

Some like it hot: Tropical ant community responses to rainforest modification and conversion are shaped by thermal tolerances

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Forest fragmentation, degradation and conversion to agroforestry or plantations are ongoing threats to forests across the humid tropics. Biodiversity invariably suffers from habitat modification (Gibson et al., 2011), but the consequences for individual species are highly variable: there are winners and losers. In insects, for example, certain taxa such as butterflies appear to do relatively well overall, at least at moderate levels of disturbance; others such as ants and termites are reduced in diversity and abundance (Barlow et al., 2007; Lawton et al., 1998). Even within an apparently homogeneous taxon such as ants, highly variable trends are often seen for individual species. It is the number and identity of 'winner' and 'loser' species that will ultimately shape the structure and function of ecological communities in human-modified tropical forest landscapes.

What factors influence the relative success of different taxa as tropical forest habitats are modified? Particular traits tend to be associated with resilience to change (e.g. Newbold et al., 2013), providing clues about the underlying mechanisms. One likely driver of varying biotic responses is a change to microclimatic conditions arising from altered vegetation structure. Logging, fragmentation and conversion to agriculture are associated with pronounced changes to vegetation structure that tend to increase mean temperatures and the frequency of high thermal extremes (Jucker et al., 2018). We expect tropical ectotherms such as insects to be particularly sensitive to such changes: most have limited capacity to maintain their temperatures at levels that deviate much from ambient, and they have evolved in an environments where daily and seasonal variations in temperature are small (Janzen, 1967). As a result, tropical ectotherms currently operate at close to the maximum temperatures that they can tolerate physiologically (Deutsch et al., 2008).

Surprisingly, there have been few studies that directly test the hypothesis that changes to tropical forest communities are causally

linked to altered thermal conditions arising from forest modification. In this issue of *Functional Ecology*, Boyle et al. (2021) compare primary forests, logged forests and oil palm plantations in Sabah, Malaysian Borneo, investigating how ants foraging on the forest floor and in the soil vary across the gradient of forest modification. Uniquely, their data on ant communities are associated with fine-scale microclimate data from the same locations, as well as data on the physiological tolerances of each ant genus. Physiological tolerances were measured using a simple, standard assay: individual worker ants, freshly collected from the field, were placed in sealed vials and submerged in a thermostatically controlled water bath. The temperature was then gradually increased until the ants stopped moving at their critical maximum temperature (CT_{max}), a widely used metric of thermal tolerance.

Boyle et al. (2021) found that ants with high CT_{max} thrive in the hotter oil palm habitats, while those with low CT_{max} were absent or rare. Conversely, the cool, shady understorey of the primary forest was dominated by ants with low CT_{max} values. While the results are in line with expectation, the mechanistic linking of community-wide shifts to altered thermal conditions and underlying variability in animal physiology is novel, demonstrating that microclimate change is the proximate driver of community reorganisation.

The 'response trait' of thermal tolerance—and hence abundance and activity across the land-use gradient—was strongly correlated with other functional traits. Ants that thrived in hot oil palm plantations tended to be large-bodied, predatory species. Ants are an abundant and functionally important invertebrate group in tropical forests and many other ecosystems, so alterations to their abundance, composition and activity are likely to have pronounced effects on a variety of ecosystem processes and the abundance of prey species such as insect herbivores.

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A variety of factors could help buffer ant communities against changes to thermal environments following habitat modification. Fine-scale heterogeneity in thermal conditions in the rainforest understorey provides the opportunity for ants to shift their foraging activities in space, while the diurnal cycle of temperatures could allow diurnal ants to forage early or late in the day to avoid thermal extremes. Such changes would likely lead to re-wiring of competitive interactions among species. A further possibility is that selection imposed by habitat modification could lead rainforest to evolve higher thermal tolerances, as has been documented for ants in urban habitats (Diamond et al., 2017).

Will other taxa show equally strong community filtering across habitat degradation gradients as a function of thermal tolerances? Certain characteristics of ants may make them especially likely to respond strongly to thermal conditions. For example, many are trophic generalists, so availability of biotic resources is less likely to drive changes in their abundance than would be the case for more specialised consumers such as tropical insect herbivores (Forister et al., 2015). Studies investigating whether thermal tolerances are a strong predictor of community changes in other insect taxa across anthropogenic land-use gradients would now be welcome. Tropical plants also operate close to high-temperature thresholds, which vary among species (O'sullivan et al., 2017), so similar processes could even contribute to structuring rainforest vegetation.

On a larger spatial scale, these and other recent results point to landscape-scale strategies that might mitigate the impacts of forest modification on ecological communities. Recent work in the same landscape on dung beetles, another functionally important arthropod group, shows that buffers of rainforest vegetation retained along the banks of streams and rivers within oil palm plantations can provide a cool, humid refuge habitat (Williamson et al., 2021). Provided they are wide enough and have high vegetation quality, these riparian buffers can support beetle communities that are comparable in their composition to those in continuous forests.

Boyle et al. argue that anthropogenic modification of forest microclimates can be viewed as a form of rapid, localised climate change. These changes are of course co-occurring with longer-term increases in mean ambient temperatures under global climate change. Understanding how communities respond to these changes provides a worrying insight into the likely fate of tropical communities in a warmer world.

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