR space. *Primary succession*, such as on bedrock, starts with stressful conditions (hot, dry, no soil, few nutrients) but conditions gradually improve when soil is formed and organic material, nitrogen and vegetation build up over time. As a result, different plant strategies dominate over time, showing an upward trajectory from S to C (Fig. 10). *Secondary succession* varies with habitat productivity. In productive habitats, succession starts out with ruderal species that rapidly colonise the open site. They are replaced by competitive species when the vegetation closes, which are themselves replaced by stress-tolerant species when light becomes limiting and nutrients are locked up in the vegetation or the microbial biomass (Fig. 10). In unproductive habitats where vegetation biomass remains low, succession moves directly from the ruderal to the stress-tolerant phase (Fig. 10). Disturbances such as grazing may modify successional pathways. Over-grazing by ungulates, geese or rabbits, may create open spots in the vegetation, thus providing establishment opportunities for annual ruderals, and setting back succession. Alternatively, moderate grazing removes the most palatable species (first the ruderals, then the
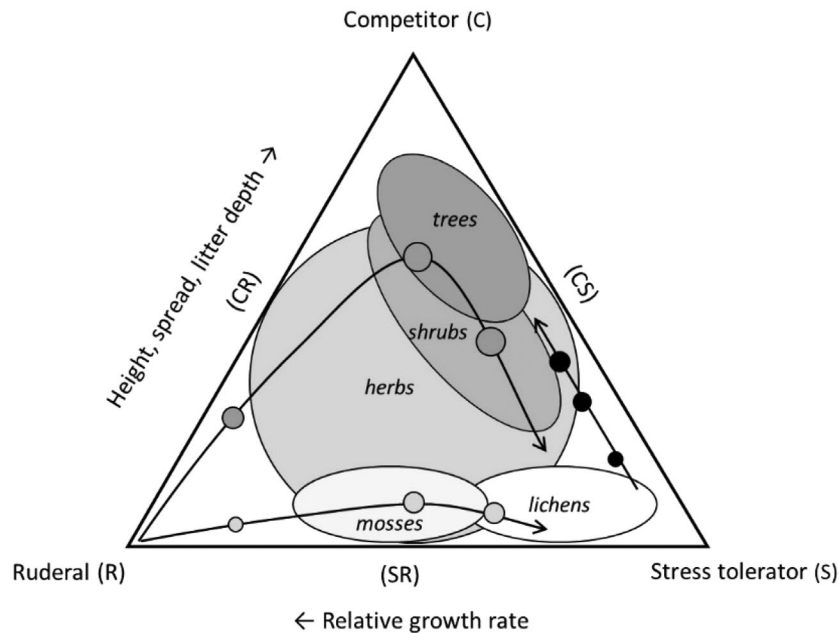
Fig. 10. Competitor stress-tolerator and ruderal plant strategies (Grime 1979, 2006). Plant species show different strategies to deal with disturbance and stress. Ruderals (R, left corner) are adapted to productive disturbed environments, competitors (C, top corner) to productive undisturbed environments, and stress tolerators (S, right corner) to unproductive, undisturbed environments. Along these axes intermediate strategies (SR, CR, CS) occur, and different life-forms tend to occupy different positions in the CSR plane (indicated by the ovals/circles). Successional pathways are shown as arrows for primary succession on bedrock (black circles), secondary succession in productive environments (dark-grey circles) and unproductive environments (light-grey circles). During succession there is a shift in the balance between disturbance, competition and mineral nutrient stress and, hence, the strategies of the dominant species as visualised by the trajectory through the CSR plane. The size of the circles reflects the vegetation biomass.

competitors), thus speeding up succession towards stress-tolerant species.

Assumptions: the scheme assumes that adaptations to different resource stresses (mineral constraints, shade, drought) and different non-resource stresses (heat, cold, extreme pH) are the same. This is not necessarily the case, so in reality there may be more strategy axes than three (Craine, 2009).

Strengths: the CSR strategy approach is highly appropriate to understand succession, as it explicitly focuses on plant responses to disturbance (R), and is globally applicable because it focuses on a wide range of environmental conditions, ranging from productive competitive environments (C) to unproductive, stressful environments (S). It is one of the first theories that makes predictions about the direction and rate of succession, and how it varies with resource supply and herbivory.

Limitations: the scheme was initially developed for temperate herbaceous vegetation, and has therefore been less applied to woody LFs or other vegetation types. Few studies have actually quantified species position in the triangle, as this requires data on seedling relative growth rates under standardised conditions (for the position along the SR axis), and data on maximum leaf canopy height, lateral spread, and litter depth (for the position along the CR axis). Therefore, most studies have used CSR strategies in a conceptual way to interpret their data.

Development: the CSR model is in line with the individualistic model of Gleason (1926), goes beyond life-history traits, and has spurred the current interest in trait-based approaches to describe species quantitatively and understand species performance.

Additional remarks: recently, Pierce *et al.* (2017) developed a global method to quantify CSR strategies using soft, continuous traits, which represents a significant advance to the use and application of the CSR strategy scheme across the globe.

(11) Vital attributes (Noble & Slatyer, 1980)

Key ideas: three groups of 'vital' life-history attributes determine the position of a species in a successional pathway following disturbance (Noble & Slatyer, 1980): (*i*) the regeneration mode (i.e. mode of arrival and persistence), (*ii*) species performance (i.e. the ability to establish and survive to maturity), and (*iii*) the timing of different life stages (Fig. 11). First, the regeneration mode indicates how species persist during disturbance (e.g. through thick bark, resprouting, or germination from the seed bank after fire) or arrive after disturbance (through dispersal). Second, species can establish and grow to maturity in three ways: *tolerant* species can tolerate a wide range of conditions and regenerate continuously, *intolerant* species can only establish immediately after disturbance because they are
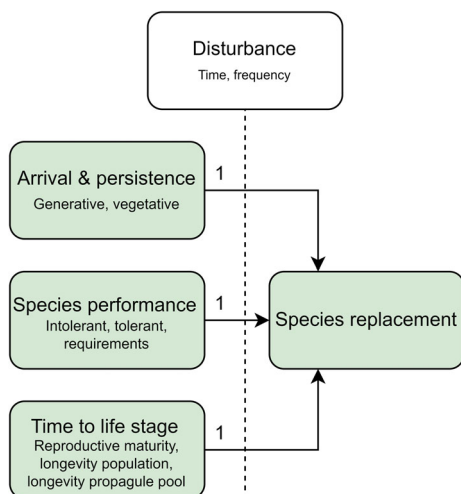
Fig. 11. Vital attributes (Noble & Slatyer, 1980). Changes in species composition during succession are determined by the disturbance regime (timing, frequency) that filters out species (as indicated by the vertical dashed line) based on their vital attributes (1). Three groups of vital attributes are distinguished, related to arrival and persistence (generative or vegetative regeneration), species performance (i.e. the ability to establish and grow in the community: intolerant, tolerant, and specific later successional requirements), and the time to reach a life stage (reproductive maturity, longevity of species population in the community, longevity of the propagule pool).

intolerant to competition by other plants, and *specialist* species require specific environmental conditions or a specific disperser and establish later in succession. Third, the timing of different life stages indicates the time to (*i*) reproductive maturity, (*ii*) maximum lifespan, and (*iii*) local extinction because all propagules are lost from the community. These three groups of vital attributes, together with the timing of disturbance, then determine the replacement sequence of species over time and hence, all possible successional pathways (Fig. 11).

Strengths: this was one of the first predictive models of successional species replacement based on very simple decision rules. It allows evaluation of how different disturbance scenarios result in different successional pathways in terms of species and functional composition.

Limitations: the model only predicts species occurrence, but not species' relative abundance.

Development: the model builds on the ideas of Gleason (1926) of individualistic species behaviour, and further develops the ideas of Drury & Nisbet (1973) that succession can only be understood based on species life-history traits related to colonising ability, performance in different environments, and longevity.

(12) Resource ratio (Tilman, 1985)

Key ideas: the resource ratio hypothesis postulates that (*i*) plants compete for two limiting resources, (*ii*) each species is

a superior competitor and becomes dominant at a certain (supply) ratio of these two resources, (*iii*) community composition should change when the availability of the resources changes (Fig. 12). The major limiting resources are often a belowground soil resource (especially nitrogen, or water) and an aboveground resource (light). During primary and secondary succession there is generally a shift from soil resource limitation to light limitation when the vegetation builds up. As a result, there is a replacement of small, short-lived, fast-growing and fast-reproducing early-successional species by tall, long-lived, and slow later successional species. Quantitative predictions of species change are made based on a simple mathematical model based on the resource supply rate, the amount of resource consumed per unit biomass, maximum biomass gain and biomass loss (e.g. due to herbivory). The process of competition is graphically illustrated by showing for multiple species the resource-dependent growth responses to two resource axes.

Assumptions: assumes that species replacement is driven only by resource supply trajectories over time and by interspecific competition amongst plant species.

Strengths: makes quantitative predictions about species turnover based on a simple and elegant mechanistic model. It is very general because it focuses on the main two limiting resources (above- and belowground) and can therefore be applied to primary and secondary succession and to mature vegetation.

Limitations: it is difficult to quantify size-dependent uptake of light and nutrient resources, especially for taller and longer-lived plants. Consequently, the model has only rarely been parameterized, and then mostly for herbaceous species. The model ignores other successional processes that are not related to competition (e.g. dispersal, facilitation).

Development: builds upon the ideas of Gleason (1926) that succession is driven by individualistic responses to the environment and develops this for competition for multiple resources. It is perhaps the only real successional theory, in the sense that it is mechanistic, quantitative, and makes clear predictions.

Additional remarks: succession is only directional or repeatable if the resource-supply trajectory is directional or repeatable. If temporal gradients during succession and spatial gradients in mature vegetation show the same resource ratio trajectories, then in both cases there should be the same replacement of species along these gradients. Importantly, successional pathways are totally dependent on the trajectory of resource supply, which therefore can explain the large variety of successional pathways observed in nature. Huston & Smith (1987) also modelled species abundance during succession based on competition for above- (light) and belowground resources (water, nitrogen). In addition, they also included inversely correlated life-history traits.

(13) Successional processes (Walker & Chapin, 1987)

Key ideas: succession is governed by a combination of different 'processes' (stochastic environmental variation, interactions,
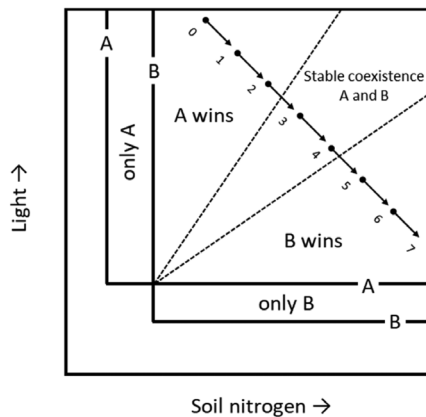
Fig. 12. Resource-ratio model (Tilman, 1985). Population growth response of two species (A and B) to two resources (soil nitrogen and light). Isoclines (the solid lines with right angles) show for each species the resource combination where net population growth is zero. Below or to the left of these isoclines species are not able to persist. The rectangular planes indicate where only one species occurs, where one species wins, or where both species stably coexist (the area between the dotted lines). Species A is an early-successional species with low N and high light requirements and species B is a later-successional species with high N but low light requirements. During succession the resource-supply trajectory (dot-arrows) changes from high light in year zero of succession to high soil nitrogen in year seven. Accordingly, the species composition changes from dominance by species A from years 0 to 2, coexistence with similar biomass from years 3 to 4, and dominance by species B from years 5 to 7.

and life-history traits). The relative importance of these different successional processes may shift during succession, and may vary with environmental conditions (i.e. favourable, productive environments *versus* severe, unproductive environments) (Fig. 13). Stochastic events such as patterns in rainfall or flooding determine plant establishment. This may be more important early in succession (in open environments), and in unproductive environments, when few resources are available. Similarly, facilitation by nitrogen fixers or nurse plants may be more important early in succession or in unproductive environments, when soil fertility is low and climatic conditions are harsh. Conversely, plant competition is more important later in succession and in productive environments, when there is dense vegetation. In productive environments, a life-history trait like rapid potential growth rate is important early in succession when pioneers rapidly colonise space, but in unproductive environments fast growth rate is only important later in succession when soil fertility has been improved by vegetation build up. Plant–microbe interactions such as mycorrhizae increase in importance during succession in productive environments and are always important in unproductive environments as they increase nutrient and water uptake. Plant–animal interactions such as mammalian herbivory are important early in succession and in productive environments, as they tend to

graze on early successional herbs, whereas insect herbivores and pathogens are important later in succession when they affect trees.

Strengths: provides a holistic view of succession by focusing on different processes, and makes clear explicit predictions on how these processes vary during succession (thus explaining species replacement) and with site productivity (thus explaining variation across seres).

Limitations: not all response variables are processes. Although the qualitative direction of the predictions makes sense, the shape of the curves (sigmoidal, bell-shaped) is in some cases somewhat arbitrary.

Development: together with Odum (1969) and Grime (1979, 2006), this was one of the first studies that actually made informed qualitative predictions about the direction of succession (i.e. on the relative importance of different mechanisms or plant strategies) (Walker & Del Moral, 2003). The predictions of this model have been confirmed for competition and facilitation, but have not been tested as widely for the other processes.

Additional remarks: Walker & Chapin (1987) suggest that their predictions can also be extended to the type of succession, where primary succession generally occurs in severe environments and secondary succession in favourable environments.

(14) Hierarchical successional framework (Pickett *et al.*, 1987*a*,*b*)

Key ideas: a series of papers (Pickett *et al.*, 1987*a*,*b*, 2011; Pickett & McDonnell, 1989; Pickett, Cadenasso & Meiners, 2009, 2013; Meiners *et al.*, 2015) present a hierarchical framework to analyse succession. They identify three hierarchical levels that affect succession, varying from proximate, direct causes at the highest level, to ultimate, indirect causes at the lowest level (Fig. 14). The highest hierarchical level presents the three main sequential *causes* of succession: (*i*) site availability, (*ii*) differential species availability, and (*iii*) differential species performance. These three causes apply to all temporal and spatial scales of vegetation dynamics, and emphasise commonalities in causes of species replacement. The intermediate level indicates the mechanisms (such as interactions, *contributing processes, or conditions*) that cause change at the highest level. The lowest level indicates the *modifying factors* that affect change at the intermediate level, for example soil conditions or presence of competitors. These organism- and site-specific features at the lowest level are thought to explain the large variation in successional pathways observed.

Assumptions: the framework assumes that succession is sequential (although immigration, germination and growth occur continuously), that the successional mechanisms are hierarchical, and that there are no feedback loops.

Strengths: the framework (*i*) provides a comprehensive understanding of succession; (*ii*) is straightforward and
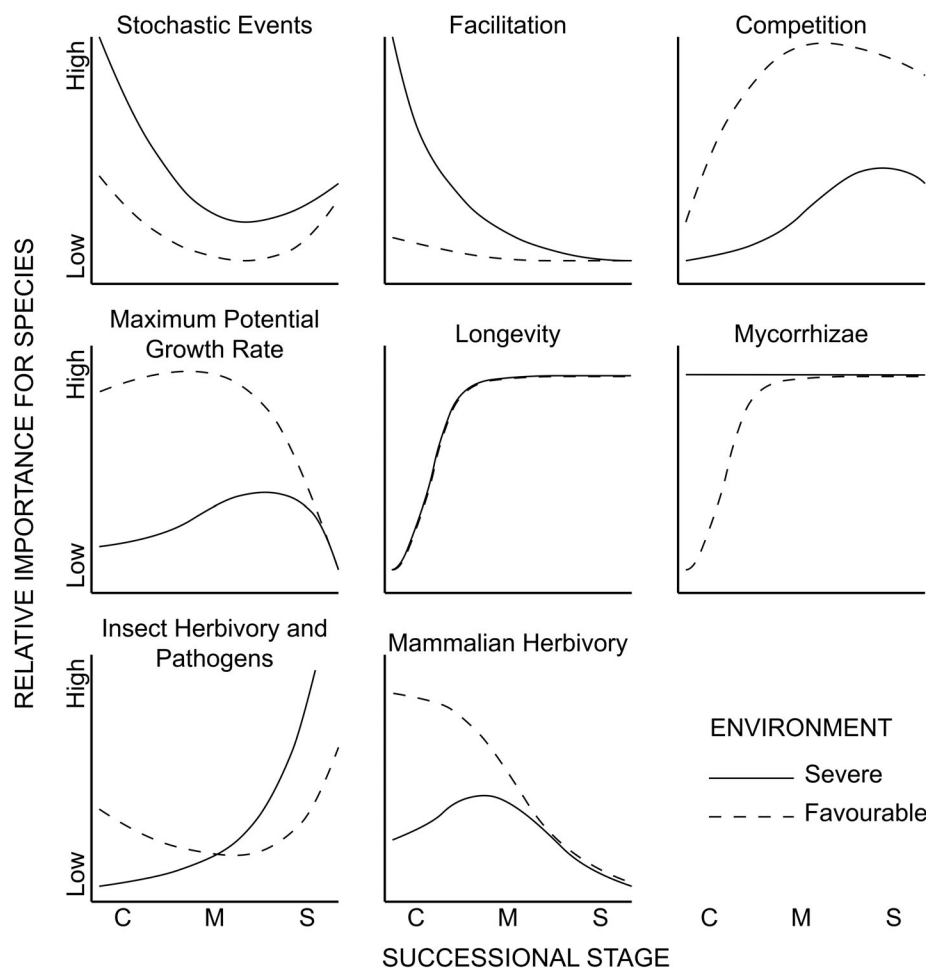
Fig. 13. Successional processes (Walker & Chapin, 1987). Relative importance of different successional processes for species replacement at different successional stages [colonisation (C), maturation (M), and senescence (S) in productive, favourable environments (continuous line) and unproductive, severe environments (dashed line)]. Each panel represents a different successional process. From Walker & Chapin (1987).

simple, because it focuses on the three main sequential causes of succession; (*iii*) is universally applicable; (*iv*) can easily be adjusted by selecting that subset of factors that is relevant for local succession; (*v*) is sufficiently general to include multiple (sub)models and to accommodate new ones; and (*vi*) allows both generality and local realism (i.e. site and situation specificity).

Limitations: because of the flexibility and the all-encompassing list of relevant factors and mechanisms, few studies have quantified all components, making it almost impossible to test the framework and leaving little room for generalisation. Initially the framework did not include feedback loops.

Additional remarks: the framework builds on Clements (1916) as the three main causes are the same as Clements' first three processes. It is not so much a successional theory that provides predictions, but a structured and very complete framework with which to analyse succession. As such, it provides the most comprehensive view on

succession, and deserves much more attention than it has received to date.

(15) Temporal scales (**Walker & Wardle, 2014**)

Key ideas: plant succession can be explained by processes that operate at different timescales (from seconds to millions of years) where short-term processes drive plant succession and long-term processes constrain succession (Walker & Wardle, 2014) (Fig. 15). Short-term processes, such as soil nutrient fluxes and plant physiology, operate at micro-timescales (seconds to days) and influence processes such as biotic interactions and plant life cycles, which operate at local timescales (days to years), and both drive the first decades of plant succession. Long-term geological, evolutionary, and soil processes operate at the timescale of thousands to millions of years and can constrain the next centuries of succession by setting boundaries to the potential rates and trajectories. For example, geology determines the parent
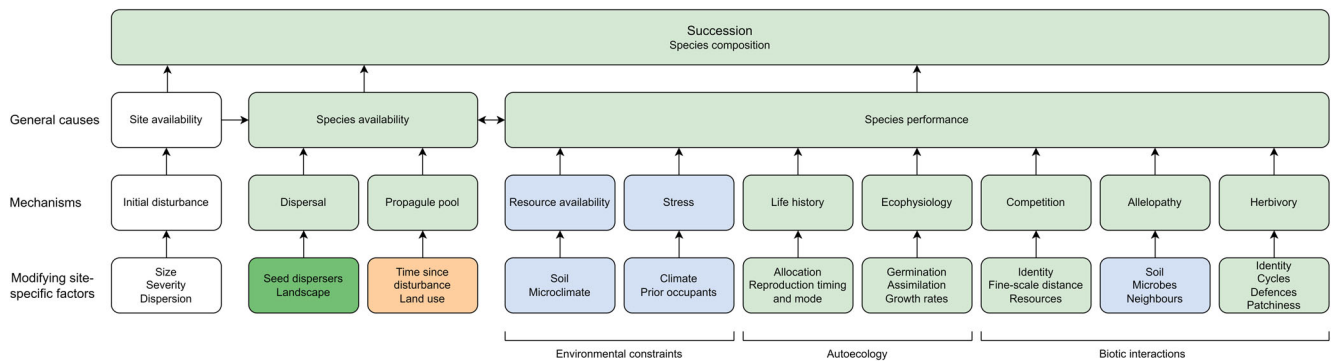
Fig. 14. Hierarchical successional framework (Pickett *et al.*, 1987*a*,*b*). Succession is the result of three general, sequential causes (second row): site availability, species availability, and species performance. The general causes are determined by underlying mechanisms (third row) which, in turn, are shaped by site-specific factors (bottom row). Species performance is shaped by a number of factors related to environmental constraints, autoecology, and biotic interactions of plants with plants, animals, and soils.

material and, hence, soil properties, and soil processes determine soil formation. Macro-evolution determines the regional species pool and which species traits and adaptations can be filtered into the local successional community.

Strengths: it provides an integrated framework to analyse how ecological processes operating at different timescales affect succession.

Limitations: it focuses only on one aspect of succession (i.e. plant species replacement) rather than ecosystem development. The framework intends to use succession, which operates at an intermediate timescale, to link ecological processes that operate at shorter and longer timescales. Perhaps for this reason it considers ecosystem processes such as decomposition and soil formation as drivers of succession, rather than components of succession.

Development: it provides a longer term perspective on succession (millions of years) than usually studied (centuries), and highlights the role of long-term soil development for succession, as loss or immobilisation of phosphorus can lead in the long term to P limitation, biomass degradation, and retrogression (Wardle, Walker & Bardgett, 2004).

Additional remarks: it highlights the role of plant–soil feedback, plant–plant interaction and multitrophic interactions in steering succession. For example, early-successional plant species can have negative plant–soil feedback loops with soil pathogens that facilitate plant species replacement, whereas later successional species can have positive feedback loops with mycorrhizal fungi that impede species replacement.

(16) Spatial scales (Arroyo-Rodríguez *et al.*, 2017)

Key ideas: succession is influenced by a set of factors that operate from broad to small spatial scales (region, landscape, and local patch) (Arroyo-Rodriguez *et al.*, 2017) (Fig. 16). The regional scale (>several km^2) sets the broad context, as it determines the climate, topography, disturbance regime, and the regional species pool. The landscape scale (hectares to km^2) refers to a spatially heterogeneous area consisting of a mosaic of different land cover types (such as forests, agricultural areas,

and corridors). It determines forest cover, edge, core area, and fragmentation, and landscape connectivity that in combination determine the availability of seeds, dispersal agents, mesoclimate, and competing invasive species. The local scale (a patch) determines patch size, shape, and isolation, microclimate and soil conditions. This local environment together with biotic interactions (plant–animal, plant–soil, plant–plant) determines plant life cycle processes (composition and structure of adult plants, reproduction, dispersal, growth and survival) that shape, in turn, forest regeneration.

Strengths: this model highlights the role of different spatial scales on succession, which may explain the large variation in successional pathways observed across and within landscapes.

Limitations: it only addresses the spatial aspects of succession; the temporal aspects (how do vegetation attributes change during succession) are not considered. Succession within a stand is said to be driven by the plant life cycle, but this is mostly treated as a black box.

Development: the model was developed because forests in human-modified tropical landscapes are increasingly fragmented and degraded, with large consequences for successional pathways. The model builds therefore on recent developments in the field of fragmentation and landscape ecology.

Additional remarks: it hypothesises that the largest variation in forest successional pathways is found at an intermediate availability of forest habitat (20–50% of surrounding forest cover), which was confirmed by a recent meta analysis (Arroyo-Rodríguez *et al.*, 2023). At low habitat amount (<20%) there are too few seed trees and dispersal agents left, leading to arrested succession; at high habitat amount (>50%), there is little seed limitation and succession proceeds rapidly and predictably, whereas at the intermediate habitat amount there is more variation in land cover type and configuration and, hence, in successional pathways. The model also emphasises that chronic human disturbance leads to ruderalization and impoverishment of the regional species pool and degradation of forest fragments.
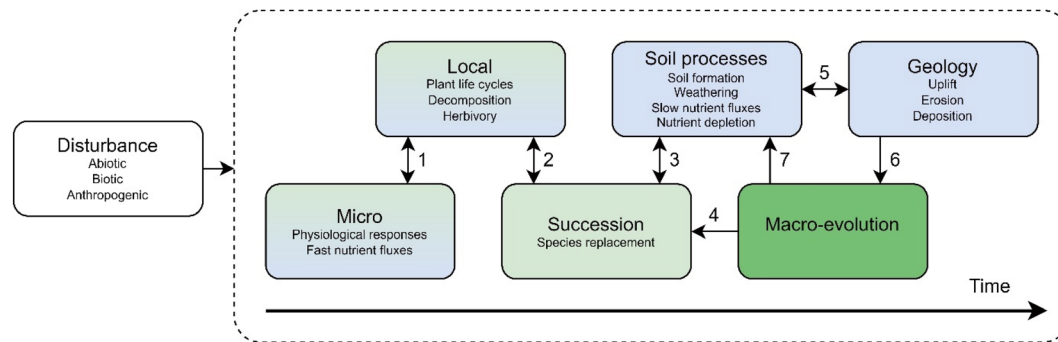
Fig. 15. Temporal scales (Walker & Wardle, 2014). Succession is shaped by factors that operate at different timescales. Micro-scale processes such as physiological plant responses affect local processes such as plant life cycles (1), which in turn drive species replacement during succession (2). Geological processes that operate at long timescales such as montane uplift and plate tectonics determine macro-evolution (6) and soil processes (5) which, in turn, constrain succession (3, 4). Macro-evolution may also affect soil processes, for example when plant species with specific adaptations (nitrogen fixation, cluster roots) increase nutrient uptake and modify soil chemistry and processes (7). The factors are ordered according to their temporal scale (*x*-axis), from seconds to the left and millions of years to the right. Factors are partly overlapping in terms of the timescale at which they operate, as indicated by the horizontal overlaps between boxes. Factors that overlap in time may influence each other mutually, as indicated by double-headed arrows. Abiotic, biotic and anthropogenic disturbances (white box) influence all factors, as indicated by the dashed box.
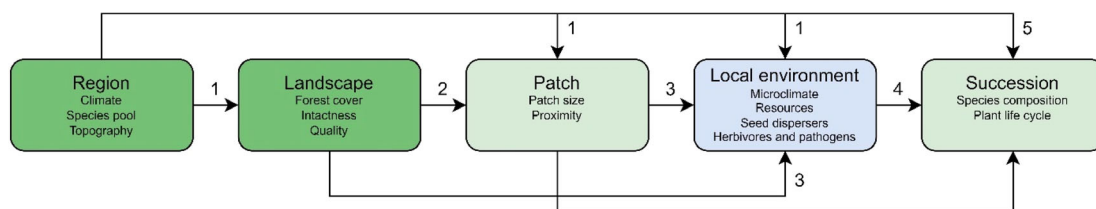

Fig. 16. Spatial scales (Arroyo-Rodriguez *et al.*, 2017). Succession is influenced by factors operating from broad to local spatial scales. Regional climate, topography, and socio-economic conditions (not shown) affect land use, and hence, landscape and patch characteristics (1). The landscape context determines patch isolation (2). Both the landscape and the patch affect the local biotic environment (seed dispersers) and abiotic environment (microclimate and resources) (3). The regional species pool (5) together with local conditions (4) shape succession by affecting the plant life cycle and species composition. The model highlights the role of landscape characteristics [forest cover, intactness (i.e. the opposite of fragmentation) and remaining forest quality in terms of diversity and old-growth species] and patch characteristics (patch size, and proximity to neighbouring forest patches) in succession.

(17) Source and disperser limitation (Dent & Estrada-Villegas, 2021)

Key ideas: the speed and direction of succession is more determined by propagule availability than by the environmental requirements of the plant species. This is especially the case for fragmented landscapes, where both seed sources and dispersers can be remote, rare, or absent, and for tropical forests where most plant species (65–95%) are animal dispersed. The interaction between the seed source and the dispersal vector determines seed movement through the landscape and, hence, local seed availability and successional pathways (Dent & Estrada-Villegas, 2021; Palma *et al.*, 2021) (Fig. 17). *Source limitation* indicates that insufficient seeds are produced to saturate potential recruitment sites, and is determined by the abundance, composition, fecundity, and location of reproductive plant species and by pollinators. *Disperser limitation* is determined by the abundance, composition, behaviour and dietary preferences of animal dispersal vectors. The interaction between source and disperser depends on

the fruit traits of the source plants and the traits (such as gape width, dietary preferences, and body size) of the animal species.

Strengths: this model highlights the importance of seed availability and animal dispersers for succession. Source and disperser limitations are especially important in human-modified fragmented landscapes.

Limitations: less relevant for succession of wind-dispersed communities.

Development: the importance of animal dispersers for succession has only recently been emphasised, as most successional models were developed in the temperate zone, where wind is the predominant dispersal vector. The decline of habitat area, landscape integrity and animal abundance has increased awareness of the importance of dispersers for plant community assembly.

Additional remarks: the relative importance of different dispersal modes is predicted to change during tropical forest succession: wind and bats are especially effective in open environments, and their importance declines during
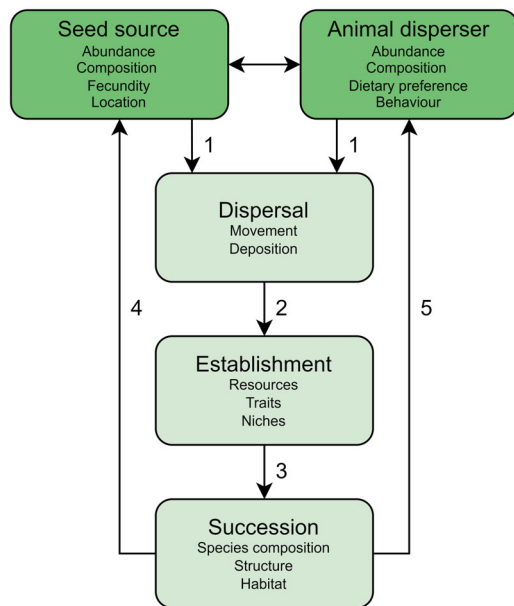
Fig. 17. Source and disperser limitation (Dent & Estrada-Villegas, 2021). Characteristics of seed source plants and animal dispersers (dark green boxes) determine seed dispersal through the landscape (1), followed by plant establishment that depends on the combination of local resource availability and species niches (2). This affects stand succession (3) creating a feedback loop, where changes in species composition lead to successional changes in local seed source availability (4) and changes in species composition and habitat affect successional changes in the local disperser community (5).

succession. By contrast, birds and non-volant mammals prefer a structurally more complex habitat and later successional plant species as their food source, and their contribution to the seed rain increases during succession.

(18) Land-use intensity (Jakovac *et al.*, 2021)

Key ideas: landscape integrity and land-use intensity affect species availability and species performance and, hence, successional pathways (Jakovac *et al.*, 2021) (Fig. 18). Higher landscape integrity refers to a higher and more continuous surrounding forest cover (see Section III.16) and more remnant trees on agricultural fields. Land-use intensity focuses on the legacies of past land use practices, and can be described in terms of the duration (time since forest conversion or continuous use), spatial extent (i.e. size), frequency (of burning, ploughing or cropping), intensity (livestock density, use of heavy machinery, use of pesticides, herbicides or fertilisers, weeding), and length of the practices. A higher land-use intensity generally leads to a higher abundance of disturbance-adapted species (weeds, lianas, and invasive species such as *Leucaena leucocephala*, *Imperata cylindrica*, and *Chromolaena odorata*) that compete with regenerating trees. Land-use practices also filter species based on their traits, leading to communities dominated by species with a

higher resprouting ability, wood density, lower leaf nutrient concentrations and a clonal habit.

Strengths: this model provides a straightforward analysis of how humans affect succession by modifying landscape integrity and land-use intensity.

Limitations: it focuses on previous land use but does not discuss the fact that local people often still use and manage regrowing secondary forests, which is difficult to quantify, as use and management are highly dynamic and vary over space and time.

Development: it expands the hierarchical framework of Pickett *et al.* (1987a,b) (Section III.14) and the spatial framework of Arroyo-Rodríguez *et al.* (2017) (Section III.16) by including the effects of landscape integrity and land-use intensity on species availability and performance (see Chazdon, 2003).

Additional remarks: the combination of landscape integrity and previous land-use intensity determines the bottlenecks for regeneration and, hence, the feasibility of different restoration strategies. In relatively intact landscapes with light land use, more seed sources are available and natural regeneration can take place. Under intermediate conditions natural regeneration should be assisted through weeding or fencing, and in fragmented landscapes with intense use, planting should be carried out. Extractive types of land use such as mine pits and soil quarries arguably represent the most intense form of previous land use. For a discussion on succession on such heavily disturbed sites, and possibilities for their passive restoration, see Prach *et al.* (2019).

(19) Socio-ecological systems (Balvanera *et al.*, 2021)

Key ideas: humans and regrowing vegetation form a *socio-ecological system*, resulting in a (shifting) mosaic of patches in which agriculture and regrowth may alternate in time and space (Fig. 19). Management practices during the agricultural phase, mediated by the interplay of societal, economic, and ecological factors such as burning and ploughing, have long-lasting legacies on vegetation development during the regrowth phase (see Section III.18), whereas the regrowth phase affects humans by providing a range of ecosystem services (Balvanera *et al.*, 2021). During forest regrowth, ecosystem processes and functions recover, resulting in an increase in ecosystem services for local and global stakeholders (Balvanera *et al.*, 2021). Local stakeholders benefit from an increase in provisioning services (e.g. number of useful species, timber volume) and regulating services (soil fertility, improved microclimate, and water availability), while global stakeholders benefit from an increase in regulating services such as carbon storage and sequestration, and from habitat services such as biodiversity conservation (Naime *et al.*, 2020; Balvanera *et al.*, 2021; Cortés-Calderón *et al.*, 2021; Siddique *et al.*, 2021).

Strengths: the model acknowledges and assesses the role of humans in succession, which allows a better understanding of land use and forest cover dynamics at the landscape scale.
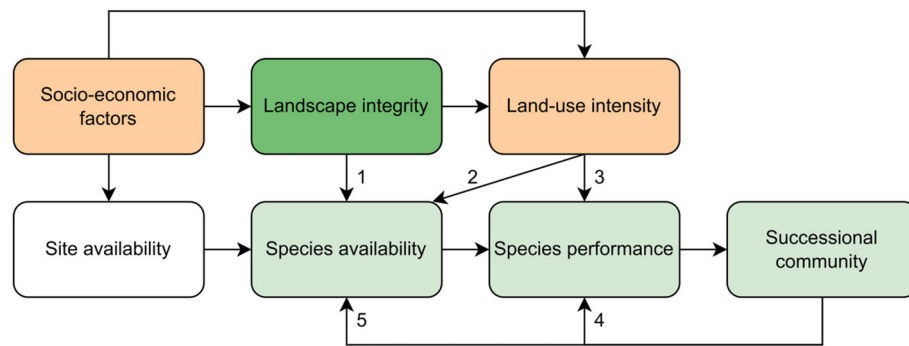
Fig. 18. Land-use intensity (Jakovac *et al.*, 2021). Humans transform the landscape (top row) and directly or indirectly determine succession (bottom row, light-green boxes). Socio-economic factors determine landscape integrity (dark-green box), land-use intensity (orange box), and site availability (white box). Site availability initiates succession. Landscape integrity affects species availability through propagule production and dispersal (1). Past land-use intensity varies in duration, extent, frequency, intensity, and length, which all leave different environmental legacies that affect species availability (2) and performance (3). The developing successional community has successional feedback loops and modifies the environment thus affecting species performance (4) and contains reproductive trees that affect local seed availability (5).

Limitations: it may result in a rather anthropocentric and utilitarian view on succession. To date, people's management practices during the successional process have been little studied (but see Lohbeck, Rother & Jakovac, 2021), while management practices, such as enrichment planting and assisted natural regeneration, may change the speed and direction of succession, increase the value of secondary forests for local people and have the potential to reduce trade-offs and land-use conflicts.

Development: in human-modified tropical landscapes, secondary forests are often the main forest type left, leading to increased human use and modification of successional pathways (see Arroyo-Rodríguez *et al.*, 2017). In such landscapes, succession can only be understood by including the human component. The more integrative socio-ecological system perspective on succession is the result of an increased realisation that long-term forest conservation and restoration is only possible by including, rather than excluding the roles, and perspectives of local people.

IV. FOUR MAIN GROUPS OF MODELS REFLECT THE DEVELOPMENT IN CONCEPTUAL THINKING

Although each model addresses multiple and sometimes overlapping issues, they can be tentatively grouped into four groups that differ in their focus on a specific integration level. They focus respectively on patch development and plants, ecosystems, landscape, and social ecological systems (Fig. 20). These groups differ in integration level and increase in hierarchical and spatial scale and scope, reflecting the increasingly broader perspective on succession over time.

Plants & Patch: the first, large group focuses on plants at the patch level, and consists of three subgroups, which all have their roots in the early 1900s. One subgroup focuses on the

processes (dispersal, establishment, and performance) that operate sequentially during succession after disturbance. This subgroup is based on the pioneering work of Clements (1916), who provided a complete and structured analysis of succession, laying the foundations for many of our current ideas about succession. A second subgroup emphasises the *individualistic* species responses during succession, and how this is driven by functional species *traits*. It is based on the visionary ideas of Gleason (1926) who challenged the orderly and predictable view on succession provided by Clements (1916), explaining why successional pathways can be context dependent and unpredictable. These ideas are implemented in recent individual-based mathematical models of forest succession (e.g. Pacala *et al.*, 1996). A third subgroup focuses on how vegetation *structure* and underlying demographic processes change during succession (Watt, 1947; Yarranton & Morrison, 1974; Oliver, 1980).

Ecosystems: the second group considers a larger hierarchical scale and focuses generally on ecosystems (Odum, 1969; Walker & Wardle, 2014) but also on how processes operating at larger spatio-temporal scales affect succession (Walker & Wardle, 2014). With the development of systems ecology in the 1960s (Fig. 21), a more holistic view of succession was provided by considering the complete ecosystem, i.e. biota, interactions, diversity, ecosystem structure, energetics and processes. Some of these aspects were already mentioned but not developed by Clements (1916).

Landscape: the third group considers a larger spatial scale and includes the effect of the surrounding landscape on succession (Arroyo-Rodríguez *et al.*, 2017; Dent & Estrada-Villegas, 2021). The distance to, and connectivity with, neighbouring forest patches determines the dispersal distance, and the quality of the neighbouring patches determines the abundance and composition of seed trees and animal dispersal vectors. Deforestation, forest degradation and fragmentation determine to a large extent the landscape quality, the regional species pool, and successional pathways.
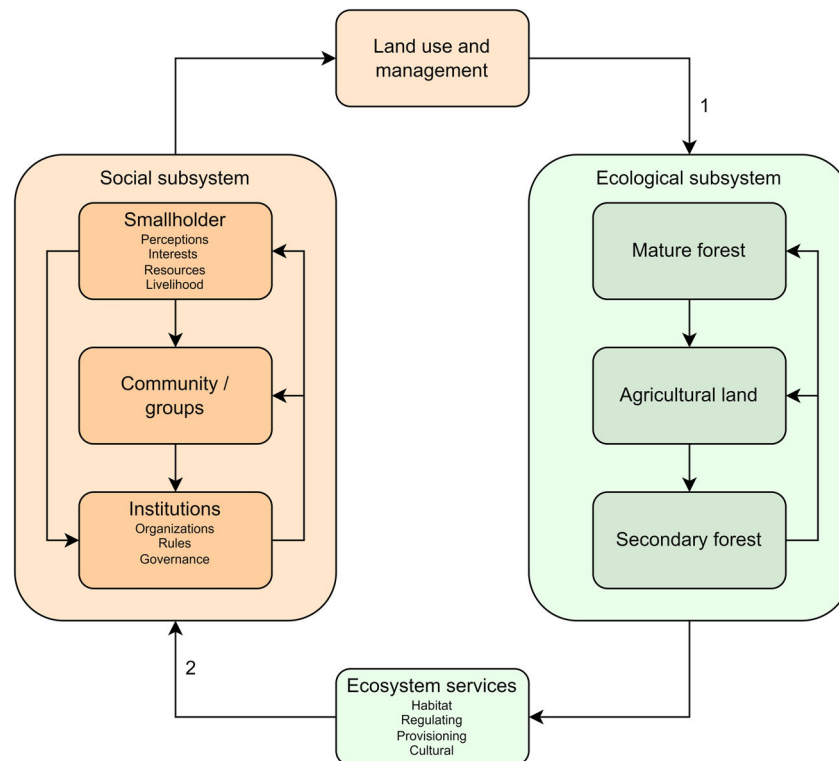
Fig. 19. Socio-ecological system (SES, Balvanera *et al.*, 2021). The SES consists of a social subsystem (orange) and an ecological subsystem (green). The ecological subsystem consists of three different land-use types (mature forest, agricultural land, and secondary forests in different stages). The social subsystem consists of smallholders, local communities or groups, and institutions that mutually influence each other. The social subsystem affects the ecological subsystem through land-use conversion (1) from mature forest or secondary forest to agricultural land, or through land abandonment that leads to natural regrowth towards secondary forest. It also affects the ecological subsystem through active management interventions. The ecological subsystems deliver different ecosystem services (also known as nature's contribution to people) to different components of the social subsystem, such as private smallholders and public stakeholders (2). Diagram after Balvanera *et al.* (2021).

Socio-ecological systems (SES): a fourth group of models includes the human component by focusing on socio-ecological systems (Balvanera *et al.*, 2021; Jakovac *et al.*, 2021). Management practices during the agricultural phase, such as burning, weeding and ploughing, have long-lasting legacies on vegetation development during the regrowth phase. In the tropics, the transition between the agricultural and regrowth (or fallow) phase is gradual, as farmers combine annual crops with perennial ones (e.g. bananas, manioc, and trees), and use the regrowth phase for animal browsing and harvesting of fuelwood and other forest products. Farmers and regrowth form, therefore, a socio-ecological system, in which regrowing forests deliver a range of ecosystem services to the local, regional, and global community.

Successional models can be classified in different ways (van Hulst, 1992). We have grouped the models based on their integration level, which differentiates clearly from the classification focus of earlier reviews. These different classifi-cations provide different perspectives on succession, and therefore additional understanding.

Walker & Del Moral (2003) grouped successional models based on contrasting perspectives on succession and science as *holistic* (i.e. an integrated view; e.g. Clements, 1916), *neo-holistic* (e.g. Odum, 1969) *versus reductionistic* (i.e. reducing the system to its parts; Gleason, 1926) and *neo-reductionistic* [e.g. Egler (1954) functional groups]. In addition, they classified some successional models based on their approach as *verbal models* that focus respectively on species interactions [i.e. autogenic succession (Connell & Slatyer, 1977; Grime, 1979, 2006; Noble & Slatyer, 1980)] or processes [i.e. a combination of allogenic and autogenic succession (Pickett *et al.*, 1987*a*; Walker & Chapin, 1987; Burrows & Burrows, 1990)] or as *mathematical models* (Shugart Jr & West, 1980; Tilman, 1985).

Meiners *et al.* (2015) classified successional models based on their approach as *phenomenological* (e.g. Clements, 1916; Gleason, 1926; Watt, 1947), *statistical* [e.g. Markov models (Horn, 1975); gap-phase models (Shugart Jr & West, 1980)], *mechanistic* [e.g. Connell & Slatyer (1977); functional groups (Grime, 1979; Tilman, 1985); individual-based models (Pacala *et al.*, 1996)], or *other* types of successional models [e.g. Odum, 1969; resilience (Holling, 1973)].
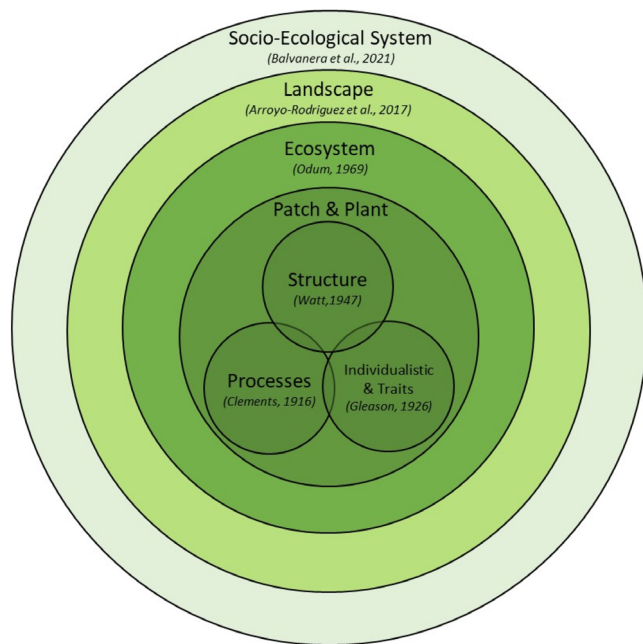
Fig. 20. Development of successional theories over time. Four main groups of theories are distinguished (Patch & plant, Ecosystem, Landscape, Socio-ecological system) that differ in integration level and increase in scale and scope, reflecting the increasingly broader view of succession over time. The first foundational paper for each group of theories is provided in parentheses. Patch & Plant consists of three subgroups, related to Processes, Individualistic species behaviour and traits, and Structure.

V. DEVELOPMENT IN SUCCESSIONAL THINKING

(1) Four periods with different views on succession

In the timeline of successional model development, four periods can be distinguished with different views on succession (blue bars in Fig. 21). These periods reflect the prevailing view of succession at that time, although note that these views continue to coexist, as indicated by the overlapping blue bars in Fig. 21. The four successional views and corresponding tentative time periods are: succession of plants (from 1910 onwards), succession of communities and ecosystems (from 1965 onwards), succession in landscapes (from 2000 onwards) and succession with people (from 2015 onwards).

Succession of plants (1910 onwards). During the period 1910–1965, succession was seen mainly through the lens of plant species replacement. This was perhaps because the field was developed by botanists and because ecology was strongly influenced by the Zurich Montpellier school of phytosociology (see Fig. 21), which focused on species assemblages (i.e. groups of co-occurring species) and their replacement over space and time. It also coincided with the rather romantic North American view of nature as wilderness, and a strong focus on natural autogenic processes in succession.

Succession of communities and ecosystems (1965 onwards). From the mid-1960s, a more holistic view on succession emerged that considered the complete ecosystem and ecosystem processes (e.g. flows of energy and matter such as carbon, nutrients and water). This coincided with the development of systems ecology, and the idea that ecosystems and the Earth were self-organised, self-regulated, and striving towards homeostasis (Fig. 21) (Odum, 1969), as for example reflected in the Gaia hypothesis (Lovelock & Margulis, 1974). It also coincided with theoretical development in community ecology that put more emphasis on community assembly, plant–plant interactions such as competition (MacArthur, 1984), and the role of plant–animal and plant–soil interactions (Connell & Slatyer, 1977).

Succession in landscapes (2000 onwards). Landscape ecology developed in the 1980s in the strongly human-transformed temperate zone (Fig. 21). This resulted in the development of the landscape and network approach in conservation biology, where nature reserves in fragmented landscapes were connected with corridors (Mace, 2014). By contrast, in the tropics most biologists studied succession in relatively sparsely populated, intact forest landscapes, where the successional forest fallow was part of the shifting cultivation system. Widespread deforestation and landscape transformation gained momentum in the tropics in the mid 1970s, and had strong effects on forest degradation and regeneration, and hence, succession. Landscape research was also facilitated by improved remote-sensing technology and the increased availability of remote sensing data of high spatial and temporal resolution. This may explain why a focus on landscape effects and dispersal limitation in succession took place from the 2000s onwards, and coincides with the increasing importance of the landscape approach in forest-restoration projects (Mansourian *et al.*, 2020).

Succession with people (2015 onwards). With the ambition of ecological research to become more relevant for society, more researchers have explicitly studied the effect of people on ecosystem functioning, rather than excluding them. This led to the realisation that succession can be strongly influenced by people. This focus coincides with an increased emphasis on the importance of ecosystem processes and services for human well-being (Costanza *et al.*, 1997), the establishment of the Intergovernmental Panel for Biodiversity and Ecosystem Services (Díaz *et al.*, 2019) and a socio-ecological systems approach in conservation that recognises the interconnectedness of nature and people, and that addresses the needs of both nature and people (Mace, 2014). Such an approach is especially relevant for the application of successional principles in the United Nations decade of restoration (2020–2030) where restoration is deemed most successful when it is done by and for local people.

(2) Facilitation and inhibition in successional model development

So when did the development in successional thinking become facilitated or arrested? When reading the different successional models, and their discourse, we noticed several things.
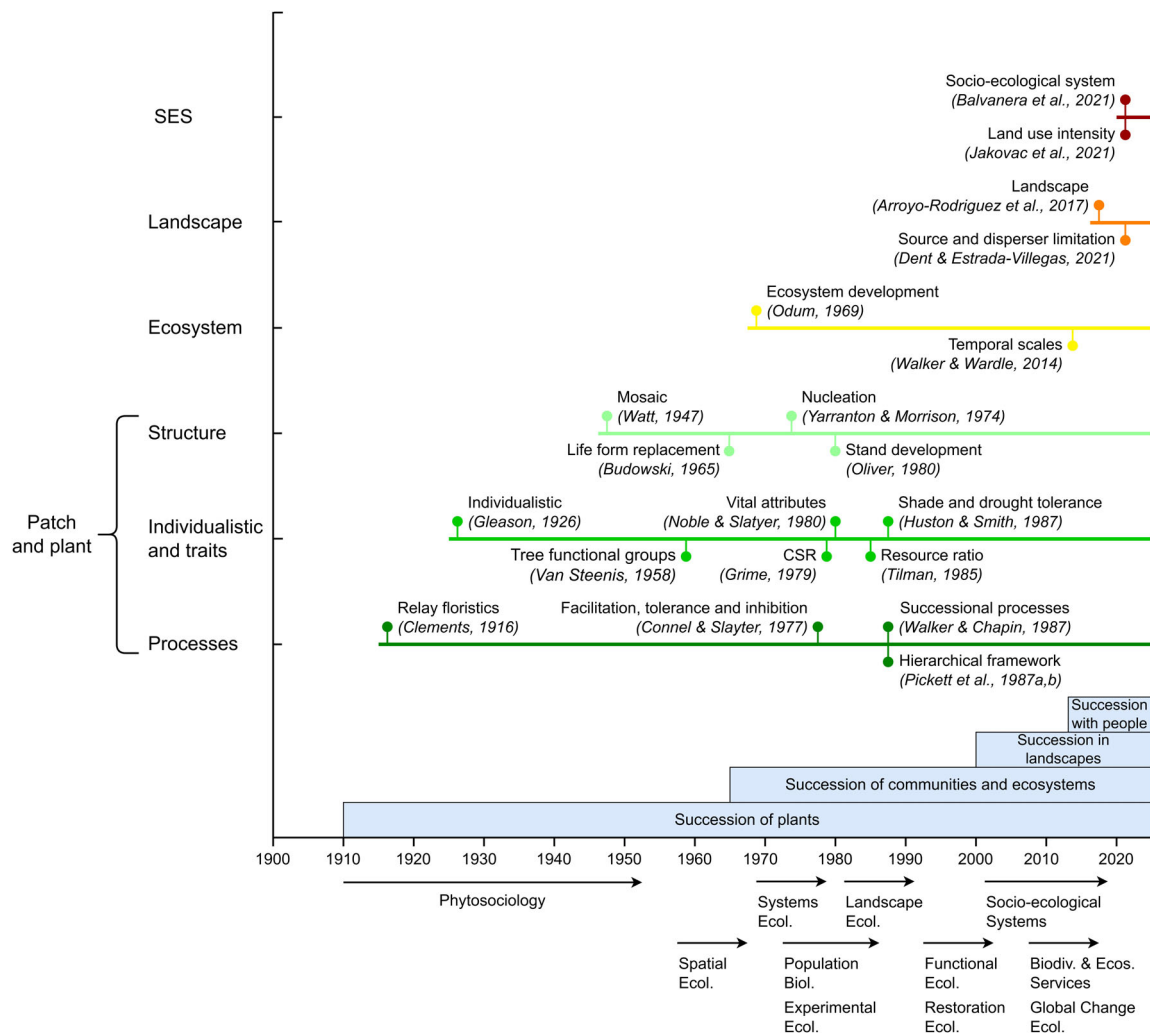
Fig. 21. Timeline of successional model development. Four main groups of models are distinguished (on left), each with its own timeline (coloured horizontal line), and the year (indicated by the pin), name, and author(s) (in italics) of the contributing models. The blue boxes along the timeline indicate four periods with different views on succession (all four views currently coexist). The arrows below the timeline indicate the time of main development of different fields in ecology (note that each of these fields continue to develop to the present). Huston & Smith's (1987) model on shade and drought tolerance is included in the figure but not discussed as an individual model in Section III, although it is briefly mentioned in Section III.12 on Tilman's (1985) resource ratio model. Biol., biology; Ecol., ecology; Ecos., ecosystem; SES, socio-ecological system.

First, there is often a priority effect followed by inhibition. Clements (1916) provided a thorough review of successional studies up to that time, and was the first to provide a structured coherent theory. Maybe as a result of this priority effect and completeness, Clements (1916) dominated successional thinking for decades, but perhaps also inhibited the development of new ideas.

Second, there is a lag-time for novel ideas. A decade after Clements (1916), Gleason (1926) published an individualistic model of succession, postulating that succession is the result of dispersal limitation and individual species responses to the environment. His visionary ideas were clearly far ahead of his time and little appreciated. It is said that for this reason he left ecology and became a herbarium curator. It took

nearly half a century before Gleason's ideas were picked up by Drury & Nisbet (1973), with an emphasis on species life-history traits. Since the 1970s a reductionist approach became dominant in ecology, leading to a revival of Gleason's ideas and an emphasis on trait-based approaches in successional ecology.

Third, new disciplines, fads, and fashions can facilitate new views on succession. Clearly, new fields in ecology and the availability of new tools has enabled new perspectives on succession. For example, the development of systems biology in the 1960s allowed Odum (1969) to develop his model of ecosystem development; the development of statistical techniques and spatial ecology in the 1960s allowed Yarranton & Morrison (1974) to develop their nucleation model; the

new emphasis on experimental ecology in the 1970s stimulated Connell & Slatyer (1977) to develop their interaction model; the emphasis on population biology in the 1970s allowed Noble & Slatyer (1980) to develop their vital attributes model; and the recent focus on human causes of global change has stimulated thinking about anthropogenic effects on successional pathways (Balvanera *et al.*, 2021; Jakovac *et al.*, 2021).

Fourth, action is reaction; recent developments tend to dominate the debate. Many successional models and reviews appeared in response to new developments in the preceding 5–10 years. For example, in response to Clements' (1916) model on the directionality of succession, Gleason (1926) formulated his individualistic model on the unpredictability of succession. The reductionistic view on species and interactions of Drury & Nisbet (1973) and Connell & Slatyer (1977) was a response to the holistic view of ecosystem development of Odum (1969). While Connell & Slatyer (1977) advocate a reductionist approach and a focus on experimental tests of species interactions such as tolerance and inhibition, Finegan (1984) argued that such ideas should be tested using field data, and for an appreciation of the role of facilitation (see Callaway, 2007).

Fifth, there are periods in which theory is based on first principles *versus* periods when theory is based on syntheses. Ecology experienced a boom in the 1960s and 1970s when many outstanding conceptual thinkers developed principles that stimulated theoretical development. In the following decades there was more emphasis on data-driven tests of these theoretical ideas through field studies, experiments, and statistical analyses, facilitated by increased computational power and more advanced statistical tools. An exponential increase in the number of published studies allowed meta-analyses and syntheses (Guariguata & Ostertag, 2001; Walker & Del Moral, 2003; Becknell, Kissing Kucek & Powers, 2012; Prach & Walker, 2020), while comparative studies (Prach *et al.*, 2014) and network-based big-data analysis (e.g. Poorter *et al.*, 2019) provided opportunities formally to compare different sites, yield generalisation, appreciate local site deviations, consolidate theory and generate new hypotheses.

Sixth, models have moved from a temperate towards a tropical view of succession. Much successional theory was developed in relatively species-poor, temperate systems. The high species diversity in the tropics led to less emphasis on pairwise species interactions, as the number of interactions rapidly becomes unmanageable, and a move away from a species-based approach to a trait-based approach. The higher species diversity also means larger diversity in LFs, more variation across species in terms of recruitment and competitive capacities, and more opportunities for niche differentiation, making the successional pathway longer and more variable. The strong co-evolution in the tropics between plants and their animal pollinators and dispersers results in slower arrival of plant species and a stronger emphasis on dispersal limitation (e.g. Dent & Estrada-Villegas, 2021), the role of landscape context, a larger number of successional pathways, and greater emphasis on the unpredictability of succession (e.g. Norden *et al.*, 2015) compared to temperate succession.

Seventh, technological advances play an important role. Initial successional ideas were based on field observations and simple measurement tools to quantify plant succession, such as rulers and diameter tapes. Technological development has greatly increased our ability to quantify plant, patch, ecosystem, and landscape structure and processes, and to scale up across space and time. This has opened up new questions, and allowed us to consider and explore the role of traits, ecosystems and landscape in succession. For example, the development of remote-sensing tools allowed Arroyo-Rodríguez *et al.* (2017) to assess landscape effects on succession, while radiotracking enables monitoring of disperser movement, and microsatellites allow quantification of dispersal distances between seedlings and parent plants (Dent & Estrada-Villegas, 2021). Advances in different technologies (e.g. spatial, physiological) now allow us to examine the same questions from a different perspective.

Finally, there is a move from scientists advancing society to society advancing scientists. In the first three quarters of the 20th century, scientists were largely autonomous, but with an increasing demand for science to become more relevant to society, science has started to follow societal trends. Many recent ideas in succession (e.g. succession in landscapes, succession with people) follow societal developments in the field of nature conservation (moving from nature despite people, to nature for people, to nature with people; Mace, 2014), the debate on land-use change and climate change (e.g. by analysing the carbon sequestration and mitigation potential of secondary forests; Chazdon *et al.*, 2016), and the importance of including people (e.g. by using the landscape approach, addressing sustainable development goals, or in the UN decade of restoration).

VI. TOWARDS A COMPREHENSIVE SUCCESSIONAL THEORY

We have provided an overview of 19 successional models that have been foundational for our thinking about succession. Many of these foundational papers and models are rich in ideas, but sometimes forgotten, and rarely tested. Part of the problem is that models have focused on different components of succession, use different terminology and approaches, and have differing views on succession. The other problem is that succession typically occurs over longer timespans than research budgets last and researchers are able to monitor. Despite the bewildering number of models, they can be classified into four groups that focus on a different spatial scale (patch, landscape) or organisational scale (plant species, ecosystem, socio-ecological system). These groups increase in scale and scope, and reflect the increasingly broader perspective on succession over time. As a result, successional models become more encompassing

and realistic, with the potential for stronger global generalisation. Unfortunately, increased complexity comes also at the expense of an increased difficulty to test them.

Currently, the hierarchical framework of Pickett *et al.* (1987*a*, *b*, 2009) and Pickett & McDonnell (1989) (Fig. 14) is the best model to develop further because it includes several factors and processes, is flexible and allows both generality and local realism (i.e. is site and situation specific) (see Section III.14). Their hierarchical framework focuses mainly on species replacement, and could be improved by including more recent developments and elements from other models (see Fig. 20), for example by including different spatial scales (plant neighbourhood, patch, landscape, region), more hierarchical scales (ecosystem, socio-ecological system), processes that operate at a wider range of timescales (months and millennia) and by taking the effects of the surrounding landscape and humans into account more extensively. The framework should also include clear predictions of how, and in what direction (increase, decrease) the mechanism affects succession, as many of the current models do not make clear predictions. An extended framework could function not only as a vehicle for verbal comparison but also for conducting meta-analyses on specific drivers, and for making predictions and developing hypotheses about how and why different ecosystem attributes recover over time. Applying such an extended framework to seres across broadscale environmental gradients in precipitation, temperature, elevation, soil fertility, and disturbance will allow better insight into the successional models and processes that matter under what conditions (Poorter *et al.*, 2019; Prach & Walker, 2020; Vítovcová *et al.*, 2021). A comprehensive successional model could allow us to address many current questions in the field of succession, it could accommodate context-dependent effects and successional pathways, and therefore meet the long-pursued goal of more accurate predictions.

The successional framework and successional models, or parts of them, such as specific cause–effect relationships or mechanisms, can be tested using a combination of complementary approaches such as empirical field studies, experiments, and modelling, that can feed and enrich each other (see van der Sande *et al.*, 2017; Chang & Turner, 2019; and references therein).

Empirical field studies can use a combination of longitudinal and chronosequence approaches (Walker & Del Moral, 2003) and novel tools. Longitudinal studies establish plots, quantify the environmental conditions, and monitor them over time. This allows us to follow community assembly, quantify variation in successional pathways, and assess the underlying mechanisms. Chronosequence studies use a space-for-time substitution, in which plots are established that differ in age since disturbance. This assumes that all plots start under similar conditions, which is not necessarily the case, but allows a long-term perspective on succession, ranging from decades to millions of years (Walker *et al.*, 2010). Such empirical studies allow us to describe succession, provide firm evidence for real-world patterns, and generate new hypotheses. Relatively new tools may facilitate empirical studies. Remote sensing allows not only

quantification of the current landscape context but also of land-use history using the LANDSAT archive (Dutrieux *et al.*, 2016), patch structure using Light Detection And Ranging (LiDAR) (Falkowski *et al.*, 2009), patch composition using hyperspectral analysis (Garcia Millan & Sanchez-Azofeifa, 2018), and monitoring of patch development over time using drones (de Almeida *et al.*, 2020). The measurement of functional traits allows comparison of taxonomically different species, and hence, different study sites using the same quantitative ecological yardstick (Westoby, 1998; Poorter *et al.*, 2021). A functional trait approach provides a more mechanistic understanding of succession as it allows to understand how plants respond to the environment (in terms of dispersal, establishment, and growth), and how plants affect the environment (in terms of ecosystem functioning) (Lavorel & Garnier, 2002). Camera trapping, acoustic monitoring, and next generation sequencing allows quantification of the distribution, abundance, and activity of animals and their effects on dispersal (Dent & Estrada-Villegas, 2021).

Experimental studies allow us to remove the large number of confounding factors and really test hypotheses and the underlying mechanisms. For example, seed and seedling addition or removal experiments can show if succession is constrained by dispersal limitation or establishment limitation (Palma *et al.*, 2021); adding or removing competing species, nitrogen fixers, mycorrhizal fungi and soil microbes can demonstrate the role of competition, facilitation, and other biotic interactions (van der Putten *et al.*, 2013); while adding or removing resources (e.g. light through shade cloth, water through rainout shelters) can demonstrate how abiotic conditions affect species performance (Berendse, 1998).

Process-based modelling studies allow for removal of confounding factors, integration of different mechanisms, scaling up across space and time, a longer time perspective on succession, and to do sensitivity analysis regarding the relative importance of different factors, to do scenario analysis and to make quantitative predictions (Shugart Jr & West, 1980; Pacala *et al.*, 1996; Schmitt *et al.*, 2020).

The increased availability of open-source data on species, traits, remote sensing and environment, and the establishment of global research networks, such as the 2ndFOR research network on secondary forests, facilitate global syntheses and comparisons (e.g. Poorter *et al.*, 2021). This will allow better testing of successional hypotheses, improved understanding of context dependence and local deviations in succession, and the improvement of current successional models. We call researchers to use and test successional models more often, rather than seeing and documenting what 'happens' in the field, and to contribute to the development of a comprehensive successional theory, for example by performing meta-analyses on elements of a comprehensive theory. This will help us to understand better and predict the impacts of land-use change and climate change on ecosystems, to design successful ecosystem-restoration

strategies that are tailored to local site conditions and needs, and to turn ecology into a more predictive science.

VII. CONCLUSIONS

(1) Four groups of successional models can be recognised based on conceptual similarities. The first group (patch & plants) focuses on plants at the patch level and consists of three subgroups which are derived from ideas from the early 20th century. One subgroup focuses on the processes (dispersal, establishment, and performance) that operate sequentially during succession. Another subgroup emphasises individualistic species responses during succession, and how these are driven by species traits. A last subgroup focuses how vegetation structure and underlying demographic processes change during succession.

(2) A second group of models (ecosystems) provides a more holistic view of succession by considering the ecosystem, its biota, the interactions, diversity, and ecosystem structure and processes.

(3) The third group (landscape) considers a larger spatial scale and includes the effect of the surrounding landscape matrix on succession as the distance to neighbouring vegetation patches determines the potential for seed dispersal, and the quality of the neighbouring patches determines the abundance and composition of seed sources and biotic dispersal vectors.

(4) A fourth group (socio-ecological systems) includes the human component by focusing on socio-ecological systems where management practices have long-lasting legacies on successional pathways and where regrowing vegetations deliver a range of ecosystem services to local and global stakeholders.

(5) The four groups of models differ in spatial scale (patch, landscape) or organisational level (plant species, ecosystem, socio-ecological system), increase in scale and scope, and reflect the increasingly broader perspective on succession over time.

(6) The four groups coincide approximately with four periods that reflect the prevailing view of succession of that time, although all views still coexist. The four successional views are: succession of plants (from 1910 onwards) where succession was seen through the lens of species replacement; succession of communities and ecosystems (from 1965 onwards) when there was a more holistic view on succession; succession in landscapes (from 2000 onwards) when it was realised that the structure and composition of landscapes strongly impact successional pathways, and increased remote sensing technology allowed better quantification of the landscape context; and succession with people (from 2015 onwards) when it was realised that people and societal drivers have strong effects on successional pathways, that ecosystem processes and services are important for human well-being, and that restoration is most successful when it is done by and for local people.

(7) The hierarchical successional framework of Pickett *et al.* (1987*a*,*b*) is the best vehicle for further integration because it already includes several factors and processes and is flexible, allowing application to different systems. The framework focuses mainly on species replacement and could be improved by including succession occurring at different hierarchical scales (population, community, ecosystem, socio-ecological system), and by integrating it with more recent developments and other successional models: by considering different spatial scales (landscape, region), temporal scales (ecosystem processes occurring over centuries, and evolution), the effects of the surrounding landscape (landscape integrity and composition, the disperser community) and societal factors (previous and current land-use intensity). Such an improved model should make clear predictions regarding how these factors affect succession.

(8) A comprehensive framework will allow us to address many current questions in successional ecology. Applying the framework to seres across broadscale environmental gradients in precipitation, temperature, elevation, soil fertility, and disturbance, will allow better insights into what successional models and processes matter under what conditions.

(9) The successional framework and successional models (or parts thereof) can be evaluated using a combination of complementary approaches. Empirical field studies can combine longitudinal plot studies that monitor community assembly with chronosequence studies that provide a long-term perspective, and with novel tools (such as remote sensing, functional traits, acoustic monitoring and genetic markers) to quantify successional processes. Experimental studies can add or remove resources, plant species, and biotic interactions, thus testing mechanisms, while process-based models can integrate different mechanisms, scale up across space and time, and make quantitative predictions.

(10) The combination of a comprehensive successional framework with the three complementary research approaches will increase our understanding of succession and advance successional theory.

VIII. ACKNOWLEDGEMENTS

IX. REFERENCES

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