© 2020 The Authors. The *Bulletin of the Ecological Society of America*, published by Wiley Periodicals, Inc., on behalf of the Ecological Society of America. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.



Meeting Reviews

Review of the Symposium Determinism and Stochasticity in Ecological Succession in ESA-Louisville, 2019

Sergio Estrada-Villegas[1,2], Niv DeMalach[3], Miguel Martinez Ramos[4], Laura M. Ladwig[5], Scott J. Meiners[6], Leland K. Werden[7], and Stefan A. Schnitzer[1,2]

[1]Department of Biological Sciences, Marquette University, P.O. Box 1881, Milwaukee, Wisconsin 53201 USA

[2]Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panama City, Panama

[3]Department of Biology, Stanford University, Stanford, California 94305 USA

[4]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Autónoma de México, Morelia, Michoacan 58190 Mexico

[5]Department of Integrative Biology, University of Wisconsin – Madison, Madison, Wisconsin 53706 USA

[6]Department of Biological Sciences, Eastern Illinois University, Charleston, Illinois 61920 USA

[7]Lyon Arboretum, University of Hawai'i at Mānoa, Honolulu, Hawaii 96822 USA

A central and recurrent discussion in ecology is how deterministic and stochastic processes dictate how communities assemble after severe disturbances. It is thought that deterministic processes hinge on biotic interactions and species-specific responses to the environment. By contrast, stochastic processes rely on random dispersal and colonization, as well as historical contingencies (e.g., previous land use, priority effects) and unforeseeable or rare severe weather events. Both determinism and stochasticity likely influence ecological succession; however, revealing the relative importance of these two processes remains elusive. Furthermore, the relative importance of these two processes is likely context-dependent; however, the role of context dependency is poorly understood. The symposium "Determinism and Stochasticity in Ecological Succession" gathered a diverse group of ecologists during the 2019 ESA conference in Louisville, Kentucky, to address this important yet unresolved topic. The symposium

Estrada-Villegas, S., N. DeMalach, M. Martinez Ramos, L. M. Ladwig, S. J. Meiners, L. K. Werden, and S. A. Schnitzer. 2020. Review of the Symposium Determinism and Stochasticity in Ecological Succession in ESA-Louisville, 2019. Bull Ecol Soc Am 101(3):e01687. https://doi.org/10.1002/bes2.1687

focused on how different deterministic and stochastic processes influence ecological succession in different ecosystems around the world, and addressed the relative contribution of determinism and stochasticity in a variety of ecological contexts.

Niv DeMalach from Stanford University began the symposium by presenting a simulation model describing competitive interactions between annual and perennial plants. The goal of the model was to predict when competitive interactions are deterministic and when stochastic initial conditions affect the final competitive outcomes (i.e., priority effects). Community dynamics were studied at various timescales to determine the presence of alternative stable states, which produce multiple equilibria, and long-term transient dynamics produced by long-term priority effects despite ultimate convergence to a single equilibrium. The simulations demonstrate that alternative stable states require similar lifetime fecundity of both species and better competitive ability of the annuals over perennial seedlings. By contrast, long-lasting transient dynamics require only similar lifetime fecundity among the species and occur in wide parameter space. In other words, even when succession has a deterministic endpoint (given enough time without disturbance), stochastic trajectories could govern the community dynamics for decades.

Sergio Estrada-Villegas from Marquette University showed that the relative importance of determinism and stochasticity changes between the levels of ecological hierarchy. Specifically, he showed that community- and ecosystem-level properties were differentially affected by edaphic factors and forest cover. He reported that during a seven-year period on 22 early successional tropical dry forest plots, the species composition of trees and lianas converged, indicating a deterministic change over time. The convergence in tree community composition was positively and significantly affected by forest cover, suggesting a strong effect of initial floristic composition. The convergence in liana community composition was positively and significantly influenced by edaphic factors, especially topography. These findings suggest that several liana species prefer wind-exposed areas that have low soil water content. Furthermore, tree biomass converged over time as forests aged, and it was positively affected by edaphic factors, especially soil fertility, implying that fertility can have a determinist effect on tree biomass accumulation. By contrast, liana biomass did not converge, regardless of forest cover or edaphic factors suggesting that liana biomass might be more regulated by stochastic processes than trees. Sergio's work highlighted the need to recognize that different levels of ecological hierarchy may be deterministic while others stochastic. Moreover, it demonstrated that different drivers had a differential effect on the convergence of community- or ecosystem-level properties, and that not all life forms respond in the same manner to the same drivers (Estrada-Villegas et al. 2019).

The third talk was by Scott J. Meiners from Eastern Illinois University, who examined the interplay between deterministic and stochastic drivers during the invasion of nonnative species into a temperate old-field succession. He used data prior to the invasion to evaluate the causes that enhanced plant invasion, and used data after the invasion to determine the impact of the invasion. The talk focused on two interesting examples. In the first, the invasive liana *Lonicera japonica* was dispersed and colonized successfully into plots with higher species richness and where two herbaceous species (*Symphyotrichum pilosum* and *Luecanthemum vulgare*) were dominant. In the second example, the establishment of the invasive grass *Microstegium vimineum* was more successful in plots with higher species richness and higher understory cover. Both examples illustrated that dispersal, a stochastic process, can be regulated by species richness, the identity of the dominant species, and resident plant cover. Both invasions reduced the species richness in the plots, suggesting that the context prior to the invasion can have a

determinist effect after the invasion. However, there was a tendency for richer plots to suffer higher probability of invasion and greater species loss after invasion (S. V. Janis and S. J. Meiners, *unpublished manuscript*).

Miguel Martínez-Ramos, from the Universidad Nacional Autónoma de México, explored how the stochasticity of secondary forest succession in tropical rainforests could be associated with interannual climate variability. Miguel studied two sites: one in a lowland tropical moist forest in southeast Mexico and another in a lowland tropical dry forest in western Mexico. At the moist forest site, rainfall variability in the dry season can change up to 20-fold (17–342 mm between February and April), and it was expected to have important potential consequences in the tree community successional dynamics. Miguel used 18 years of continuous census data from early successional forest plots (<18 years of fallow age) to examine the effect of interannual rainfall on annual rates of change in plant density, recruitment, and mortality. As expected, recruitment increased in years with higher rainfall. Unexpectedly, mortality rates showed a positive relationship with annual rainfall. In rainy years, less light resources are available for plants, and natural enemies such as herbivores and pathogens might increase mortality. However, the interannual rainfall explained less than 18% of the variation in the rates of change in the community. Fallow age, in contrast, had a higher predictive and deterministic effect because it explained 20–50% of the temporal variation in community dynamics. For these moist forest plots, climatic variability can only partially explain the stochastic trajectories of early successional forests. Other unaccounted factors, such as plant–plant interactions and natural enemies, might have a more important role on successional trajectories (Van Breugel et al. 2012). In comparison with the moist sites in southeast Mexico, a study conducted in a strongly seasonal tropical dry forest in western Mexico showed that interannual rainfall variation had a significant predictive effect on annual rates of community change. Between 29% and 45% of the annual rates of community change were explained by interannual rainfall variation, while fallow age did not have any influence (Martínez-Ramos et al. 2018). More studies are needed to test a hypothetical deterministic effect of climate variability on tropical forest succession, which should increase from wet to dry environments.

The fifth talk was by Leland K. Werden, a postdoctoral associate at the University of Hawai'i at Mānoa, who examined how seed-to-seedling transitions of tropical trees might be influenced by restoration treatments, canopy cover, and species' life-history traits. While seed-to-seedling transitions in old-growth forest are commonly driven by deterministic factors (e.g., seed mass), it is unclear what factors have the greatest influence on seed-to-seedling transitions in regenerating tropical forests. Leland used a 3.5-year record of seed rain and seedling recruitment to examine limitations on tree recruitment for 43 premontane tropical forest species. He determined how seed-to-seedling transitions varied across passive (natural regeneration) and active restoration treatments (applied nucleation and tree plantations) after a decade of recovery. He showed a gradient in which seed-to-seedling transition rates were higher across all restoration treatments than in minimally disturbed remnant forests. This result implies a transition from seed limitation, related to stochastic factors at early successional stages, to deterministic factors related to niche requirements at later successional stages. Moreover, large animal-dispersed seeds showed higher transition rates, consistent with the idea that seed mass can be a deterministic factor of plant recruitment. Overall, his results showed that accelerating canopy formation via applied nucleation or tree plantations becomes a determinist factor during succession as these approaches can accelerate seed dispersal to sites, and improve seed-to-seedling transitions for larger-seeded species (L. K. Werden et al., *unpublished manuscript*).

The final talk of the symposium was by Laura M. Ladwig, a postdoctoral associate from University of Wisconsin, Madison. She showed how changes in the disturbance regime and climate change can create a deterministic shift from temperate prairies and savannas to temperate forests. Laura and colleagues revisited 50 prairie and savanna sites that were originally surveyed in the 1950s to examine the effect of fire suppression and climate change on community composition and species persistence. They found that land management history can have a strong determinist effect on prairies and savannas. Specifically, when fires were absent and grazers excluded, many prairies and savannas became closed-canopy woodlands (Ladwig et al. 2018). The probability of extinction increased fourfold for prairie species when fires were completely absent or infrequent over the past 60 years. Laura emphasized that the synergistic effect of fire suppression and climate change has produced a deterministic shift between temperate ecosystems.

Following the talks, the panel of speakers and the audience participated in a roundtable discussion, where we exchanged different ideas about the theme of the symposium, as well as discussed how to move the field forward. One of the topics was the current disagreement on terminology, and how discrepancies confuse the field. For example, the term stochasticity can have multiple interpretations, and how to model stochasticity in the study of ecological succession can be a contentious issue. Most of the attendees suggested that seed dispersal was a paradigmatic example of a stochastic process. Several speakers cited Vellend et al. (2014) arguing that seed dispersal could be considered stochastic because it can be stochastic with respect to the species bearing fruit in a community. Dispersal can also be considered stochastic because the location of where the seed will be dispersed is indeterminate or very hard to predict, particularly with respect to the species-appropriate edaphic conditions. However, general spatial patterns of seed dispersal can be predictable, leading some to argue that dispersal should not be considered stochastic. Similarly, divergence among communities across time could be related to demographic stochasticity if the changes in abundance are random with respect to species identity.

Members of the audience suggested that different types of noise (white or pink) could be added as a factor to emulate stochasticity when analyzing short time series, and determine the contribution of stochasticity in the changes in trajectories through time. Other members of the audience reminded the attendees that methods that compare the direction and magnitude of trajectory vectors could also help describe unpredictability and perhaps stochasticity among successional trajectories (Fulton and Harcombe 2002). Yet, discrepancies in defining stochasticity remained. Terms such as stochastic, neutral, random, divergent, and unpredictable are often used interchangeably, and the subtle similarities and differences among these concepts are often confused. For example, if an event is probabilistic, does it become predictable and therefore not stochastic? If that is the case, stochastic and random might share the same meaning. The panel and the audience agreed that a review of such concepts and delimiting the boundaries among them would provide a great service to the field. The recent and timely contribution by Shoemaker et al. (2019) addresses some of the concerns of our discussion and provides clarity for some of the concepts we examined.

Another interesting discussion was related to alternative stable states. Some of the attendees view alternative stable states as deterministic because once initial conditions are known, the outcome is predictable. By contrast, other attendees and some panelists suggested that initial conditions can be deeply affected by random colonization processes, and are therefore stochastic. If the initial conditions are stochastic, the direction and outcome of successional trajectories might be less predictable, and the array

of alternative stable states is less deterministic. Two of the presentations in this symposium (DeMalach and Estrada-Villegas) illustrated this point.

Another topic of conversation was the interrelationship between stochastic and determinist processes. As Scott Meiners stated, "stochastic processes become the context for deterministic processes and vice versa as successional dynamics proceed." This issue can be either practical or philosophical. Practical in the sense was that we just need to evaluate the deterministic consequences of a stochastic event or process. For example, the dispersal and colonization of an invasive species into a plot (Meiners), or the occurrence of a severe drought event, are usually considered stochastic events (Martínez-Ramos). These two processes/events create determinist and tractable processes such as the reduction in species richness or biomass after the colonization of the invasive species, or the increase in mortality that follows a severe drought. Another practical consideration is related to spatial scales; at larger spatial scales, communities tend to show convergent trajectories and modulated by deterministic factors such as land management (Ladwig). At smaller spatial scales, trajectories tend to show divergent trajectories and modulated by stochastic factors such as dispersal or mortality (Werden and Martínez Ramos). However, the switch from stochastic to deterministic is also a philosophical issue because it depends on our capacity to find an ultimate state/cause that might render the stochastic process a determinist process. For example, predicting the occurrence and spatial extent of a severe drought can provide reliable estimates of future mortality, or accurately predicting seed dispersal can provide reliable estimates of recruitment. In a sense, stochasticity is partially a problem of unaccounted variables (Clark 2009) that can be resolved once we have a statistical distribution around a mean probability of the event or process of interest.

This symposium illustrated that the relative importance of stochastic and deterministic processes in succession is context-dependent. Each study in the symposium exemplified a different dimension of contingencies; some studies showed that stochastic and deterministic processes depend on the community property, the life form, and the spatial scale under consideration. Short-term trends appear to be more stochastic, whereas long-term trends appear more deterministic. The conversation that followed highlighted ongoing concerns that have been in the field of ecology for decades. However, this symposium demonstrated that the predictable changes in communities during succession can be understood when ample information about determinist and stochastic processes is identified and incorporated in the sampling designs or in the modeling process. The field of ecology will continue to advance from one of its oldest topics of interest, and the discussion between deterministic and stochastic processes in ecological succession is yet to be concluded.

Literature Cited

Clark, J. S. 2009. Beyond neutral science. Trends in Ecology & Evolution 24:8–15.

Estrada-Villegas, S., M. Bailón, J. S. Hall, S. A. Schnitzer, B. L. Turner, T. Caughlin, and M. van Breugel. 2019. Edaphic factors and initial conditions influence successional trajectories of early regenerating tropical dry forests. Journal of Ecology 180:160–174.

Fulton, M. R., and P. A. Harcombe. 2002. Fine-scale predictability of forest community dynamics. Ecology 83:1204–1208.

Ladwig, L. M., E. I. Damschen, and D. A. Rogers. 2018. Sixty years of community change in the prairie-savanna-forest mosaic in Wisconsin. Ecology and Evolution 8:8458–8466.

Martínez-Ramos, M., P. Balvanera, L. F. Arreola, F. Mora, M. Maass, and S. Maza-Villalobos Méndez. 2018. Effects of long-term inter-annual rainfall variation on the dynamics of regenerative communities during the old-field succession of a Neotropical dry forest. Forest Ecology and Management 426:91–100.

Shoemaker, L. G., et al. 2019. Integrating the underlying structure of stochasticity into community ecology. Ecology 101: e02922.

Van Breugel, M., P. van Breugel, P. A. Jansen, M. Martínez-Ramos, and F. Bongers. 2012. The relative importance of above- versus belowground competition for tree growth during early succession of a tropical moist forest. Plant Ecology 213:25–34.

Vellend, M., et al. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. Oikos 123:1420–1430.