

ANNUAL MEETING

Can Nucleation Bridge to Desirable Alternative Stable States? Theory and Applications

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Can Nucleation Bridge to Desirable Alternative Stable States? Theory and Applications – A Review of the 2021 ESA Annual Meeting Symposium 8

Ecosystem recovery is full of wicked problems that result in nonlinear responses to management interventions. As the United Nation's call for a Decade on Ecosystem Restoration highlights, there is an urgent need to identify and address restoration barriers and enhance the efficacy of our restoration strategies in a rapidly changing world (United Nations 2019, Aronson et al. 2020, Fischer et al. 2021). Ecological nucleation is an emerging framework that shows promise as a restoration strategy across a variety of ecosystems. Unlike many other restoration strategies, ecological nucleation recognizes that many vital ecological interactions occur at the local scale and that these local interactions can be leveraged to initiate desirable landscape-scale changes in ecosystem structure and function. Past applications of ecological nucleation have used it as an analogy to describe the growth of recently established patches of the desired state, which can accelerate that state's spread (Yarranton and Morrison 1974, Corbin and Holl 2012, Hulvey et al. 2017, Shaw et al. 2020). More recently, autocatalytic nucleation has been more

Michaels, T. K., M. B. Eppinga, C. Angelini, K. D. Holl, and J. D. Bever. 2021. Can Nucleation Bridge to Desirable Alternative Stable States? Theory and Applications. *Bull Ecol Soc Am* 00(00):e01953. <https://doi.org/10.1002/bes2.1953>

strictly defined in ecology as the process by which a critical patch size of the desired state can lower resistance thresholds and catalyze rapid growth through local positive feedback dynamics (Michaels et al. 2020). In this way, nucleation leverages local-scale interactions to facilitate transitions between alternate stable states at the landscape scale. This symposium served as a conversation between architects of the ideas and practice underlying the notion of “nucleation.”

The goals of this symposium were to (1) provide a theoretical framework that compared the key mechanisms often associated with nucleation or nucleation-like processes, (2) demonstrate how the principle of nucleation can be leveraged to promote ecological recovery in a variety of systems, and (3) promote discussion about future research needs. This symposium, moderated by Dr. James D. Bever from the University of Kansas, brought together Dr. Maarten B. Eppinga (University of Zurich, Switzerland), Dr. Karen D. Holl (University of California, Santa Cruz), Dr. Christine Angelini (University of Florida), and PhD candidate Theo K. Michaels (University of Kansas). We provide brief summaries of the individual presentations and then summarize the conversation on future research directions, the potential for nucleation to address restoration needs, and the challenges of integrating nucleation into restoration practices.

Presentation Summaries

Models of nucleation and nucleation-like processes

Maarten Eppinga noted that a variety of mechanisms have been proposed in the literature that potentially cause introduced patches to become nuclei from which desired ecosystem properties can be re-introduced and propagated throughout the landscape. The presentation focused specifically on three of these mechanisms: autocatalytic nucleation (defined above, Michaels et al. 2020), directed dispersal, and resource concentration. Here, directed dispersal refers to patches of trees and shrubs increasing the local seed rain, by attracting dispersers in the surrounding landscape toward these patches (Cole et al. 2010, Caughlin et al. 2016, Holl et al. 2020). Resource concentration refers to organisms within a patch harvesting resources from their surroundings, improving growth conditions within the patch at the expense of resource availability at larger spatial scales (Rietkerk et al. 2004, Rietkerk and van de Koppel 2008). The three mechanisms were included in a theoretical model framework that could show how the occurrence of each mechanism is reflected in spatiotemporal patch dynamics of an ecosystem. Eppinga linked these theoretical results of spatiotemporal patch dynamics to ecosystem restoration and analyzed the implications of observed patch dynamics for the optimal design of restoration strategies.

The main finding was that qualitative differences in spatiotemporal patch dynamics depended on which of the three mechanisms was driving these dynamics. Specifically, Eppinga showed that patch expansion accelerated over time when driven by the autocatalytic nucleation mechanism, whereas patch expansion decelerated over time when driven by directed dispersal or resource concentration. While patch expansion was independent of patch position in the landscape when driven by autocatalytic nucleation, proximity of other patches affected patch expansion either positively or negatively when driven by directed dispersal or resource concentration. From these differences among the three mechanisms, several implications for ecosystem restoration could be inferred. For example, the model results suggested that introducing a single large patch was the most effective

restoration strategy to initiate the directed dispersal mechanism, whereas introducing many small patches was most effective to reach a restored ecosystem state when driven by resource concentration. For autocatalytic nucleation, many small patches were also a favorable strategy, provided that each individual patch exceeded a critical patch size. As discussed during the symposium, these hypotheses create opportunities for the testing of nucleation theory in future empirical studies. In addition, ideas were exchanged about additional modeling scenarios that could be considered within the presented framework.

Test of autocatalytic nucleation in tallgrass prairie restoration

Theo Michaels shared early findings from her research that utilizes nucleation to explore restoration in tallgrass prairie systems. Her research employs the stricter definition of nucleation (Michaels et al. 2020) and as such, tests for local scale positive feedback and the patch size needed to generate an autocatalytic nucleation event. Michaels shared how tallgrass prairies are a model system for testing these principles of nucleation, as the transition from dominance of early- to dominance of late-successional prairie plant species is governed by positive plant-soil feedback generated by dynamics of beneficial arbuscular mycorrhizal (AM) fungi (Koziol and Bever 2019). Following the large-scale agricultural disturbance, post-agricultural fields often remain stuck in early successional stages of tallgrass prairie recovery and are often resistant to the reestablishment of late-successional native plant species because of the disruption of the mutualisms between late-successional species and AM fungi (Middleton and Bever 2012, Koziol and Bever 2017, House and Bever 2018).

Michaels detailed an experimental design that sought to test whether plant-AM fungi relationships of late-successional prairie patches could generate the local feedback dynamics necessary for nucleation. Remnant prairie patches were transplanted in small-, medium-, and large-patch sizes into three recipient sites that differed in their post-agricultural histories. To detect the presence and spread of local positive feedback, she planted sterile test plants from the same plant family but that differed in successional status and AM fungal dependence. Plants were planted inside, adjacent to, and four meters from the patches, and survival and fitness were measured over three years. Michaels and colleagues found evidence for local positive feedback based on test plant response at the patch edge. They also found evidence that suggests that when a critical patch size is met, patch configuration, specifically dispersed patches, may be important in leveraging additional benefits of nucleation. Lastly, they reported that recipient site characteristics can modify these results. Michaels' talk underscored the ways in which mechanisms and patch size dynamics could be tested to enhance our understanding of nucleation dynamics. With this, Michaels also shared ways to bridge theory to practices, suggesting restoration strategies could include late-successional plant species inoculated with their fungal partners clustered in a critical-patch size.

Mechanisms of patch survival and spread in salt marshes

Christine Angelini focused on the factors controlling patch dynamics in coastal salt marshes of the southeastern United States. She noted that these intertidal grasslands exhibit nucleation dynamics, highlighting that system recovery hinges on clonal expansion of surviving cordgrass patches after disturbance events (Angelini et al. 2016). Despite the evidence that patch dynamics govern the resilience of the desired state in this system (Angelini and Silliman 2012), relatively little is known about the

mechanisms controlling patch survival and expansion rate, or whether such mechanisms shift in relative importance of disturbance type. Angelini shared findings from several studies that illuminate our mechanistic understanding of nucleation dynamics in salt marsh systems.

The first experiment focused on determining the relative importance of mutualistic partners in mediating cordgrass patch survival and expansion under drought-generated die-back events. Angelini and colleagues found that the ribbed mussel, *Geukensia demissa*, functions as “keystone” mutualist in drought-stricken salt marshes by promoting cordgrass survival and patch expansion through fertilization. Numerical simulations highlighted that, by forming stress-resistance nuclei for cordgrass clonal expansion within die-off areas, mussels dramatically accelerate recovery from drought (Angelini et al. 2016). These findings were then tested in the field. Cordgrass was planted with and without mussel mutualists and then subjected to disturbance in which plants aboveground were removed. This two-year experimental study revealed that mussels dramatically increased cordgrass survival and shoot production after disturbance (Derksen-Hooijberg et al. 2017). These studies demonstrated a key nucleation principle: resilience of salt marshes to drought and other disturbances depends on the local positive feedback generated here by the cordgrass-mussel mutualism. Angelini concluded her presentation by summarizing another field experiment that explored the interaction between nucleation dynamics and disturbance type. This study focused on disturbance created by invasive feral hogs (*Sus scrofa*), which can intensively disrupt the soil and give rise to anoxic, waterlogged soil conditions. In the context of these hog-generated disturbances, nucleation dynamics are dramatically stifled; in essence, surviving cordgrass patches failed to spread (Sharp and Angelini 2016). She noted that disturbances which disrupt local positive feedback dynamics in the system may pose a specific challenge to the utility of nucleation, so disturbance type is a key consideration when characterizing nucleation dynamics.

Applied nucleation in tropical forests

Karen Holl discussed research on applied nucleation (i.e., planting patches or nuclei of trees) and other spatially patterned (Shaw et al. 2020) planting methods (e.g., planting in strips) as more promising methods to accelerate forest succession and create more heterogeneous habitat than standard, plantation-style tree planting approaches. She summarized key lessons learned from the long-term, well-replicated applied nucleation study that she, Dr. Rakan Zahawi, and many other collaborators have been conducting in southern Costa Rica. Their results indicate that applied nucleation and plantation restoration strategies are similarly effective in enhancing the recovery of most floral and faunal groups, vegetation structure, and ecosystem functions, as compared to natural regeneration (Holl et al. 2020). Nonetheless, after 17 yr of recovery, the species composition in restoration treatments still differs substantially from reference forest. Larger tree nuclei more effectively attract faunal seed-dispersers and shade out grasses (Fink et al. 2009, Holl et al. 2020). The applied nucleation strategy is cheaper than mixed-species tree plantations, but there may be social obstacles to implementing this technique in agricultural landscapes, such as perceptions that the land is not being used productively (Zahawi et al. 2014).

Holl also discussed more recent collaborative experiments to scale up spatially patterned planting methods to meet the many ambitious international forest restoration commitments. She and Dr. Pedro

Brancalion are testing both applied nucleation and strip planting in the Brazilian Atlantic forests; initial results suggest that strip planting has similar benefits to applied nucleation in facilitating recovery and creating habitat heterogeneity, while being more practical and cheaper to implement using machinery. Furthermore, interplanting strips of native species with fast-growing Eucalypts, which are logged after 5–7 yr, are local; however can achieve comparable ecological outcomes and help offset restoration costs (Brancalion et al. 2020). She also mentioned work with collaborators at Conservation International to create an applied nucleation guide for restoration practitioners (Wilson et al. 2021) and examples of restoration projects in both the Brazilian Amazon and Atlantic forest regions that are applying spatially patterned planting methods in larger-scale restoration projects.

Lessons Learned and Future Directions

Nucleation provides a useful lens through which to view ecological theories. Alternative stable states are a common feature of many ecological systems and are frequently identified as a potential problem for restoration because of the concern that a system may be trapped in a degraded state. For systems in which interactions are local, however, autocatalytic nucleation theory identifies that transitions between alternative states can be facilitated by spatial processes, potentially effectively reducing the region of hysteresis (Michaels et al. 2020). Because most ecological systems might be thought of as “local” at some scale, a general question for theoretical ecology discussed in the symposium is whether inference from mean-field models has overstated the problem of alternative stable states. An overall challenge of systems with positive feedback and alternative stable states is to understand the spatial dependence of the resulting dynamic. This, in turn, will govern the critical patch size to initiate nucleation and therefore will determine the feasibility of applications of this approach.

Advancing our understanding of nucleation for the benefit of restoration depends on vital connections between theory and application. This symposium highlighted the importance of recognizing differences in the mechanistic drivers governing patch dynamics across a variety of systems, as they influence context-dependence of the benefits of initiation of patches of desirable states in restoration. Testing nucleation principles for restoration, such as the optimal nuclei size, distance, and species composition, can be challenging, given constraints on conducting large-scale, replicated field experiments. Theoretical models may allow us to advance our understanding of nucleation by exploring patch size and feedback strength in a variety of ecosystems, illuminating the effects of patch spacing, and creating targeted restoration scenarios that could be put into practice. Integrating these model results into an application could enhance our understanding of how interactions between local positive feedback and disturbance characteristics of the degraded state influence nucleation dynamics. Finally, expanding the utility of nucleation requires testing the feasibility of implementing nucleation methods, which may require finding innovative ways of adapting nucleation principles to the needs of restoration practitioners and landholders. This symposium illustrated the utility of nucleation as a conceptual and practical approach to meeting the challenges of ecosystem recovery.

Open Research

No data were collected for this study.

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