Succession Theory and Imprints of Vegetation Restoration

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Abstract

The Kunming-Montreal Global Biodiversity Framework proposes the high-quality protection and restoration of 30% of land respectively, aiming to maximize the achievement of biodiversity conservation and climate change mitigation objectives. Succession theory and vegetation restoration can serve these 30% protection and restoration targets. Succession theory constitutes a core theory in vegetation ecology; succession refers to the process whereby the structure or composition of living organisms comprising different species at a given site changes over time. Vegetation restoration is a process primarily involving plant cultivation and configuration to restore or reconstruct plant communities, or to restore plant communities through natural regeneration; it represents a process of ecosystem structure and function evolving from simple to complex and from lower to higher levels, with the ultimate objective of establishing healthy and stable plant communities. Succession forms the foundation of vegetation restoration, while vegetation restoration is regarded as a manipulation of the succession process to achieve the restoration of damaged vegetation ecosystems. Succession theory can guide vegetation restoration, and vegetation restoration also contributes to the development of succession theory. Succession can be categorized into primary succession and secondary succession based on the nature of bare ground; some studies propose treating the restoration process as tertiary succession, which would facilitate understanding of management options for promoting vegetation restoration success through human intervention, particularly by emphasizing management options for environmental and biological legacies in degraded ecosystems. Furthermore, scientific and technical issues that may become future research priorities for vegetation restoration theory and succession theory have been proposed.

Full Text

Preamble

Succession Theory and Vegetation Restoration

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Abstract

The Kunming-Montreal Global Biodiversity Framework proposes to protect and restore 30% of land with high quality to maximize biodiversity conservation and climate change mitigation. Succession theory and vegetation restoration can serve these 30% protection and restoration targets. Succession theory is the core theory in vegetation ecology, describing the process by which the structure or composition of living organisms—comprising different species at a given site—changes over time. Vegetation restoration is the process of restoring or reconstructing plant communities, primarily through plant cultivation and configuration, or through natural regeneration. It represents a process of ecosystem structural and functional change from simple to complex and from low to high levels, with the ultimate goal of establishing healthy and stable plant communities. Succession forms the foundation of vegetation restoration, while vegetation restoration can be viewed as the manipulation of successional processes to achieve the goal of restoring damaged vegetation ecosystems.

Succession theory can guide vegetation restoration, and vegetation restoration can also benefit the development of succession theory. Succession can be divided into primary and secondary succession based on the nature of bare land. Some studies suggest treating restoration processes as a third type of succession, which would help understand management options for promoting vegetation restoration success through human intervention, particularly by emphasizing the management of environmental and biological legacies in degraded ecosystems. This paper also proposes future scientific and technical issues that vegetation restoration theory and succession theory may focus on.

Keywords: succession, ecological restoration, tertiary succession, biodiversity, nature-based solutions

1. Succession Theory

Succession theory falls within the scope of community dynamics and refers to the process by which one community replaces another at a given site (Knap, 1985). Community succession types can be classified as primary or secondary succession based on bare land characteristics; as hydric or xeric succession based on substrate properties; as progressive or retrogressive succession based on direction; as linear or cyclic succession based on pattern; as endogenous, exogenous, or mixed succession based on driving factors; as small-scale, local, or regional succession based on spatial extent; and as contemporary or century-scale succession based on temporal scale (Peng, 1996; Ren et al., 2001; Song, 2001).

The main theories explaining community succession include the monoclimax hypothesis, the polyclimax hypothesis, and the climax-pattern hypothesis (Horn, 1975). These theories can be categorized into two philosophical perspectives: individualistic (emphasizing reductionism in community succession) and organismic (emphasizing holism in community succession). Key perspectives explaining succession mechanisms include the relay floristics hypothesis, initial floristic composition hypothesis, competition and resource ratio hypothesis, three-species interaction mechanism hypothesis, life history strategy theory, Odum-Margelef ecosystem development theory, McMahon system concept model, shifting mosaic steady-state hypothesis, hierarchical system perspective of succession, and spiral ascending succession theory (Ren et al., 2001; Sun, 2001). Research methods for studying succession mainly include community change indicator measurement, long-term permanent plot experiments, compositional analysis, model simulation, functional trait analysis, and molecular biology techniques (Chang & Turner, 2019).

Succession involves the process by which the structure or composition of living organisms—comprising different species at a given site—changes over time. Key aspects include: succession is driven by interactions among organisms and between organisms and the physical environment (i.e., biological, physical, and chemical driving hypotheses); successional patterns are determined by interactions among individuals; multiple trophic levels participate in driving these interactions; successional outcomes depend on disturbance processes, the availability of different species at a site, and species performance; successional causes can operate at any scale; interactions among different individuals may involve tolerance, inhibition, or facilitation; species composition at a site tends toward equilibrium with that site's environment; successional trajectories are determined by initial conditions, colonization stochasticity, and species interactions; and succession creates temporal gradients in physical environment, biological communities, and interactions between organisms and environment (Pickett et al., 2011). These aspects of succession can be used to guide vegetation restoration practice.

Christensen (2014) argues that succession is ecosystem change caused by discrete disturbances, and current understanding of succession mechanisms, trajectories, and endpoints has diverged from Odum's succession theory. Succession models have become more complex, stochastic, and context-dependent, making a single unified theory unlikely to explain successional changes. These shifts in understanding have important implications for restoration and conservation practice. Buma et al. (2019) found that primary succession on glacial forefields does not support the classic facilitation model; instead, stochastic early community assembly followed by inhibition dominates, meaning that early species interactions cannot form predictable successional trajectories. Vegetation succession is driven by seed dispersal or by stochastic processes of ecosystems that determine vegetation structure and species richness, or combinations thereof (Abella et al., 2018). Dent and Estada-Villegas (2021) found that seed source and disperser limitation determine seed production and arrival at suitable colonization sites throughout succession, thereby affecting community succession. Changes in soil microorganisms of plant communities can alter plant-herbivore interactions, affecting community succession, and aboveground-belowground interactions in plant communities also influence successional processes (Howard et al., 2020). During community succession, species-specific facilitation between nurse and target species is a mechanism promoting beta diversity (Paterno et al., 2016). Additionally, numerous studies have examined succession from a plant functional trait perspective. For example, Buzzard et al. (2016) found that community-weighted mean trait values align with the "productivity filtering" hypothesis, where water and light availability shifts physiological strategies from "slow" to "fast," while patterns of community trait dispersion align with abiotic filtering and/or competitive hierarchy hypotheses.

2. Vegetation Restoration

Vegetation restoration is the process of restoring or reconstructing plant communities, primarily through plant cultivation and configuration, or through natural regeneration (Peng, 1996). Ecological restoration originated from vegetation restoration, namely early afforestation activities, and vegetation restoration remains an important component of forestry. Early vegetation restoration emphasized "utilization" and "management" of vegetation resources, with single restoration objectives achieved through artificial planting interventions (Ren et al., 2004). By the mid-to-late 20th century, classified forest management began in forestry, and vegetation restoration for ecological public welfare forests focused on comprehensive objectives and ecological benefits, shifting the philosophy from "natural resource management" to "ecosystem approach." Restoration objectives expanded to include resource utilization, biodiversity conservation, pollution control, and ecosystem service provision. Currently, due to global change and sustainable development challenges, the philosophy of vegetation restoration has shifted again from "natural ecosystems" to "socio-economic-ecological complex systems," with restoration goals ensuring ecological security and achieving harmonious coexistence between humans and nature (Ren et al., 2014; Fu et al., 2023).

Vegetation restoration is a process of ecosystem structural and functional change from simple to complex and from low to high levels, with the ultimate goal of establishing healthy and stable plant communities. This process constructs various types of forest ecosystems with high biodiversity, functionality, stress resistance, and stability. The primary task is selecting appropriate constructive plant species to ensure the system rapidly develops in a positive direction (Ren et al., 2014). In practice, vegetation restoration involves human-designed transformation of degraded ecosystems, with the most direct method being planting single or multiple species. However, considering ecosystem complexity, vegetation restoration must also create ecological factors such as light, temperature, water, soil, air, and organisms required by target organisms and vegetation succession (Wali, 1999). For example, Zhang et al. (2021) found that soil microorganisms showed no significant changes during the first 0–5 years of natural restoration succession in degraded grasslands, but bacteria, fungi, and actinomycetes increased significantly during years 6–10. Vegetation restoration is also a practice focused on effective and efficient outcomes, involving three processes: overcoming harsh physical environments, seed source arrival, and reestablishing interspecific relationships. When implementing succession-based vegetation restoration, practitioners must consider: setting clear objectives, assessing site environmental conditions, determining whether spontaneous succession is an appropriate way to achieve objectives, predicting successional processes, and monitoring outcomes. This process necessitates interdisciplinary approaches and communication among scientists, engineers, and decision-makers (Prach et al., 2001).

3. The Relationship Between Succession Theory and Vegetation Restoration

Succession is a key ecological process that underpins much vegetation restoration. Vegetation restoration is viewed as manipulating successional processes to achieve the goal of restoring damaged ecosystems or landscapes. Walker et al. (2007) argue that succession and restoration are intrinsically linked because succession involves temporal changes in species and substrate, while restoration purposefully manipulates these changes. While ordered and unpredictable patterns emerge during succession, some general principles provide theoretical and practical insights for restoration activities. Because restoration operates at shorter time scales, it is more goal-oriented, whereas succession occurs over longer periods, and related concepts may not be directly applicable. Restoration may provide practical insights into how communities assemble during succession, but a lack of scientific research during restoration processes hinders the connection between the two.

Succession theory can guide vegetation restoration. For example, the relay floristics hypothesis can "provide a pattern for introducing secondary successional species" in ecological restoration; the initial floristic composition hypothesis can "guide the design of vegetation restoration to preserve soil seed banks"; facilitation theory can "posit that primary successional species improve conditions for secondary species entry"; and inhibition theory can "posit that primary successional species hinder and delay secondary species entry" (Ren et al., 2019). Similarly, landslides can achieve self-sustaining community restoration through techniques such as stabilizing original ground cover, applying nutrient amendments, promoting dispersal to overcome species colonization bottlenecks, emphasizing functionally redundant species, and promoting connectivity with neighboring landscapes. This demonstrates that recovery time can be shortened using techniques that facilitate successional processes (Prach et al., 2001).

Vegetation restoration also benefits the development of succession theory. Restoration practice can validate succession theory, particularly by providing information on community structure, function, and dynamic sustainability during successional processes. Vegetation restoration can provide objectives and trajectory predictions for applied succession theory.

Succession theory and vegetation restoration differ in scale, theme, and underlying paradigms (Walker et al., 2007). Succession often emphasizes nature-related disturbances, while vegetation restoration focuses on human-related disturbances. Succession theory concentrates on serial stages within a single ecosystem, whereas vegetation restoration focuses on adjacent multiple ecosystems and their series within a watershed or landscape. Succession theory originates from natural history and observations of temporal change, while vegetation restoration stems from human disturbance-oriented practice (Ren et al., 2019).

Artificial intervention based on succession theory can accelerate vegetation restoration, avoid early positive promotion of degraded vegetation ecosystems to pre-degradation levels in poor habitats, and prevent resource waste caused by disordered competition and low efficiency among communities. Appropriate community species combinations (near-natural uneven-aged forests, near-natural mixed forests, near-natural multi-layered forests) can accelerate soil quality improvement. In later stages, restoration can promote plant communities to develop toward climax stages by reducing disturbances, restoring original structure and function, achieving equilibrium, and ultimately evolving into stable climax communities (Yu & Zhang, 2020).

Phylogenetics is relatively new in vegetation restoration and succession but has the potential to provide novel insights into the dynamics of community structural changes during succession. Phylogenetic community tools can describe evolutionary relationships among coexisting species. In succession studies, these tools can identify evolutionary lineages most suitable for specific successional stages and habitat restoration. Shooner et al. (2015) found that compared to vegetation restored on mines, adjacent vegetation was phylogenetically denser, while restored mine vegetation showed weaker phylogenetic community structure. In other words, early colonizers represent phylogenetically random subsets of species from the local species pool, and over time, there appears to be selection for specific lineages that are filtered in space and environment. Therefore, species most suitable for mine restoration may depend on community successional stage and local species composition.

The Convention on Biological Diversity requires considering global ecosystem restoration priority areas to maximize biodiversity conservation and climate change mitigation while minimizing conservation costs, which can be addressed through Nature-based Solutions (NbS). NbS are actions for sustainable ecosystem management and restoration that emphasize utilizing natural and healthy ecosystems, optimizing infrastructure, and safeguarding ecosystem integrity and biodiversity (Li et al., 2022). NbS can provide solutions for climate change mitigation and adaptation, disaster prevention and reduction, economic and social development, human health, food security, water security, ecological environment degradation, and biodiversity loss (IUCN, 2020). NbS considers restoration under disturbance conditions and addresses species diversity, community composition, species interactions within communities, interactions among communities, and the trade-offs between biodiversity and ecosystem services from different vegetation restoration approaches.

4. Tertiary Succession Theory

To address climate change and biodiversity loss, current vegetation restoration efforts focus heavily on wetlands, forests, and grasslands. This is primarily because logging, mining, fires, floods, landslides, and agricultural activities have created large areas of degraded ecosystems. But what succession theory drives vegetation restoration?

Vegetation restoration is a human-manipulated activity aimed at accelerating the achievement of stable vegetation. While using succession theory to guide vegetation restoration is appropriate, problems remain. For instance, comparisons of primary succession, secondary succession, and vegetation restoration reveal almost no overlap among these concepts. Rapson (2023) proposed treating restoration processes as tertiary succession, which would help understand management options for promoting vegetation restoration success through human intervention, particularly by emphasizing the management of environmental and biological legacies in degraded ecosystems. A comparison of primary succession, secondary succession, and ecological restoration is presented in Table 1 . Rapson also suggested that “initializing succession” and “regeneration succession” are more appropriate terms than “primary succession” and “secondary succession.”

Using tertiary succession theory to guide vegetation restoration can focus on three aspects: promoting natural succession in restored vegetation, rewilding vegetation with strong artificial traces, and native-species transformation of plantations constructed from exotic species.

5. Research Trends in Succession Theory and Vegetation Restoration

The United Nations has proposed the UN Decade on Ecosystem Restoration (2021–2030) and the Kunming-Montreal Global Biodiversity Framework, while China has issued the National Master Plan for Major Projects of Important Ecosystem Protection and Restoration (2021–2035). These conventions and plans all include content on protecting and restoring ecosystems for the benefit of humanity and nature, thereby promoting sustainable development. Implementation of these plans will strengthen global and Chinese vegetation protection, restoration, and sustainable use while also advancing vegetation restoration and succession theory. Future research may focus on the following scientific and technical questions:

Scientific questions: Mechanisms of degradation in various typical degraded ecosystems and vegetation restoration strategies; interactions between aboveground and belowground processes during vegetation succession; trade-off mechanisms between biodiversity and ecosystem services during vegetation restoration; the role of historical contingency, disturbance severity, dispersal limitation, functional traits, and belowground community processes in determining ecosystem successional processes; impacts and mechanisms of global change on vegetation ecosystem succession and restoration (Wilson et al., 2004); and how to quantify the relationships between biodiversity and ecosystem function, stability, and resilience during vegetation restoration.

Technical questions: Diagnostic technology for biodiversity health status and identification of priority restoration areas in typical vegetation ecosystems; natural-community-structure-based construction and optimization technology for carbon sequestration and productivity enhancement; understory vegetation induction and restoration technology based on water conservation and biodiversity protection; soil acidification and nitrogen deposition remediation and nutrient use efficiency improvement technology in vegetation ecosystems; multi-scale restoration technology development and demonstration combining plants, animals, and microorganisms; technology for achieving multi-objectives and managing trade-offs between biodiversity and ecosystem services during degraded ecosystem restoration; technology for synergistically improving vegetation ecosystem quality, ecological service functions, and ecological stability during ecological restoration; near-natural habitat creation and urban biodiversity restoration technology based on habitat-food-disturbance considerations; technology for synergistically enhancing urban biodiversity with ecological functions such as carbon sequestration and climate regulation; plant-microorganism-soil amendment combined technology for heavily contaminated land remediation; multi-scale optimization models for synergistically enhancing ecosystem structure and function; and integrated "space-air-ground-network" monitoring systems for typical ecosystem protection and ecological restoration.

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Note: Figure translations are in progress. See original paper for figures.