Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2012, **81,** 937–939 doi: 10.1111/j.1365-2656.2012.02016.x

IN FOCUS

Unpacking the impoverished nature of secondary forests

An ant worker of the genus *Diacamma* foraging in the understorey of a lowland rain forest in Papua New Guinea. These ants belong to the species usually nesting in aerial soil in the canopy of primary forest trees (Photo and copyright: M. Janda, www.newguineants.org).

Klimes, P., Idigel, C., Rimandai, M., Fayle, T.M., Janda, M., Weiblen, G.D. & Novotny, V. (2012) Why are there more arboreal ant species in primary than secondary forests? *Journal of Animal Ecology*, **81**, 1103–1112.

In a world where even documenting species declines in tropical systems is challenging enough, Klimes *et al.* raise the bar by addressing the deceptively simple, yet inherently complex, question of why species richness is lower in secondary forests. Using the first plot-scale inventory of arboreal ant nests, combined with an innovative rarefaction technique, they quantify the relative importance of a range of successional factors and highlight the contribution of beta diversity to the higher richness in primary forest.

There is concern about the high rates of deforestation in tropical ecosystems that have resulted in an unprecedented loss of biodiversity; indeed, secondary forests are now estimated to cover more than 30% of the total tropical forest area (Chokkalingam *et al.* 2000). Overwhelming evidence indicates that these habitats are species-poor, containing lower biodiversity values than adjacent primary forest (Gibson *et al.* 2011). Disturbances, such as the conversion of forest to oil palm, result in a loss of biomass, and as a consequence, there is often considerable simplification of habitat structure (Grime 1979; Floren & Linsenmair 2005). Changes to habitat structural complexity are some of the most important and obvious direct effects of disturbance, although there are others, such as change in species composition and loss of food resources. The structure and functioning of biotic communities also can be influenced in many indirect ways linked strongly to habitat structure, including changes to microclimate, predation risk and modification of competitive interactions (Tews *et al.* 2004; Table 1).

Table 1. Direct and indirect effects of disturbance on biotic communities

Direct	Indirect
Change in habitat structure	Change in microclimate
Change in plant species composition	Change in competitive interactions
Loss of food resources	Change in predation risk
Loss of nest sites	Change in nest site availability
	Increased likelihood of stochastic events having detrimental effect/ increasing extinction risk

For ants, diversity peaks in tropical forest canopies, and they dominate these systems in terms of their biomass and abundance (Hölldobler & Wilson 1990). Past work has focused on how competitive interactions (resulting in ant mosaics), resource availability and tree diversity contribute to the structure of local arboreal ant assemblages (e.g. Blüthgen *et al.* 2000; Blüthgen, Stork & Fiedler 2004). Yet others suggest there is evidence that assem-

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blages in secondary and primary forests are structured differently with stochastic factors important in primary forest and deterministic processes such as competition more important in secondary forests (Floren & Linsenmair 2005). To date, however, there have been no explicit tests, and little is known about the relative importance of plausible modifiers.

In this issue, Klimes *et al.* take a closer look at the question of why secondary forests have fewer species than primary forests. Applying a novel approach combining the first-ever complete inventory of arboreal ant nests at a plot scale and a clever rarefaction technique, they were able to partition the relative contribution of different succession-related factors in explaining this difference. In a result that might surprise some ecologists, the taxonomic composition of the trees played less of a role than tree density or size. Indeed, their study instead stresses the importance of habitat heterogeneity in promoting species diversity. Although the recognition of the role of habitat complexity is not itself new, the study advances understanding of disturbance and key factors structuring assemblages in tropical forests and importantly provides information on the relative importance of these.

As part of a large-scale, intensive study across Papua New Guinea, Klimes *et al.* took the opportunity to make complete inventories of patches of forest designated for clearance; clearance of the forest vegetation was performed systematically enabling a full inventory. Thus, within two 0·32-hectare plots (one primary forest and one secondary forest), the authors searched intensively all trees and associated vegetation (e.g. lianas and epiphytes) for ant nests, with nests classified by location and structure. Addressing some of the main predictors of ant species richness, they also collected additional data on tree density, tree size and vegetation taxonomic diversity. Although the study is unreplicated, and thus variability across the forests is not quantified, this highly labour-intensive and challenging task represents a major advance on previous studies. This is because canopy-fogging studies cannot distinguish exclusively arboreal species from epigaeic forager species, tend to focus only on larger trees and have limited replication. Typically, only a handful of trees are sampled, and owing to logistical constraints, fogging is rarely replicated at different times of the day; this is problematic as many arboreal ant species have distinct foraging windows, and at any one time, only a fraction of species will be sampled.

To partition the contribution of each succession-related factor, the authors controlled for the number of trees by randomly selecting a subset of 96 trees from both forest types so that sample size was equal and the number of trees in the primary forest data sets matched that found in the secondary forest sample. Size distributions of trees and tree taxonomic structure were also matched. Three simulated data sets were thus drawn from their empirical data and used to partition the difference in species diversity of ants into the effect of tree density, tree size and tree taxonomic diversity.

Although the mean number of species per tree in each forest type was the same, there was much higher beta diversity between primary forest trees than secondary forest trees, thus promoting local richness. Klimes *et al.* (2012) found the high ant beta diversity was matched by equally higher turnover of nest sites between primary forest trees, and they attribute the higher beta diversity in these forests to more complex vegetation structure, providing more nest site opportunities. Epiphytes in particular enhance the structural diversity of primary forests and are far less abundant and diverse in secondary forests; these plants play a dual role in the provision of physical niches (nest sites) and food resources (e.g. honeydew and nectar) and can thus contribute to increasing local ant species richness (Schultz & Wagner 2002; Yanoviak *et al.* 2012). Klimes *et al.* result concurs with a study from the Cerrado in Brazil where Powell *et al.* (2011) highlighted the importance of nest cavity availability and diversity for promoting arboreal species co-existence and species richness in newly colonized cavities. For twig-dwelling epigaeic ants too, richness was enhanced where a diverse array of twigs was provided (Armbrecht, Perfecto & Vandermeer 2004).

Although there is some evidence to suggest that diversity of nest sites plays a role in contributing to the higher beta diversity in primary forests, Klimes *et al.* (2012) are cautious in this assertion; this is because there are many other possible explanations they did not explicitly consider. First, food resource quality, quantity and stability have long been considered important in structuring local ant assemblages, particularly where the provision of a consistent supply of carbohydrates (from honeydew and extrafloral nectaries) affects species interactions (Davidson 1997; Blüthgen *et al.* 2000; Blüthgen & Feldhaar 2010); as such, changes to the availability of food resources as a result of disturbance are likely to have profound effects on the local ant communities. Second, recent studies have highlighted the role habitat connectivity can play in promoting species diversity; Powell *et al.* (2011) found that greater canopy connectivity facilitates access to resources and increases local arboreal ant richness. The more continuous canopy cover provided by primary forest enables ants to move across the canopy, finding new food and nest resources. Third, disturbances have a major effect on microclimate (Didham & Lawton 1999; Savilaakso *et al.* 2009): daytime temperature increases and humidity decreases, while the buffering effect provided by the canopy is reduced, and consequently, diurnal variation also increases. Possible impacts on arboreal ants include a reduced foraging window, while the effect of altered microclimatic conditions on growth and development in nests is virtually unknown. Finally, the role of stochastic processes warrants further attention (e.g. Hubbell 2001; Andersen 2008); can greater niche availability in primary forest account for the higher richness, or are there more opportunities for stochastic processes affecting colonization and extinction to operate?

The study raises a number of other interesting questions about species co-existence mechanisms and the functioning of forest ecosystems. In a system where ants can constitute 85% of biomass (Hölldobler & Wilson 1990; Davidson *et al.* 2003), the finding that such a large proportion of trees did not contain any nests (a third of primary forest trees and 23% of secondary forest trees) is intriguing. Other studies have also reported a large number of 'empty' nest niches, for example, 57% of hollow epiphytic pseudobulbs were uninhabited by ants (Yanoviak *et al.* 2012), while in a manipulative experiment, Sagata *et al.* (2010) found on average only 11·2% of twigs were colonized. Although in many systems nest site cavities are typically a limited resource and consequently competition for nest sites is intense (e.g. Carroll 1979), nest site availability and colonization is complex varying with land-use type, disturbance history, biogeographical context and with the characteristics of the nest sites themselves (e.g. size, shape) (Powell *et al.* 2011). Are arboreal nest sites limited in these Papua New Guinean forests? What are the particular characteristics of the nests that make them more or less favourable for colonization (e.g. too small, too large)? To what extent do ants nesting on one tree forage widely across other trees? Or is nest site availability potentially a red herring in this instance, with other factors such as pathogens and parasites (Anderson *et al.* 2012), or recruitment limitation (Philpott & Foster 2005), possibly being more important for explaining the patchy distribution of ant colonies?

Secondary forests can differ enormously in age, land-use history and other characteristics, so it is likely that the determinants of richness will vary too (Floren & Linsenmair 2005). Klimes *et al.* (2012) examined a relatively young (10-year-old) secondary forest. Questions therefore remain as to how the relative contribution of different factors changes with successional age, and whether changes are gradual or thresholds exist (e.g. development of epiphytes provides more nest sites)?

To provide better predictions and management of biodiversity for the future, ecologists and conservation biologists need to understand both pattern and process; elucidating those mechanisms is the trickier part of the equation. Klimes *et al.* (2012) have made an important contribution to our understanding; yet as with all good studies, more questions have been generated than answered.

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Received 12 May 2012; accepted 20 June 2012
Handling Editor: Corey Bradshaw