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COMMENTARY

Successional convergence, stochastic assembly and the future of tropical forests

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Abstract

In this issue of the *Journal of Vegetation Science*, Dent et al. take advantage of a century-long chronosequence of forest succession in central Panama, and highlight a lack of convergence to the tree composition of old-growth stands. Does this suggest tropical forests assemble randomly, or is this an expected consequence of high diversity and patchy recruitment?

Fig. 1. Forest regrowth in the Canal Watershed of central Panama (Credit: D. Dent).

Humans tend to 'patchify' landscapes, creating islands of habitat that together operate as metacommunities – that is, a network of communities linked to similar habitats by dispersal and continually at risk of 'extinction' or conversion into new habitat (Hanski et al. 1995). As long as suitable habitat is available and species can move between patches, temporary habitat loss need not drive widespread extinction, or so the theory goes (e.g. Perfecto & Vandermeer 2010). For example, forest habitats in eastern North America have experienced over the past 400 yr very few extinctions despite massive reductions in area from European settlement that peaked in the 19th century, in part because forest losses were not coincident or permanent (Pimm & Askins 1995). Would the same reasoning suggest that widespread tropical species extinctions could be avoided if deforestation is coincident with adjacent forest regrowth?

A key component to this question, as posed by Dent et al. (2013) in this issue, is whether regrown forests resemble today's primary forests, in both composition and function. Assuming land use has not significantly altered site properties (a big assumption, and one not ignored by Dent et al.), succession theory traced all the way back to Frederick Clements and his cadre of environmental determinists suggests a predictable and convergent trajectory of forest composition; the only question being the duration required for the establishment of late-successional species that dominate primary stands. But much has happened in succession theory since Clements' time (Crawley 1997). Community ecologists pondering such questions today do so under the guise of community assembly theory (Chase 2003), and warn that convergence may be thwarted by species interactions that depend on the order in which species arrive (i.e. 'history') or, more ominously, randomness itself (Lepš & Rejmánek 1991), which we now call *stochastic assembly*.

Dent et al. focus on forest stands in Barro Colorado Nature Monument, Panama. Using a chronosequence approach involving old-growth stands and those last disturbed 20–100 yr ago as farms were abandoned, they surveyed tree seedling, sapling and overstorey layers and measured the compositional similarity of each layer across disturbed and undisturbed stands. Although tropical forest succession studies are not uncommon, such a lengthy chronosequence is rare. Combined with the general perception that forest succession proceeds rapidly in the tropics (Norden et al. 2009), Dent et al. reasoned that convergence patterns, if real, would be evident as a pattern of increasing compositional similarity to old-growth stands across the chronosequence.

Did the forests converge? The simple answer, as emphasized by Dent et al., is no. Although shade-tolerant species became more abundant over time, 100-yr-old forests remained compositionally distinct from old-growth stands, particularly when comparing adult trees. At face value this is intriguing in the context of community assembly theory, in that it points toward stochastic immigration and extinc-

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tion processes, a core tenet of neutral theory that has visited these old-growth stands before (Hubbell 2001). But a closer look suggests that Dent et al. may have been too quick to dismiss determinism in the assembly of these forests, for two reasons. First, a failure to reject the null hypothesis that compositional similarity does not increase between primary and secondary stands over time, as opposed to the alternative hypothesis of convergence, is driven in part by statistical power, which was here low (two stands per age category) due to obvious logistical constraints in surveying complex tropical landscapes. A glance at their successional trajectory figures, expressed in both ordination space and as pair-wise similarity comparisons over time, suggests a convergence trend, particularly for adult trees, as would be expected in a deterministic model of succession. Use of a negative statistical result to argue for stochastic assembly brings to mind Clark et al.'s (2007) critique of neutral theory as merely subsuming niche-based differences into unmodelled error ("neutral models are not 'trade-off' free, they are 'knowledge-free'").

Second, one might ask to what extent hyper-diverse tropical forests are expected to fully converge in composition anyway, given low species dominance and patchy seedling distributions even in old-growth stands. Clustered dispersal and low dominance do not necessarily indicate stochastic assembly – indeed these are the same conditions predicted by the Janzen–Connell hypothesis, recently shown to be highly predictive of species abundances in these same forests (Comita et al. 2010). To Dent et al.'s credit, they compare the similarity between adjacent old-growth stands (about 80% for adults) and conclude that it is twice as high as the similarity of those to 100-yr-old stands, but old-growth stands are more spatially clustered than disturbed stands so it is difficult to assess whether theirs is an appropriate null model. Given that successional convergence has been shown to be scale-dependent even in relatively species-poor temperate forests (Woods 2007), more consideration of convergence expectations in a spatial context seems a promising way forward.

Concerns about the role of stochasticity aside, an important take-home message from Dent et al.'s study is that species-rich tropical forests are complex enough to defy the simple expectation that a regenerating forest will closely resemble the forest that was cut down, at least within a time-frame that is relevant to metacommunity dynamics. Whether this will be a serious threat to the persistence of a particular species depends on many other considerations, including range size (endemism), dispersal ability, sensitivity to edge effects, degree of edaphic specialization and trophic cascades that are difficult to predict (Laurance et al. 2002). Nonetheless, studies like that of Dent et al. are crucial for understanding the fate of tropical forest species under the increasing threat of habitat loss, even under a rosy scenario of substantial forest regrowth in the decades ahead.

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