Merging Multiple Equilibrium Models and Adaptive Cycle Theory in Forest Ecosystems: Implications for Managing Succession

Daniel P. Soto & Klaus J. Puettmann

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Merging Multiple Equilibrium Models and Adaptive Cycle Theory in Forest Ecosystems: Implications for Managing Succession

Daniel P. Soto[1,2] · **Klaus J. Puettmann**[2]

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Abstract

Purpose of Review We review the dynamics of multiple equilibrium models with the adaptive cycle concept and propose a unified theoretical framework. We highlight how the shape of basins of attraction changes along secondary succession and how the shape is influenced by the properties of the adaptive cycle (i.e., potential, connectedness, and resilience) and by ecological traps such as poverty, rigidity, and lock-in. We use degraded forest ecosystems undergoing arrested succession as an example, how the new framework can improve our understanding of restoration and management options.

Recent Findings Here, we highlight how the adaptive cycle uses three properties to describe ecosystem dynamics and how this information can be useful for management decisions at the stand level. "Potential" is related to biomass accumulation along succession; "connectedness" to the rigidity of internal control to resist external influences (e.g., disturbances), as quantified by the depth of the basin of attraction; and "resilience" to the ability of ecosystems to stay in a basin of attraction, as determined by the basin width. We integrate these aspects of the adaptive cycle with the basins of attraction model, ecological trap properties, and succession and disturbance concepts into a conceptual framework and highlight the resulting conceptual insights by contrasting forests that follow typical successional development (and associated provision of multiple ecosystem services) and forests that have arrested succession (e.g., degraded forests that do not provide desired ecosystem services). We use restoration practices aimed at overcoming arrested succession as examples how our framework can be downscaled to stand-level conditions. The framework views restoration practices as disturbances of different severities that may modify connectedness and resilience through the manipulation of species composition and the enhancement or constraint of resources (i.e., modifying a desirable basin of attraction by deepening and widening its shape to facilitate typical successional development or vice versa for an undesirable basin).

Summary Our review led to a unified theoretical framework. The resulting conceptual basis will improve the general understanding of vegetation development, which is especially important for restoration efforts in novel, no-analog conditions, as expected under global change.

Keywords Adaptive cycle · Arrested succession · Basin of attraction · Ecological traps · Recalcitrant understory vegetation · Resilience theory

Introduction

Ecological systems are dynamic, and species turnover and successional direction have been an important research topic [1]. These dynamics are often strongly influenced by natural disturbances and human activities [1, 2], leading to successional pathways that are considered either desirable or undesirable by humans [3, 4•]. The vegetation response after small- and large-scale disturbances can be anticipated in terms of general trends in species composition and structure [4•, 5, 6]. At the same time, the specifics of successional dynamics can be unpredictable, due to spatial variation in disturbance intensity, random events, non-linear ecological interactions, and feedbacks [4•, 6, 7]. A special case of successional development, and thus one that may potentially provide insights, is arrested succession [8–10, 11•]. This phenomenon can be due to the direct effects of endogenic and anthropogenic disturbances [9, 10], the invasion of competing vegetation [12], or a

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✉ Daniel P. Soto
daniel.soto@uaysen.cl

[1] Departamento de Ciencias Naturales y Tecnología, Universidad de Aysén, Coyhaique, Chile

[2] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

combination of both [11•, 12, 13]. For example, treefall gaps or selective harvesting can lead to shrub, grass, or herbaceous vegetation dominating forest understories for decades or longer, thus stalling or delaying succession by preventing the establishment of mid- to late-successional tree species [8–10, 12, 13].

Arrested succession is an exception to the typical successional development [9, 10, 11•]. It is not particularly common globally, but where it happens, it receives attention for various reasons. First, it is viewed as a type of forest degradation because desirable forest ecosystem processes and functions (in this case, the development of trees) are being retarded [14••]. Second, as an exception to the conceptual successional pathways, it provides great learning potential to improve our understanding. Consequently, arrested succession has been investigated in detail in several forest ecosystems. Examples of arrested succession after disturbance, due to the dominance of bamboo species, have been documented in temperate rainforests in Chile [11•, 15, 16] and New Zealand [17]; tropical rainforests in Peru [18]; Iguazu neotropical forests [19], Amazonian rainforests [12], and Atlantic forest in Brazil [20]; and subalpine Abies-Betula forest in China [21]. Dwarf bamboo in cold temperate forests in Japan also has been reported to arrest succession [22]. In addition, selected ferns species have been shown to be responsible for arrested succession in northwestern Pennsylvania hardwood forests [10], Puerto Rico [23], and Hawaii [24] in the USA; in southern Chile [25]; and in temperate forests in New Zealand [26]. Similarly, members of the Ericaceae family have been reported to interfere with successional dynamics in different forest types, such as salal (*Gaultheria shallon*) in the temperate rainforests of the Pacific Northwest of the USA [27–29], *Kalmia* spp. in the eastern USA [10], *Empetrum hermaphroditum* [9] in the European boreal forests, and *Calluna vulgans* in western Europe [30]. Another example of arrested succession is the long dominance of *Rubus* spp. in temperate forests of the Pacific Northwest [27] and Europe [31]. Different grass species have also been reported to promote arrested succession, such as *Sacharum spontaneum*-dominated grasslands in Panama [32, 33]. Other examples of arrested succession include *Imperata* spp.-dominated grasslands in northeast Vietnam [34], Singapore [35], in highlands of Sri Lanka [36], in Panama [37], and Indonesia [38]. All these examples suggest that selected understory vegetation can arrest successional trajectories of vegetation. In the case of forests, understory vegetation that is shade tolerant and has several different regeneration modes, including sprouting or suckering, appears to be particularly apt to arrest succession [39].

Forest restoration activities informed by succession models and historical disturbance regimes are common management strategies for overcoming arrested succession [4•, 6, 8, 40]. Goals of such activities typically focus on altering vegetation and/or soil conditions to encourage development along desirable successional pathways [2, 41, 42]. However, scientific understanding is not always sufficient to ensure successful outcomes [see 2, 4•, 6, 7, 41, 42]. Undesirable results have occurred when biotic (e.g., proliferation of understory vegetation) and abiotic factors (e.g., limited or overabundant resources, such as light, nutrients, and water) and their interactions were not considered adequately, for example, when the high production of leaf litter prevented the germination of tree seeds [16, 43]. These types of issues are garnering special interest now, as the responses of forests to novel forest ecosystem disturbances due to climate change or the introduction of exotic species may promote and result in novel conditions that may lead to the rapid proliferation and domination of undesirable species [8–10, 44]. For example, drier and warmer climate conditions may encourage alternative or novel successional trajectories that allow small and aggressive shrubs or small undesirable trees to dominate the landscape by creating savannas [45].

To provide a solid conceptual basis for forest ecosystem dynamics, with a special focus on conditions leading to arrested succession and the associated implications of management or restoration activities, we linked succession theory to multiple equilibrium models [4•, 7, 46••, 47••] and the adaptive cycle metaphor [48••, 49•]. These concepts all relate to the topic of how disturbances during a given successional stage may influence the future forest ecosystem development. The multiple equilibrium model by itself describes multiple distinct states or “basins of attraction” and how ecosystems cross thresholds to move from one state or basin to another [46••, 47••, 48••]. The basin-of-attraction and “ball-and-cup” landscape metaphors are closely linked [46••, 47••, 49•, 50]. For the latter, the ball (i.e., ecosystem) remains fairly stable in the bottom of a cup or basin, if disturbances are absent or are not sufficient to change the forest ecosystem’s structure, processes, and functions [14••]. Although small disturbances may move the ball throughout basin, the ball does not leave the basin [46••, 47••] and will eventually return to its predisturbance position through the natural processes of succession [49•]. If a disturbance severity or frequency is great enough to disrupt the ecosystem’s structure and composition, however, the successional trajectory will change: the ball will go over the basin’s threshold and into another basin of attraction [46••, 47••]. For example, on sites with moderate moisture regimes, the presence and absence of fires have been shown to determine a potential shift of forest to savanna ecosystems, as alternative stable states [51].

In a restoration context, forests with arrested succession may be viewed as being in an undesirable basin of attraction. In contrast, forests following typical successional progression would be in a desirable basin. However, this concept can be viewed as “static,” as it deals with an ecosystem at a given stage along successional development. Thus, it provides limited insights into the dynamic nature of forest succession. In this review, we describe how multiple equilibrium models can be integrated with adaptive cycles into a dynamic overall framework that not only offers theoretical insights but also provides a conceptual basis for restoration and management efforts.

Brief Review of Successional and Disturbance Theories in the Context of Arrested Succession

Forest succession is viewed as vegetation development over time along trajectories of compositional and structural change [1, 3, 5, 6, 52, 53]. It is a well-developed and established concept and has provided an important basis for understanding forest ecosystem dynamics and for the development of management practices [5, 54–56]. Current understanding of forest succession emphasizes multiple pathways that ecosystems can follow as a function of the timing, type, and severity of disturbances, resource availability, and abiotic and biotic interactions [55–57], specifically, as influenced by biophysical conditions and legacies (structural and compositional) left after disturbances [55, 58, 59]. For example, residual overstory trees influence the availability of various resources (e.g., light, water, and nutrients) for regenerating vegetation [58, 59]. These resources shape regeneration niches as related to resource requirements of different plant species and thus play a fundamental role in determining successional development [1, 11, 52]. Figure 1 highlights four examples out of many possible trajectory patterns [sensu 60] to illustrate differences between typical and arrested succession after stand-replacement and partial disturbances. Figure 1.1 shows a trajectory that differs initially but then converges rather quickly with the typical successional trajectory used as a reference pattern. Examples of this convergent pattern include the classical models of forest ecosystems and stand dynamics [1, 60–62] (Fig. 1, black circle d). After the initial trend towards convergence, the successional trajectory in a forest could deviate from a typical pattern (e.g., due to feedback loops or the effects of a sudden partial tree mortality episode caused by a drought) but then converge again over time (Fig. 1.2). Examples of this pattern have been documented in insect outbreaks in Patagonia [63], the Rocky Mountains region [64], and boreal forests [65]. In contrast, arrested succession shows trajectories that do not converge with the typical successional trajectories for extended time periods (Fig. 1.3). In cases where management or restoration activities alter the factors leading to arrested succession and change the successional pathway, the system then shifts towards a typical succession trajectory (Fig. 1.4).

A wealth of ecological literature has documented how disturbance frequency and severity control species composition and thus influence successional trajectories [e.g. 52, 66–68]. ,In forests with fairly stable disturbance regimes, disturbance frequency is often related to life span of the dominant tree species [6] and disturbance severity to their life histories and physiological traits [69]. For example, ecosystems with very frequent disturbances are often dominated by ruderal species [70]. Alternatively, forest ecosystems with infrequent disturbances may be dominated by long-lived tree species [71, 72] (see Fig. 2). However, in forest ecosystems with a mixed-

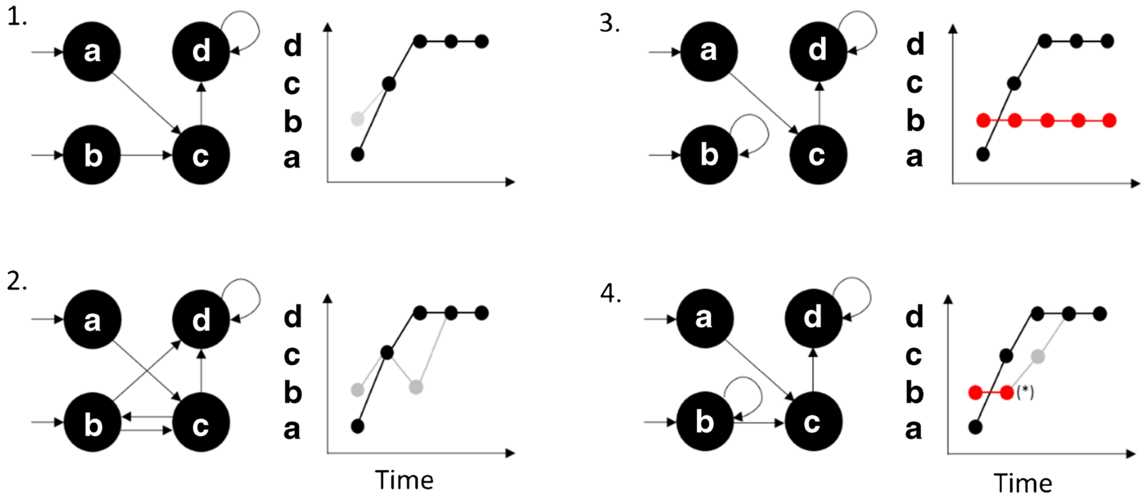

Fig. 1 Four of many possible patterns of successional dynamics (e.g., biomass accumulation) after stand-replacement disturbance, in which (**a**) is the initial state after disturbance (e.g., bare ground); (**b**) is an early successional stage after partial disturbance; (**c**) is an intermediate stage; and (**d**) is the final state (i.e., basin of attraction), typically late successional. The solid black line and black dots represent typical successional trajectories leading to late-successional conditions in terms of composition and structure; in contrast, the gray or red line and dots show alternative trajectories, where red dots indicate stages of arrested succession. The example patterns are as follows: (**1**) trajectories differ initially but converge quickly to the same late-successional state; (**2**) trajectories converge initially, then diverge, but ultimately converge to reach the late-successional state; (**3**) arrested succession, where the trajectory never moves into a late-successional state (red dots and lines); and (**4**) initial arrested succession (red line and dots), but then natural processes or management actions (*) shift the trajectory towards convergence and a late-successional state (gray line and dots)

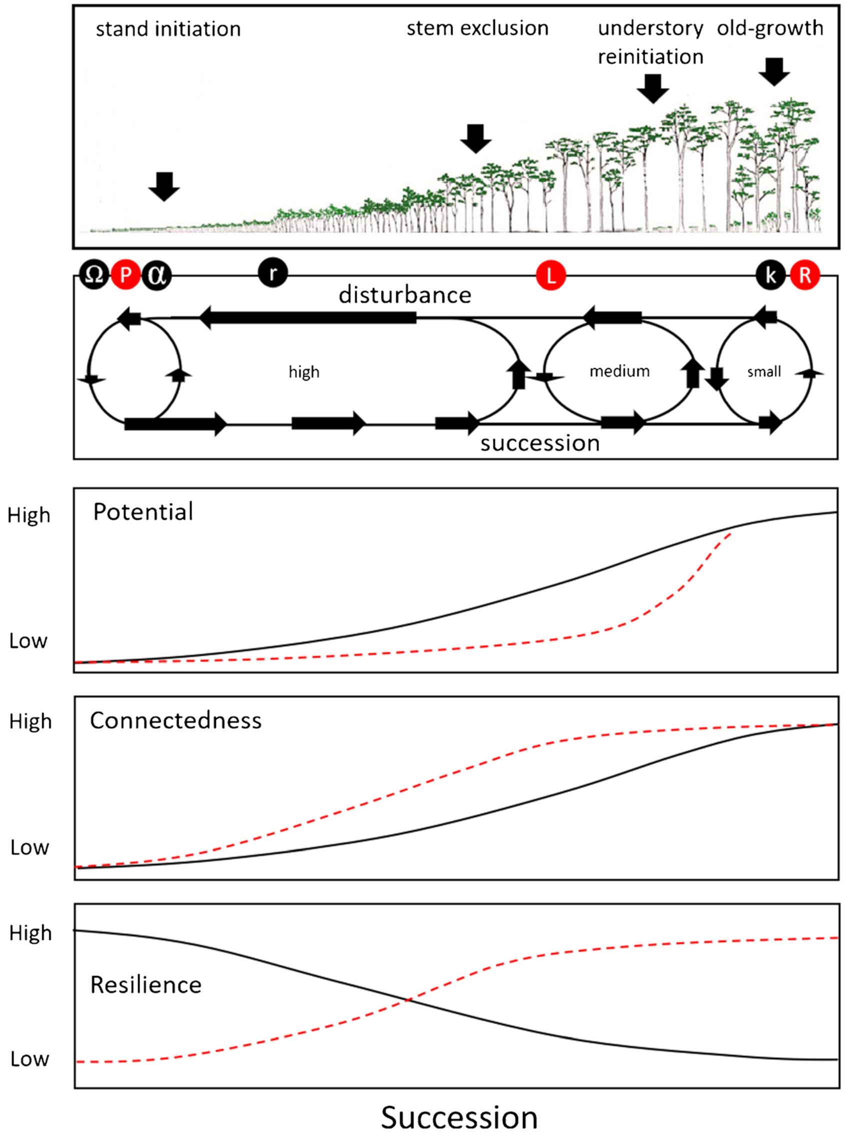

Fig. 2 The three properties (potential, connectedness and resilience) of the adaptive cycle (black line; [48••]) and for ecological traps (red dashed line; [48••, 73••, 74]) along succession (lower three panels). Disturbance impact on successional trends as related to disturbance size (in the case of forests this is also related to severity) is presented in the panel above. Arrows lengths are reflecting the speed and direction of vegetation development. For example, the short downward arrows are indicating the retarding effects of traps. The four phases of the adaptive cycle (black circles: exploitation (*r*), conservation (*k*), release (Ω), and reorganization (*α*) [48••]), as well as ecological traps (red circles: poverty trap (*P*), lock-in trap (*L*), rigidity trap (*R*) [58, 59]), are aligned above this panel. The top panel depicts a typical successional development with stand dynamic stages [sensu 62]

severity disturbance regime, and thus a higher influence of structural and compositional legacies, succession may be more variable [6]. This variability exhibits itself both in terms of different structural and compositional pathways but also due to heterogeneity at smaller spatial scales [6, 59, 71].

Theoretical Framework Using Basin of Attraction and Ecological Traps

Integration of Successional Theory and the Basin of Attraction Metaphor

The stability of a basin of attraction is defined by two attributes: resilience and resistance [48••, 50]. Resilience is quantified as the horizontal distance between two of the summits adjacent to a basin of attraction (i.e., thresholds) [50]. It represents how much a system can change without losing its functioning and the capacity to reorganize after disturbance [48••, 50]. In contrast, resistance is quantified as the depth of the basin. It represents the effort necessary to switch to another state, for example, the severity of a disturbance that an ecosystem can tolerate without losing its capacity to reorganize [14••, 50]. Late-successional forests are the typical example of an ecosystem in a narrow, deep basin, i.e., with low resilience and high resistance to change [73••].

Linking the basin-of-attraction model to successional dynamics highlights the limitations of the typical single ball-and-cup display due to its "static nature" [see 50]. Even with the "static" limitation and no specific information about potential successional trends, basin of attractions have been used successfully to explain ecological phenomena and anthropogenic influences on ecosystems [14••, 48••, 50]. We propose that it is more useful to view a ball-and-cup model as part of a dynamic landscape [46••], where the location, depth, and shape of a ball-and-cup or basin of attraction vary over time in relation to successional development (see Fig. 3.1 a–e). It is crucial to understand the ecosystem properties that define the basin of attraction, specifically width and depth and how they change over time and how they can be manipulated using management or restoration practices.

Review of Properties of Adaptive Cycle Phases and Ecological Traps

The adaptive cycle [48••] can provide conceptual insights into factors determining the shape of basins of attraction and how these factors change over time (e.g., succession). The adaptive cycle can be viewed as an expanded, more conceptual version of the stand dynamics model [62], with an additional emphasis on the role of disturbances [49•]. It uses three properties as defining features to understand ecosystem dynamics (Fig. 2):

(1) Potential, quantified as stored energy or biomass.
(2) Connectedness, defined as the rigidity of internal control of the ecosystem to external influences.
(3) Resilience, as mentioned above, is the capability of a system to react to disturbance without losing its functioning and the capacity to reorganize. In the context of the adaptive cycle, resilience can be interpreted as the number of potential pathways an ecosystem can take while maintaining a functioning forest and as an indicator of adaptive capacity, sensu Puettmann [74].

These three properties can be used to sort ecosystem dynamics into four phases: exploitation (*r*), conservation (*k*), release (Ω), and reorganization (*α*) [48••]. The exploitation and conservation phases basically represent the periods when typical successional dynamics play out [49•]. During these phases, forests gradually increase in potential and connectedness but decrease in resilience [48••, 49•] (Fig. 2). The typically high diversity of conditions and species in conjunction with low connectedness during the reorganization phase results in high resilience, as the system can withstand a variety of disturbances and still develop into a forest. Starting in the exploitation phase, as connectedness (e.g., competition and facilitation) and potential (e.g., biomass) increase, resilience is reduced as, for example, species loss and decreased opportunities for establishment of new species result in fewer possible pathways of forest development [48••]. In practical terms, a high potential can mean a high fuel load and an increased likelihood of high severity fires with the resulting major shift in vegetation structure and composition [49•, 50, 73••]. In contrast, in the absence of large-scale disturbances,

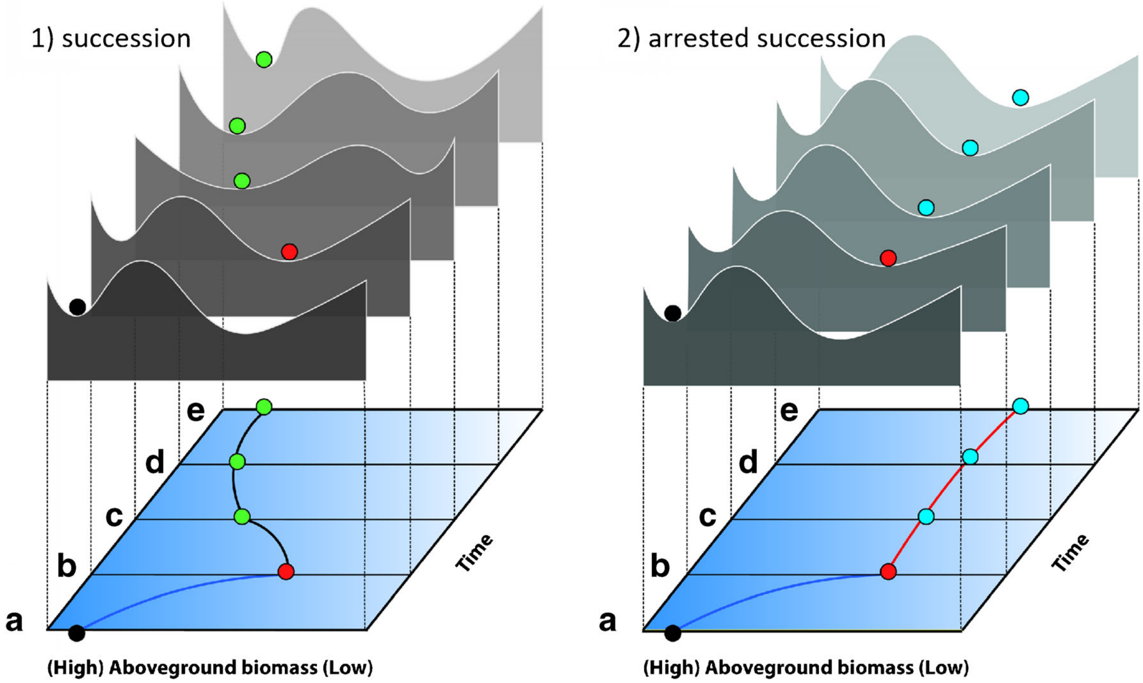

Fig. 3 Multiple equilibrium model displayed in terms of basins of attractions following a partial disturbance (a–e in all models), with Panel 1 showing typical successional and Panel 2 showing arrested successional trajectories. In Panel 1, disturbance (red ball) is not intense enough to produce a change in the system state and attributes (e.g., structure and composition), and the potential to build up biomass is not affected after disturbance. That means that green balls are kept in the desirable basins of attraction while succession progresses. Alternatively, as shown in Panel 2, if disturbance is intense enough to remove competing vegetation, it may produce a shift in species composition and structure, due to changes in biophysical conditions in the forest (red ball in time b). In this state, the succession is arrested, and the potential to build biomass is locked into an alternative stable state in the long term by the high connectedness and resilience of this state (blue balls)

the high connectedness ensures higher resistance [48••, 49•, 50, 73••] and lower resilience. For example, openings created by small disturbances in late-successional forests typically are filled in with late-seral tree species already present in the mid- or overstory layers, leading to minor changes in structure and composition [73••] (Fig. 2).

To understand arrested succession, it is useful to integrate the adaptive cycle with the ecological trap concept [48••, 73••], as the relationship between the ecosystem properties described as part of the adaptive cycle and ecological traps can provide useful insights. The concept of ecological traps—or phases when ecosystem development is slow to static [see 73••, 75••]—viewed in terms of a basin of attraction, also helps to provide an understanding of ecosystem dynamics as they relate to arrested succession. Arrested succession is a prime example of an ecological trap [sensu 73••]. In unmanaged systems, ecological trap conditions are typically overcome by large-scale disturbances [73••, 75••]. Gunderson and Holling [48••] described two types of ecological traps: "poverty" and "rigidity," and Allison and Hobbs [75••] described a third one called "lock-in" trap. The poverty traps (*P*) are characterized by ecosystems having low potential and low connectedness (Fig. 2). Such traps are found in landscapes with frequent disturbances that remove biomass (lower potential) and free up resources (lower connectedness). The resulting variability, for example, in soil conditions, and potential for species invasion, including undesirable species, are an indicator of high resilience, as they indicate a high number of potential pathways [4•, 60]. Examples of poverty traps include open savanna or grassland ecosystems that are stabilized or trapped through frequent fires [73••, 75••]. In contrast, rigidity traps (*R*) are defined by high potential and connectedness and low resilience [73••](Fig. 2). Late-successional forests are a prime example of a rigidity trap [73••]. Unless more severe disturbances lower the potential (by removing biomass) and connectedness (by freeing up resources sufficiently for early-seral species to dominate), late-successional forests are stable over long periods in the absence of major disturbances [73••]. Long-term dominance of few selected tree species has also been found in some tropical forests [76–79] and has been hypothesized to be due to the superior competitive ability and/or better resistance to adverse physical and biological conditions, which may be due to selected species traits [80].

Lock-in traps (*L*), which are characterized by their low potential and high connectedness, but intermediate to high resilience [sensu 75••], can be described as falling between poverty and rigidity traps (Fig. 2). The typical example of this trap is degraded forests, where some structural legacies (i.e., potential) remain after disturbances and the understory is dominated by dense thickets of shrubs, lianas, or ferns, which delay or stop successional development [8–10, 11•, 80, 81]. Figure 2 illustrates the relative importance of potential, connectedness, and resilience of ecosystems following typical successional development with ecosystems in arrested succession (red and dashed lines). Based on the relative positions of the three properties, one can distinguish the three types of traps [48••, 73••, 75••]. As noted above, arrested succession is a prime example of a lock-in trap [75••]: potential is lowered due to natural or anthropogenic disturbances; connectedness is driven by the dominance of selected few understory species; and resilience is relatively high, mostly due to the pervasive behavior of the selected understory species (e.g., their resprouting traits) [10].

Figure 2 also aligns events in the disturbance and successional dynamics with the stand dynamics model [sensu 62]. Thus, Fig. 2 provides insights why selected forest stands may or may not follow the typical stand dynamic development, i.e., successional trajectories. Specifically, it shows that selected combinations of connectedness, potential, and resilience resulting in the respective traps are only found in specific stages of stand dynamics. Similarly, an integrated framework also provides insights into the inhibition model, which has been discussed as a potential driver of successional development [sensu 82], and manipulating connectedness, potential, and resilience may be used to overcome inhibition mechanisms at various successional stages. Compared with relay and initial floristics, the inhibition model has received less attention in the ecological and restoration literature.

Developing a Conceptual Framework

Figure 3 visualizes a framework that integrates successional theory, basin of attraction, ecological traps, and the adaptive cycle. For simplicity, we depict only two dynamic basins of attraction: Fig. 3.1 shows typical successional ecosystem development, and Fig. 3.2 shows ecosystems in arrested succession. At time (**A**), the black ball always depicts a late-successional forest. The shape of the basins of attraction in these conditions indicates high potential (i.e., fairly high elevation), high connectedness (i.e., fairly deep), and low resilience (i.e., fairly narrow). As described above, small-scale disturbances do not lower connectedness sufficiently and thus do not lead to major changes in structure and composition. However, the low resilience suggests that major disturbances can lower the potential and connectedness to a level that allows the ecosystem to move into a new basin of attraction, in our example, a basin representing early-successional stages (time **B**).

Depending on the specific vegetation and growing conditions at time (**B**), an ecosystem can take different successional pathways. In Fig. 3, two possible successional trajectories that differ, starting at time (**C**), are used to visualize our conceptual framework. Figure 3.1 represents an ecosystem that follows typical successional trajectories (see Fig. 1.1 or 1.2) leading to the buildup of biomass (i.e., potential) and connectedness; it is thus moving in a basin of attraction that eventually leads to late-successional conditions (green balls), i.e., conditions similar to those found at time (**A**). In this condition, the resources freed up by the disturbance produce several changes in the shape of the basin of attraction along time. Graphically, it means that the basin of attraction is shallower and wider after the disturbance (3.1, time **C**), but the new shape is not different enough to modify the essential ecosystem processes and functions, for example, natural regeneration that promotes early successional development. Thus, in the absence of major disturbances, the potential and connectedness level will recover with time.

In contrast, Fig. 3.2 represents an example of an ecosystem that has moved from a late-successional state (time **A**) to an alternative stable state or basin of attraction (time **B**), where low potential, high connectedness, and intermediate levels of resilience after the initial disturbance prevent the development of the potential (Fig. 3.2 C–E, blue balls). This is an ecosystem that is undergoing arrested succession, such as those with dominant, recalcitrant, and pervasive understory vegetation. In ecosystems in a state of arrested succession, the connectedness is high, the resilience is intermediate, but the potential (or biomass, in this case) is low, and these conditions remain stable for long periods.

Figure 4 depicts an example of how successful restoration activities can push an ecosystem out of a lock-in trap, i.e., how arrested succession that prevents typical stand development (as shown in Fig. 3.2) can be overcome through management activities. To move a stand out of an arrested-succession basin of attraction requires specific disturbances or management activities [16, 38, 83•, 84•]. For efficient restoration, such activities should be designed to effectively reduce the system's stability, i.e., break down the connectedness [60] and lower resistance and increase resilience to encourage forest development [14••, 47••, 48••]. Thus, undesirable states can be overcome theoretically by:

(1) Moving the ball through the basin of attraction landscape
(2) Modifying the width and depth of the basin of attraction [see details in 47••]

Managers can erode or enhance the connectedness and resilience of a basin of attraction by altering the resources (e.g., the amount of light, nutrients, and water) or safe sites conditions (mineral soil, litter or downed wood, and lack of competition) for key dominant species that lead the ball to remain stable in a basin of attraction [46••, 47••]. For example, breaking connectedness can be accomplished by preventing existing vegetation from taking up key resources [47••, 75••]. The freed-up resources are then available for other species, which can become established and thus break the system out of the trap (dashed lines in Fig. 4). The section below explains how management may break connectedness and influence resilience of undesirable basins and provides specific examples.

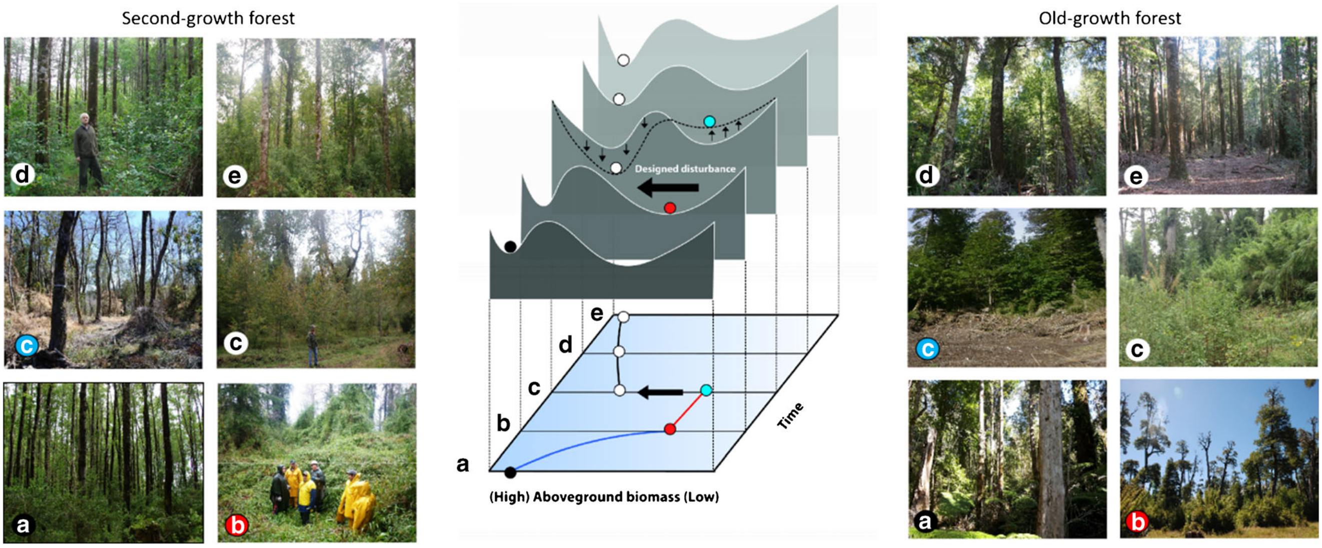

Fig. 4 Multiple equilibrium model represented by basins of attraction and their associated photos depicting how second-growth (left panel) and old-growth (right panel) forest stages reacted through the proliferation of a dense and recalcitrant understory vegetation that arrested succession (b, red balls). Designed disturbance treatments were implemented to overcome the arrested-succession state (c, blue balls) by controlling its high resilience and connectedness. The restoration treatments reshaped the basin of attraction (c, black arrow) and allowed ecosystems to follow desirable successional patterns through the establishment of tree species (c, white balls) through underplanting (left panel) and natural regeneration (right panel), thereby promoting desirable states of resilience and connectedness. Photos e and e show how successional progression is taking place in both examples after some small-scale disturbances and how management actions can improve forest potential, resilience, and connectedness

Translating the Framework into Restoration and Management Practices

The overall framework can provide a conceptual perspective for three different settings at the stand level: (1) restoration practices to overcome arrested succession; (2) management of ecosystems following typical successional patterns (including those restored from arrested succession); and (3) management to maintain ecosystems in a desirable successional state.

Restoration Practices to Overcome Arrested Succession

Management practices to overcome arrested succession are not designed by practitioners with shapes of basins of attraction in mind. In practical terms, management practices manipulate forest components, such as by outplanting seedlings or removing vegetation, as well as changing how these components interact, for example, by altering resources. Such resources may erode or foster resilience or break down the connectedness of a given basin of attraction (Fig. 4). For example, reducing the presence of the species that promote arrested succession is a key activity for breaking down connectedness and influencing the resilience of a forest stand in arrested succession by modifying the shape of the basin of attraction of this trap (Fig. 4c, blue circle). Alternatively, management may foster resilience through enhancing species diversity, for example, by underplanting tree species that initiate the successional process or by creating safe sites for the establishment of such trees (Fig. 4c, white circle) [14••, 16, 40]. Underplanting to establish advanced regeneration is a prime management example of this principle. It has been used to restore forest structure and composition in, e.g., *Nothofagus*-dominated forests in the Andes of Chile [85]; the redwoods and Douglas fir old-growth forests in California and Oregon, respectively [86]; the Sri Lankan rainforest [83•, 87]; and the Pacific coastal areas of Panama, Costa Rica, Nicaragua and Mexico dry tropical forests [88]. Typically, such restoration activities include the manual or mechanical removal of undesirable vegetation (Fig. 4c, blue ball [89, 90]; or the removal of topsoil through mechanical scarification when undesirable understory vegetation has a pervasive sprouting behavior (Fig. 4c, blue ball) [e.g. 16, 22]. ,Thus, restoration activities that modify resources and safe site conditions can make the basin of attraction shallower, through reduced connectedness and, narrower, through influencing resilience of the arrested-succession or trap condition, and vice versa for those conditions that promote successional development (Fig. 4c).

Management of Ecosystems Following Typical Successional Patterns

To accelerate successional development towards desirable conditions, for example, late-successional stages, additional management activities can improve growing conditions for selected species that promote successional development by increasing the system's connectedness and resilience (Fig. 4 d-e). For example, dense patches of desirable natural or artificial regeneration may result in reduced tree growth due to high intra- and inter-specific competition [57, 91]. In these cases, restoration thinning [92] or variable density thinning [93, 94, 95•] can be used to accelerate successional progression by decreasing connectedness (i.e., increased resources availability) to a level that results in increased growth of the remaining trees but still prevents the establishment of early-seral tree species (Fig. 4d). Late-seral tree species can become established under the canopy of the early-seral trees, either naturally, if seed sources of these species are already present [96] or aided by seeding [97] or planting [85–87, 89] (Fig. 4e). Under these management approaches, resilience will likely increase, which means widening the basin of attraction by creating safe sites for the establishment and growth conditions for late-successional tree species (Fig. 4d).

Management to Maintain Ecosystems in a Desirable Successional State

Once a desirable forest ecosystem state is reached (e.g., late-successional forests; see right panel, Fig. 4d), managers may want to maintain forests in this stage for longer time periods, because of carbon storage and biodiversity concerns [98] or to provide other ecosystem services [99]. However, late-successional forests have low resilience and high connectedness (Fig. 3.1E). Thus, management goals would include enhancing resilience by widening the basin of attraction. For example, simple partial control of understory vegetation to avoid the proliferation of undesirable vegetation would promote forest resilience (Fig. 4e) [16]. Other management activities aimed at encouraging resilience and maintaining a system's connectedness include low-intensity canopy removals that encourage the regeneration of mid- to late-seral tree species. These types of low-intensity management activities limit the reduction in connectedness while maintaining a relatively high potential (biomass) [100•, 101••]. In practical terms, management approaches with low-level tree removals have been used extensively in selected locations, for example, under the label of uneven-aged or close-to-nature or multi-aged silviculture [102, 103•, 104, 105]. While not designed with these concepts in mind, these management approaches allow ecological processes and functions to be maintained in forest stands and maintain levels of connectedness and potential that maintains the system in the basin of attraction for extended periods of time [49•, 50, 51].

Outlook

The main goal of this review was to encourage forest managers and restoration ecologists to view ecosystems through an integrated framework that incorporates the basins of attraction, the adaptive cycle, and ecological trap properties with succession and disturbance concepts [4•, 14••]. Specifically, analyzing forest conditions in terms of the properties of adaptive cycles and traps, potential, connectedness, and resilience along successional trajectories can provide useful insights to understand why successional development might be arrested. The resulting better understanding of the scientific basis for forest restoration practices [6, 42] can guide selection of specific, stand-level management practices aimed at promoting successional development and/or maintaining forest ecosystems in desirable successional stages. For example, analysis of conditions with extremely low resilience using our theoretical framework can suggest the need to overcome dispersal limitations or other landscape-level drivers [e.g. 106]. ,In the case of arrested succession, our model results in recommendations to enhance the resilience and connectedness for species that encourage successional development and erode the connectedness and resilience for those species that promote arrested succession. Clearly, operational restoration treatments need to be designed and implemented in the context of the larger ecological, political, and social landscapes [107–112]. We suggest that relying on basic fundamental understanding of ecosystems, for example, by assessing connectedness, resilience, and potential, and utilizing that information in an integrated framework will increase the likelihood of successful restoration and management efforts [42, 58, 86].

Conclusions

In this review, we link several theories to provide a deeper conceptual understanding of the successional dynamics in forests. Specifically, we apply ecosystem properties as used in the adaptive cycle (i.e., potential, connectedness, and resilience) and to the basin of attraction concept to better understand successional development and the potential conditions and stages where ecological traps can develop. Our model allows restoration ecologists and forest managers to view their activities in the context of altering ecosystem properties and thus influence the shape of the basin of attractions to overcome undesirable conditions at the stand level. For example, in the case of arrested succession, disturbances or restoration activities should be aimed at breaking down or enhancing the connectedness and increase the resilience through the release or constraint of resources (amounts of light, nutrients, and water), respectively. This can be achieved, for example, by activities that efficiently remove an undesirable understory competitor species may break down connectedness. At the same time, resilience can also be encouraged by an external input, such as planting tree species that foster succession towards desirable conditions. Thus, modifying connectedness and resilience through the manipulation of species composition and resources, restoration ecologists and/or forest managers effectively alter the width and depth of a basin of attraction to either encourage or discourage successional dynamics and/or transition to an alternative basin of attraction. Last, as with any theory, the integrated framework per se is a general concept developed to apply to a broad set of conditions. Thus, any application to restoration and management activities in specific settings requires a detailed analysis and local adjustments.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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