Four opportunities for studies of ecological succession

Karel Prach¹,² and Lawrence R. Walker³

¹Faculty of Science USB, Branisovska 31, CZ-370 05 Ceske Budejovice, Czech Republic
²Institute of Botany, Academy of Sciences of the Czech Republic, Dukelska 143, CZ-379 82 Trebon, Czech Republic
³School of Life Sciences, University of Nevada Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154, USA

Lessons learned from the study of ecological succession have much to offer contemporary environmental problem solving but these lessons are being underutilized. As anthropogenic disturbances increase, succession is more relevant than ever. In this review, we suggest that succession is particularly suitable to address concerns about biodiversity loss, climate change, invasive species, and ecological restoration. By incorporating modern experimental techniques and linking results across environmental gradients with meta-analyses, studies of succession can substantially improve our understanding of other ecological phenomena. Succession can help predict changes in biodiversity and ecosystem services impacted by invasive species and climate change and guide manipulative responses to these disruptions by informing restoration efforts. Succession is still a critical, integrative concept that is central to ecology.

Succession is still a vital part of ecological studies

Succession, the sequential replacement of species following a disturbance (Box 1), has been a central theme throughout the 110 year history of ecology [2]. However, its lessons have not been adequately integrated into efforts to tackle modern environmental problems. Too often, succession is considered an esoteric study of plant dynamics on abandoned agricultural fields [5] or volcanoes [6,7]. In fact, succession provides a broad conceptual background to address most temporal dynamics of communities and ecosystems.

As humans adapt to a world that they increasingly modify, succession can aid in the prediction and interpretation of disturbance responses, including the novel ecosystems and successional trajectories that are now appearing. We outline four areas in which successional studies have an opportunity to develop a modern, interdisciplinary and effective approach to our altered world: biodiversity loss, climate change, invasive species, and restoration. Succession provides a framework in which to evaluate and predict the effects of these changes on altered rates or pathways of successional trajectories and losses of ecosystem services.

Succession was a pivotal concept in the early development of ecology [1,2,8] and has been studied with field observations based on chronosequences or long-term plots [9,10], experimental manipulations [11], and models [12-15]. Interest in succession as an organizing concept in ecology has been maintained in part because of the century-long but constructive debate (summarized in [2]) between those that argue that community assembly is predictable [16] versus those for whom it is perceived as being more random [17]. As evidence that this debate is not over, concepts originating in the early 1900s are currently being revisited and their relevance to succession re-examined. These concepts include facilitation [18,19], retrogression [4] and the use of chronosequences [9,10]. The questions of how species assemble into communities or how ecosystems change following a disturbance are still not fully resolved. Prediction of trajectories is still difficult, reminding us of Cowles’ [20] statement that succession “is a variable approaching a variable”. Despite the lack of a unified framework for the study of ecological succession, much progress has been made in successional theory. In addition, successional studies have undergone gradual but important methodological shifts that can help address current concerns in ecology. We present two such shifts (experimental manipulations of succession and meta-analyses of successional data across ecological gradients) and argue that they can help integrate successional studies with other fields.

Promising methodological approaches

The increased use and sophistication of experiments can elucidate the mechanisms driving succession. Experimental manipulations of abiotic factors, especially nutrients and moisture, have shown that vegetation reacts less stochastically than was often expected [21,22], although detailed predictions of vegetation change still remain elusive [23]. The manipulation of biotic factors by the introduction and removal of individual species or functional groups of species has shown the importance of interspecific interactions in determining successional trajectories [11,24,25]. Future experimental studies that conduct parallel experiments under different site conditions across gradients of abiotic and biotic variables [26] will improve our understanding of successional mechanisms, particularly when methods are standardized [27]. Understanding successional mechanisms helps clarify how they are modified by climate change and invasive species and how they impact biodiversity.

The recent development of meta-analyses has also aided our understanding of succession. These analyses consider data about temporal change across broad geographical
Successional stages and trajectories (Box 1) are considered components of succession, i.e., mechanisms, successional concepts but also improve predictability of successional changes because of climate change and invasive species. Successional stages and trajectories can occur spontaneously or be altered by various tools of conservation or restoration. In any case, successional changes should be observed by using properly designed, permanent research plots or other kinds of repeated sampling.

The four opportunities

**Biodiversity loss**

The first opportunity for successional studies stems from the justified concern about increased rates of reduction of species richness and local species extinctions, primarily through destruction and usurpation of habitat by humans and changing management in remaining habitats. Changes in biodiversity during succession have been evaluated in many studies, often demonstrating a peak in early but not initial stages of succession [2], suggesting the importance of early stages of succession for the maintenance of biodiversity [47]. Studies of succession can help focus on vulnerable species, determine their responses to disturbance, and indicate which life stages are most susceptible to local extirpation. Mechanisms responsible for the decline of biodiversity can be revealed by experiments that manipulate population fitness of the species [11,32]. Successional studies can also determine if populations of vulnerable species are sustainable, if their meta-populations are still functional, and thus predict future population dynamics [33,48]. On the community level, permanent plot research can reveal trends in biodiversity in habitats of concern [49]. Biodiversity can also be threatened by successional changes because of climate change and invasive species. Without repeated analyses of successional populations, either experimentally manipulated or not, changes in biodiversity, causes of species loss, and methods to restore them are difficult to determine.

**Climate change**

The second opportunity for succession is one of the biggest challenges for humanity: climate change. Succession can help address this challenge in several ways. Manipulative experiments, such as installation of open-top-chambers in

---

**Table 1. How studies of successional mechanisms, stages and trajectories (see Box 1) are related to other topics in contemporary ecology**

<table>
<thead>
<tr>
<th>Topic</th>
<th>Successional Links</th>
<th>Goals</th>
<th>Tools</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Biodiversity</strong></td>
<td>Mechanism</td>
<td>Stop competitive exclusion of rare and vulnerable species</td>
<td>Manipulative experiments</td>
<td>[11,32]</td>
</tr>
<tr>
<td>Stage</td>
<td>Keep most desirable stage</td>
<td>Conservation management</td>
<td>[33]</td>
<td></td>
</tr>
<tr>
<td>Trajectory</td>
<td>Reach most desirable stage</td>
<td>Restoration management</td>
<td>[34,35]</td>
<td></td>
</tr>
<tr>
<td><strong>Climate change</strong></td>
<td>Mechanism</td>
<td>Find how climatic factors determine competitive and facilitative relations among organisms</td>
<td>Manipulative experiments</td>
<td>[36]</td>
</tr>
<tr>
<td>Stage</td>
<td>Monitor vegetation change</td>
<td>Permanent plot network</td>
<td>[37,38]</td>
<td></td>
</tr>
<tr>
<td>Trajectory</td>
<td>Prediction of vegetation change</td>
<td>Scenarios based on permanent plot research</td>
<td>[39]</td>
<td></td>
</tr>
<tr>
<td><strong>Invasive species</strong></td>
<td>Mechanism</td>
<td>Avoid undue interference or facilitation</td>
<td>Experimental removals or additions</td>
<td>[40]</td>
</tr>
<tr>
<td>Stage</td>
<td>Preserve original sequence</td>
<td>Eradication or control of non-natives</td>
<td>[41,42]</td>
<td></td>
</tr>
<tr>
<td>Trajectory</td>
<td>Reduce occurrence of novel trajectories</td>
<td>Manipulation of succession</td>
<td>[43]</td>
<td></td>
</tr>
<tr>
<td><strong>Restoration</strong></td>
<td>Mechanism</td>
<td>Mimic natural mechanisms</td>
<td>Experimental manipulation of abiotic and biotic factors</td>
<td>[44-46]</td>
</tr>
<tr>
<td>Stage</td>
<td>Achieve and prolong desired stages</td>
<td>Conservation or restoration management</td>
<td>[2,35]</td>
<td></td>
</tr>
<tr>
<td>Trajectory</td>
<td>Restore original trajectory</td>
<td>Restoration projects</td>
<td>[2,35]</td>
<td></td>
</tr>
</tbody>
</table>
the field [36,50], can reveal mechanisms of community change. Long-term monitoring of permanent plots can elucidate how fast and in what ways organisms respond to climate change. A well-designed network of permanent plots could serve as an effective warning system, indicating changes in biodiversity or other ecosystem structure and functioning due to climate change. The National Ecological Observatory Network in the USA [37] and the Ecological Change Network in the UK [38] are designed to become such networks. Re-analysis of data collected for other purposes such as vegetation mapping, biomass analysis or soil sampling [51,52] can address climate change effects on population, community or ecosystem dynamics [53]. Climate change alterations of competitive and facilitative species interactions [18] can alter successional rates and trajectories as well as species composition of successional communities, providing support for the nonequilibrium view of succession [8]. As climate change effects on composition and successional trajectories accumulate, we are losing reference systems to compare to emerging novel communities [44]. Expanded studies of existing successional dynamics are therefore crucial.

**Invasive species**

The third opportunity for successional studies is provided by invasive species. Succession has often been radically altered by invasions of non-native organisms that initiate many changes in the impacted communities [54]. Incorporating...
ration of new species can create novel communities with new ecosystem properties [55]. Studies of succession can demonstrate the impact of non-native organisms on ecosystem structure and function and help to predict the community and ecosystem consequences of both their further spread and their eradication or control [43]. Mechanisms of succession, such as establishment dynamics, facilitation and competition (including inhibition) can be tested through studies of invasive organisms [54]. A particular question, having both theoretical and practical consequences, is which successional stages are susceptible to invasions [56] (i.e. when is the ‘invasion window’ open)? Studies of succession, either experimental or observational, might indicate threshold conditions when non-native organisms can start to invade. Non-native invasives might arrest or divert succession, thus initiating new successional pathways and increasing compositional divergence at broader scales but monopolizing space at smaller scales. One way in which novel or divergent pathways can occur is when the non-native invasive introduces a new function, such as nitrogen fixation [41,55]. Another alteration of successional pathways can occur when non-native invasive species decrease establishment of or outcompete existing native species, thus modifying turnover during succession [42]. Intriguingly, some species that are early successional but rather weak competitors in their native range become strong competitors in later stages of succession when they invade other ecosystems in their secondary range [57]. Experimental manipulations of succession are needed to explain which traits are responsible for such role changes. Establishment of successional dominants and non-native invasive species is probably based on similar mechanisms [58], and parallel sets of traits could be responsible for expansion of both native and non-native species. Among them, mass production of easily dispersed diaspores, extensive vegetative spread, fast growth, robust stature, and ecological plasticity can be considered. The link between succession and invasion could certainly be better exploited [59] to help interpret both processes.

Restoration ecology

Finally, successional studies have recently been challenged to address restoration that is essentially the manipulation of succession to generate a desired outcome. Restoration can be seen as an effort to initiate, accelerate, slow down, turn back, or mimic succession. Restoration can also attempt to recreate ecosystem services provided by successional communities. As the type and intensity of disturbances increase, so do the challenges of restoration. Therefore, better integration of these two disciplines is critical [60]. When properly documented, both successes and failures of practical restoration efforts can clarify successional mechanisms and lead to further development of theoretical concepts concerning succession [44], essentially providing a test of those theories [61]. In turn, successional theoretical concepts can guide future restoration activities by suggesting the most effective techniques and the best timing for manipulations to mimic natural successional mechanisms. However, we lack long-term data that can evaluate the success of a particular manipulation. Monitoring permanent plots in restored sites is a basic and effective tool [60]. Some information, including long-term data, is available on spontaneous succession, which can be used in restoration [2,60]. Minimal intervention and maximal reliance on spontaneous succession can be a successful approach (Box 2) when site conditions reflect intermediate productivity and stress [63], when desired species are present in a local species pool with vectors to transport them [64], and when non-native invasives are not a threat. Results of a detailed successional study in a particular habitat can be immediately exploited for local restoration projects [45], whereas comparative studies across habitats can enable extrapolation of the results and delineate limits of restoration efforts. As most ecosystems are now anthropogenically influenced, successional studies that are closely coupled to restoration activities will substantially increase the efficiency with which we manipulate ecosystems in the future.

Conclusion

Succession provides a conceptual framework in which to examine many ecological topics of immediate concern. Use of modern tools, such as experiments employed across resource gradients, meta-analyses of multi-site data sets, mathematical modeling, and expert systems, links studies of succession to a better understanding of the ecological implications of biodiversity loss, climate change, invasive species, and restoration. We can imagine a study that investigates succession after invasion of a non-native as a result of climate change that might be used to suggest restoration measures to protect local biodiversity. Thus, we are convinced that succession remains a central concept in ecology that makes critical contributions to understanding the implications of current environmental challenges.

Acknowledgments

K.P. was supported by the following grants: MSM 6007665801, AVOZ 60050516 and GACR P505-11-0256. L.R. W. was supported by the Department of Botany at the University of Hawai`i at Manoa through the Wilder Chair Program and the NSF-funded Luquillo Experimental Forest Long-term Ecological Research Program (grant DEB-0920910). We thank Marcel Rejmanek, Rob Marrs and anonymous reviewers for their valuable comments.

References

Opinion


23 Walker, L.R. et al. (2006) Plant characteristics are poor predictors of microsite colonization during the first two years of primary succession. *J. Veg. Sci.* 17, 397–406


42 Yurkonis, K.A. et al. (2005) Invasion impacts diversity through altered community dynamics. *J. Ecol.* 93, 1053–1061


