



Original Articles

Ants as indicators of environmental change and ecosystem processes



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ABSTRACT

Environmental stressors and changes in land use have led to rapid and dramatic species losses. As such, we need effective monitoring programs that alert us not only to biodiversity losses, but also to functional changes in species assemblages and associated ecosystem processes. Ants are important components of terrestrial food webs and a key group in food web interactions and numerous ecosystem processes. Their sensitive and rapid response to environmental changes suggests that they are a suitable indicator group for the monitoring of abiotic, biotic, and functional changes. We tested the suitability of the incidence (i.e. the sum of all species occurrences at 30 baits), species richness, and functional richness of ants as indicators of ecological responses to environmental change, forest degradation, and of the ecosystem process predation on herbivorous arthropods. We sampled data along an elevational gradient (1000–3000 m a.s.l.) and across seasons (wetter and drier period) in a montane rainforest in southern Ecuador. The incidence of ants declined with increasing elevation but did not change with forest degradation. Ant incidence was higher during the drier season. Species richness was highly correlated with incidence and showed comparable results. Functional richness also declined with increasing elevation and did not change with forest degradation. However, a null-model comparison revealed that the functional richness pattern did not differ from a pattern expected for ant assemblages with randomly distributed sets of traits across species. Predation on artificial caterpillars decreased along the elevational gradient; the pattern was not driven by elevation itself, but by ant incidence (or interchangeable by ant richness), which positively affected predation. In spite of lower ant incidence (or ant richness), predation was higher during the wetter season and did not change with forest degradation and ant functional richness. We used path analysis to disentangle the causal relationships of the environmental factors temperature (with elevation as a proxy), season, and habitat degradation with the incidence and functional richness of ants, and their consequences for predation. Our results would suggest that the forecasted global warming might support more active and species-rich ant assemblages, which in turn would mediate increased predation on herbivorous arthropods. However, this prediction should be made with reservation, as it assumes that the dispersal of ants keeps pace with the climatic changes as well as a one-dimensional relationship between ants and predation within a food-web that comprises species interactions of much higher complexity. Our results also suggested that degraded forests in our study area might provide suitable habitat for epigeic, ground-dwelling ant

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assemblages that do not differ in incidence, species richness, functional richness, composition, or predation on arthropods from assemblages of primary forests. Most importantly, our results suggest that the occurrence and activity of ants are important drivers of ecosystem processes and that changes in the incidence and richness of ants can be used as effective indicators of responses to temperature changes and of predation within mega-diverse forest ecosystems.

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1. Introduction

Biodiversity provides the basic elements for species interactions within food webs and ecosystem processes and is therefore a key factor for the stability of ecosystems (Cardinale et al., 2012; Chapin III et al., 1997; Tilman et al., 2012). However, rapid anthropogenic environmental and land-use changes increasingly modify the structure and extent of natural ecosystems, which can lead to a dramatic loss of biodiversity (Foley et al., 2005; Walther, 2010). As such, we urgently require a continuous monitoring of the status of biodiversity and ecosystems (Scholes et al., 2008) that not only focuses on the presence or absence of certain (keystone) species, but monitors functional changes in species assemblages and their effects on food webs and ecosystem processes (Noss, 1999; Palmer and Febria, 2012).

Predation is an important process within food webs; predators can act at different trophic levels (De Ruiter et al., 1995) and can modify species abundances (Holt, 1977), composition of assemblages (Pace et al., 1999), and evolution of traits (Peacor and Werner, 2001). Ants are one of the most important generalist predators of arthropods in terrestrial ecosystems, particularly in the tropics (Hölldobler and Wilson, 1990; Seifert et al., 2016). They are crucial for numerous ecosystem processes, e.g., soil turnover, nutrient cycling, plant defense, seed dispersal, and regulation of herbivores, which has led to them being widely accepted as keystone taxa (Parr et al., 2016; Underwood and Fisher, 2006 and references within). Furthermore, their simple and cost-efficient sampling (Andersen and Majer, 2004; Underwood and Fisher, 2006) makes them a suitable indicator of even subtle abiotic, biotic, and functional changes of ecosystems (Folgarait, 1998).

The monitoring of responses to various environmental changes requires measures that match the habitat and degradation type in question (Carignan and Villard, 2002; Dale and Beyeler, 2001; Read and Andersen, 2000; Ricotta et al., 2015; Siddig et al., 2016). Different measures of ant diversity have been successfully used to indicate ecological responses to natural abiotic changes within local habitats, such as temperature, humidity, soil, and vegetation type (Hoffmann, 2010). For ants, species richness alone usually provides rather limited information on ecosystem changes, whereas data on ant abundance, species composition, and richness of functional traits (functional richness) better reflect the biotic response of the entire ecosystem (Folgarait, 1998; Hoffmann and Andersen, 2003; Yates et al., 2014). Many ant species are stenothermic, and thus temperature is often the main determinant of abundance, species richness, and composition of ant assemblages, with generally decreasing ant abundances and species richness with decreasing temperature (Jenkins et al., 2011; Kaspari et al., 2003; Longino et al., 2014; Sanders et al., 2007, 2003). Therefore, the projected global warming might lead to shifts in the latitudinal or elevational distribution of species as well as to an overall loss of species (Colwell et al., 2008; Gibb et al., 2015a,b; Hughes, 2000), with consequences for ant-mediated food web interactions and ecosystem processes (Del Toro et al., 2015). In addition, seasonality influences ant assemblages; high amounts of rainfall can decrease

the size of colonies and activity of ants, thereby influencing the composition of assemblages (Andersen, 1986; Delsinne et al., 2013).

Beyond abiotic changes, anthropogenic habitat degradation also alters richness and composition of ant assemblages mediated through changes in habitat characteristics (Hoffmann, 2010; Underwood and Fisher, 2006). In general, a decrease in the complexity of habitats (e.g., the amount or characteristics of leaf litter) leads to changes in species composition (Gibb and Parr, 2013; Gibb et al., 2015b; Wiescher et al., 2012). Thereby, the effect of habitat degradation on ants depends on its type and severity. In complex habitats, such as forests, fragmentation or selective logging does not necessarily affect the abundance or species richness of ants (Donoso, 2017; Underwood and Fisher, 2006 and references within; Woodcock et al., 2011). However, secondary forest patches of differing ages in Brazil contain ant assemblages with fewer species and lower functional diversity compared to old-growth forests (Bihn et al., 2010, 2008). Furthermore, forest degradation is expected to affect the composition of ant assemblages when it is associated with changes in habitat structure, e.g., canopy openness, vegetation structure, and plant richness (Underwood and Fisher, 2006; Yusah and Foster, 2016). In New Guinea, higher density, larger size, and higher taxonomic diversity of trees explains more than 50% of the observed higher ant species richness of primary forests compared to secondary forests (Klimes et al., 2012).

The multitude of species responses to environmental change depend on the functional traits of species, as traits are related to habitat preference, diet, and foraging strategy (Gibb and Parr, 2013; Gibb et al., 2015b; Wiescher et al., 2012). For example, the overall body size of epigeic ant assemblages is linked to habitat complexity and trophic level (Gibb and Parr, 2013), where larger ants forage at the surface rather than in the litter (Donoso and Ramón, 2009; Weiser and Kaspari, 2006). Epigeic predatory ants also have larger bodies than omnivorous species (Gibb et al., 2015b), and head and mandible size are linked to prey size (Davidson, 1977; Fowler et al., 1991; Kaspari, 1996) and leg length is linked to foraging speed (Bartholomew et al., 1988). Given these close relationships of functional traits with habitat conditions and trophic position, it is thought that functional richness of ants is more directly linked with food web interactions and ecosystem processes than species identity *per se* (Mouchet et al., 2010). However, it is important to note that the strength of an assemblage-wide contribution to ecosystem processes will be determined not only by the number of species and their functional richness but also by the number and activity of individuals (Stuart-Smith et al., 2013).

Abiotic conditions and species traits jointly affect the composition of predator and prey assemblages, which in turn affects predation (Hooper et al., 2005; Lavorel and Garnier, 2002; Lebrija-Trejos et al., 2010; Yates et al., 2014). By controlling herbivorous arthropods, predators can positively influence plant growth and regeneration (Snyder et al., 2006) and might promote persistence and stability within assemblages (Chapin III et al., 1997). Overall, rates of predation on herbivorous arthropods decline with increasing elevation, whereby the relative contribution of the various predators might change (Hodkinson, 2005; Sam et al., 2015a). However, estimating predation rates along environmental gradients is

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