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RESEARCH HIGHLIGHTS

Community form, function and phylogenetic diversity respond differently across microhabitat and recovery gradients

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Abstract

Research Highlight: Hoenle, P. O., Staab, M., Donoso, D. A., Argoti, A., & Blüthgen, N. (2023). Stratification and recovery time jointly shape ant functional reassembly in a neotropical forest. *Journal of Animal Ecology*, https://doi.org/10.1111/1365-2656.13896. Space, time and abiotic variation are primary axes across investigations of community ecology and disturbed ecosystems offer tractable systems for assessing their relative impact. While recovering forests can act as isolated case studies in understanding community assembly, it is not well understood how individual microhabitats respond to recovery and ultimately shape community attributes. Hoenle et al. (2023) leverage the ubiquity and microhabitat-specific diversity of ants across a gradient from active agricultural sites to old-growth forest and assess how recovery and stratification together shape communities. The authors find distinct stratification across phylogenetic, functional and trait diversity as forest recovery time increases, while also recovering unique recovery trajectories contingent on trait sampling. While stratified, phylogenetic and functional diversity did not increase along this recovery gradient. Ten out of 13 sampled traits were jointly influenced by both stratification and recovery time. In contrast to intuitive predictions, a majority of trait means converged throughout the recovery period. Results highlight the multifaceted nature of recovery-based community assembly and the capacity of multidimensional sampling to uncover surprising patterns in ecologically diverse lineages.

KEYWORDS
ants, functional traits, microhabitat, recovery, stratification, trait-based ecology

How do communities assemble over time? Answers to this foundational question are fundamentally multifaceted in nature and so assembly is well illuminated by multivariate perspectives (Weiher et al., 2011). Investigations of community assembly that couple both dynamic ecosystems and ecologically diverse organisms may reveal important nuances that are otherwise difficult to discern. Disturbed and recovering agricultural ecosystems are pervasive and provide innate spatiotemporal variability while space and time are frequent primary axes across investigations of community ecology. These dynamic spatial settings have therefore revealed key processes governing how species composition changes over time (Cramer et al., 2008). Ants are a ubiquitous component of both disturbed and undisturbed terrestrial habitats, evidenced by their frequent use as biodiversity indicators in land management (Majer et al., 2007). The phylogenetic, ecological and morphological diversity of ants (Hölldobler & Wilson, 1990) further allows for increased resolution in elucidating fine-scale variation across study sites as many species are obligate specialists of microhabitat strata.

Hoenle et al. (2023) effectively leverage the diversity of their study critters, ants, and inherent variation in disturbed forests to provide a fresh view of community assembly in all of its complicated glory. The authors assessed micro-habitat community composition across a three-decade long recovery gradient and nearly 250 ant species. There are three factors at play in the work: (i) Diversity: species-, trait- and phylogeny-level diversity of sampled ant communities; (ii) Recovery: a sample series spanning agricultural land, recovering forest plots and old-growth forests; and (iii) Microhabitat: three distinct strata from leaf litter to trees that tend to yield distinct ant fauna. The authors couch their work as simultaneously evaluating how recovery and stratification both might act as environmental filters that shape community assembly. While sometimes used more strictly to refer to only abiotic influences (Kraft et al., 2015), here the term environmental filtering is less focused on contributory process but instead on observable pattern. The authors found most traits were influenced by both microhabitat and recovery time, while each microhabitat stratum exhibited distinct patterns of diversity for a majority of functional traits. Even as trait means differed along a recovery gradient, patterns of change were unique to strata and means unexpectedly became more similar with increasing forest recovery time. Surprisingly, functional and phylogenetic diversity did not appear to increase with recovery time, complicating an otherwise intuitive prediction that aspects of diversity might increase as ecosystems recover. Taken together, the results underscore the multidimensional nature of community assembly and sensitivity of pattern recovery to sample scale.

Trait-based ecology is well-suited to the detection of community shifts in the context of disturbed habitat (Mouillot et al., 2013). Hoenle et al. (2023) employ a primarily trait-based approach along a disturbance gradient rendered as recovery time. The authors undertook a tripartite sampling approach at field sites comprising current pastures and cacao plantations, former agricultural land abandoned 1–34 years before sampling, and old-growth forest with no known human disturbance (Hoenle et al., 2022). At each locality, three microhabitat subsamples were captured by well-defined collecting regimes across leaf litter, ground and tree trunk strata (Agosti et al., 2000). For collected species, the authors measured morphological traits suspected to correlate to ecology (Parr et al., 2017); these ranged from captures of body shape and mouthpart morphology to cuticle colour and spinosity. Trait- and community-level data were distilled into stratum-specific trajectories (via linear mixed-effects models) across rank-transformed axis of recovery from present-day agricultural land to old-growth forests. The authors formulated, tested and found at least limited trait-dependent support for each of three hypotheses describing the relationship between microhabitat strata and recovery time: a strict stratification pattern defined by unique stratum-specific trait means or community indices unimpacted by recovery time; a recovery pattern in which trait means or community indices were unique to each stratum but changed over recovery time in a similar direction; and an interaction hypothesis in which each stratum exhibited a unique trajectory, either converging on the same trait- or community-level mean or diverging away from any one central mean. A strict pattern of stratification was recovered only for head width, a trait with wide variability due to a range of ecological and phylogenetic factors (Kaspari & Weiser, 1999). Two traits were consistent with hypothesized recovery trajectories, while a clear majority of traits—eight ranging from body size to cuticle colour—exhibited a pattern of interaction, most converging on a uniform mean (Figure 1).

In some ecosystems, as many as 75% of ant species may only be reliably sampled in one microhabitat strata (Brühl et al., 1998). Species within strata are often highly specialized; extreme examples include certain species of arboreal ant that are incapable of walking on solid ground (Khalife et al., 2018) while workers of some leaf litter dwelling taxa may be entirely eyeless (Weiser &

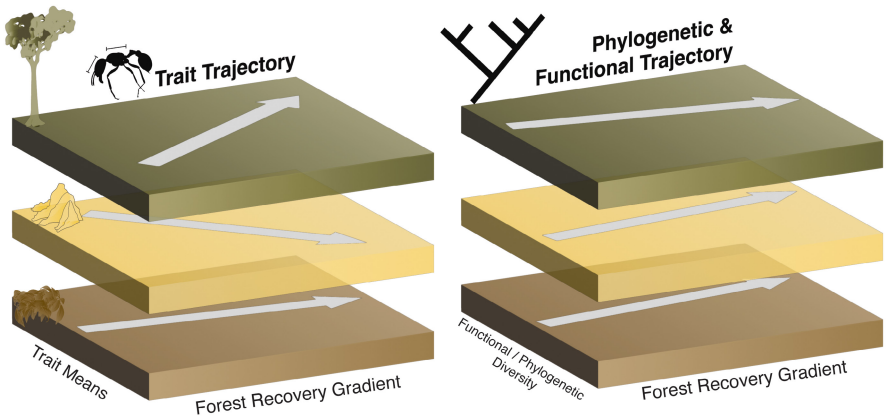

FIGURE 1 Responses of trait and community attributes across recovery and microhabitat gradients. Simplified trajectories in response to forest recovery across three distinct vertical strata, in order from top to bottom: tree-trunk, epigaeic/ground and leaf litter sampling. Forest recovery gradient spanned present-day cacao plantations and pastures, a range of abandoned agricultural plots ranging from 1 to 34 years in age, and old-growth forest. (Left) Idealized trajectories for a hypothetical trait exhibiting distinct trajectories across strata. Hoenle et al. (2023) captured 13 morphological measurements, eight of which exhibited unique trajectories within strata (Right) Simplified depiction of phylogenetic and functional diversity trajectories, neither community-level attribute increased over recovery time. Tree, rock and leaf silhouettes modified from Tracey Saxby, Integration and Application Network (http://ian.umces.edu/media-library).

Kaspari, 2006). That each stratum sampled by Hoenle et al. (2023) contains a unique community recovered through the lens of trait means is perhaps not surprising. What is particularly surprising, however, is that most trait means became more similar over this powerful recovery gradient. In ants as in other lineages, generalist taxa may be more common in disturbed habitats (Fotso Kuate et al., 2015). Because specialists tend to occupy distinct morphospace relative to more generalist taxa (Sosiak & Barden, 2021), it would be reasonable to predict that functional diversity should increase as an ecosystem recovers. Ants are also specifically sensitive to the particular disturbance surveyed by Hoenle et al. (2023); habitat openness is a primary driver of variation in some disturbed ant communities (Andersen, 2019; Ibarra-Isassi et al., 2021), and a slight majority of sampled sites relate to current or recovering pasture land. How could strata become more functionally similar as forests recover? Hoenle et al. (2023) suggest that functional redundancy may be responsible; however, there is yet no direct insight into this mystery. As other recent work suggests that certain community-level attributes recover within stratified timescales that may differ by as long as a century (Poorter et al., 2021), it appears to be important to consider each metric, sample size and temporal perspective carefully.

How do communities assemble over time? In short, it is complicated. When reading this paper, it is easy to imagine how the loss of any one axis, say, by grouping all strata into one community sample, would obfuscate the more interesting patterns here. This is true for microhabitat sampling as well as trait selection. Community-level attributes surveyed here such as species richness support results of previous work (Marques et al., 2017); however, the inclusion of trait-specific trajectories uncovered a suite of new, and complex, patterns. There are myriad opportunities for incorporating recovery time into evaluations of community assembly. Forests are regularly converted to new agricultural land (Gibbs et al., 2010) and are also increasingly abandoned or actively restored (Lambin & Meyfroidt, 2011). It may not be surprising that individual strata exhibit distinct recovery patterns, however, as additional taxa are viewed through the lens of stratification, it seems likely that more community-level surprises are in store.

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CONFLICT OF INTEREST STATEMENT

The author has no conflict of interest to declare.

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