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Tropical ant communities are in long-term equilibrium

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ABSTRACT

Communities change with time. Studying long-term change in community structure permits deeper understanding of community dynamics, and allows us to forecast community responses to perturbations at local (e.g. fire, secondary succession) and global (e.g. desertification, global warming) spatial scales. Monitoring efforts exploring the temporal dynamics of indicator taxa are therefore a critical part of conservation agendas. Here, the temporal dynamics of the Otongachi leaf litter ant community, occurring in a cloud forest in coastal Ecuador, were explored. By sampling this community six times over eleven years, I assessed how the ant fauna caught by Winkler traps (more diverse and cryptic fauna) and caught by pitfall traps (larger, more mobile fauna) changed over time. The Otongachi leaf litter ant community was dynamic. Although species richness in the community remained constant, temporal turnover of species was high: on average, 51% of the ant species in Winkler traps, and 56% of those in pitfall traps, were replaced with other ant species from one year to the other. Shifts in the rank abundance of species in the community were also large across the eleven years and, on average, shifts in the rank abundance of species collected by Winkler traps doubled those occurring in pitfall traps from one census to the other. In spite of these trends, the Otongachi ant fauna showed no (Winkler) or weak (pitfall) evidence of directional change (towards a new community). Thus, this tropical ant community can be divided in two community compartments. The Winkler compartment composed by a more diverse and cryptic ant fauna appears to be resilient and stable in time. The pitfall compartment composed by larger and more mobile ants may be prone to respond to disturbance. This study suggests that 1) species appearing/disappearing from a site may be rather the rule, difficult to separate from responses to ecological stress. 2) Conclusions made in short-term studies, or studies comparing two (e.g. before and after) snapshots of a community, should thus be revisited. Finally, 3) the ant fauna caught by pitfall traps (a rather simple and cheap survey method) is the most likely community compartment to indicate ecological perturbation. This study adds to the growing evidence that using ants as ecological indicators should incorporate long-term temporal dynamics.

1. Introduction

Natural communities change over time (Butchart et al., 2010; Magurran et al., 2010). Studying temporal community dynamics is of interest because the relative importance of different processes structuring ecological communities changes with time (Matthews et al., 2013; Baez et al., 2016). Examining long-term community dynamics also allow us to test how ecological stressors (e.g. anthropogenic disturbance, global warming, invasive species, El Niño Southern Oscillation) impact communities (Magurran et al., 2010; Colwell et al., 2008). As such, these dynamics can provide helpful insights to improve conservation efforts (Butchart et al., 2010). Unfortunately, temporal changes of naturally occurring communities are difficult to measure. It requires long-term funding and institutional support, as well as expertise in taxonomy (Bonada et al., 2006; Majer et al., 2007; Lenoir and Svenning 2013). As a consequence, our knowledge of the temporal dynamics that communities experience under natural conditions is limited. This is especially true for insect communities in tropical environments, and refrain us from using insect taxa as effective ecological indicators (Agosti et al., 2000).

Despite difficulties, interest in long-term community dynamics has grown with time, and long-term ecological research is now well incorporated into mainstream ecological research agendas (e.g. Long Term Ecological Research Network, Callahan 1984; National Ecological Observatory Network, Kampe et al., 2010; CTFS-Forest GEO Network, Anderson-Teixeira et al., 2015). New conceptual frameworks exploring how communities change over time measure trajectories of multiple species simultaneously in a

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multivariate space (Magurran et al., 2010). These temporal analyses emphasize the role of direction and gradualism of community trajectories (Collins et al., 2000; Matthews et al., 2013). Communities are considered to be stable if changes in community structure do not accumulate with time. Alternatively, communities show direction if changes in community structure accumulate with time and either diverge from, or converge towards, an original state, which is usually assumed to be the reference community sampled first (Collins et al., 2000; Matthews et al., 2013). Another important aspect of temporal dynamics is the rate of change in community structure (Collins, 2000). Gradual changes are considered the norm, and occur when communities experience minor and constant changes from one year to the other. Contrary to gradual change, saltatory change is expected to occur when communities experience rapid major disturbances (Collins, 2000). Generally, the ability of a community to return gradually to its original state is considered as positive, especially within conservation or restoration agendas (Majer et al., 2013). Communities are said to be in equilibrium if, despite year-to-year variability, community structure remains constant (Collins, 2000).

Ants are conspicuous organisms in soil ecosystems, and participate in a myriad of ecological interactions (Del Toro et al., 2012; Tiede et al., 2017). Several authors have proposed ants as good ecological indicators (Andersen 1990; Arcila and Lozano-Zambrano, 2003) and methods exist to monitor ants (Agosti et al., 2000). However, most studies examining ant communities through time compare two points; and thus they do not constitute 'temporal' studies in a strict sense (defined here as communities surveyed three or more times). These studies tend to compare disturbed plots (after a certain time) with nearby control treatments (Table 1). For example, recently, Belcher et al. (2016) resampled M.R. Smithís 1926 survey of invasive ants in Urbana (Illinois, USA) after 87 years. Whereas they found that the four most common house ants differed between the two sampling times, the similarity of the complete faunas was unanticipated. In a different approach, some studies have used chronosequences, i.e. a space-for-time substitution (Hoffman and Andersen, 2003; Majer et al., 2007) to monitor temporal change (Table 1). In Australia, for example, ants have been used to monitor restoration of mining sites (Majer et al., 1982; Majer, 1983; Hoffman and Andersen, 2003) and ecosystem responses to fire (Andersen 1991). Evidence thus far suggests that ant communities can show directional (Gosper et al., 2012) and stable trajectories (da Conceição et al., 2015). In Brazil (Bihn et al., 2010) and Puerto Rico (Barberena-Arias and Aide 2003), ants have been used to monitor secondary succession. These studies show directional and saltatory trajectories with little or no sign of communities returning to the original state (Barberena-Arias and Aide 2003, Bihn et al., 2010). However, in Costa Rica, Patrick et al. (2012) found that, after 12 years, treefall gaps had little or no effect on the structure of ant communities living in those gaps. While the number of published studies is likely too small to suggest strong patterns (Table 1), the majority of these studies show that ant communities are certainly responding to disturbance, but see Tiede et al. (2017).

To the best of my knowledge, no temporal survey of naturally occurring ant communities has been documented to date. Here I surveyed the leaf litter ant fauna of the Otongachi forest six times (2003, 2006, 2008, 2009, 2011, and 2013) over eleven years. I aimed to understand the changes in structure that a tropical leaf litter ant community experiences naturally over a decade. Using what is the longest dataset available for any ant community, I ask 1) are temporal changes occurring in a gradual or saltatory way? 2) Is there evidence of changes in the general abundance of species with time? And 3) is there evidence of directional or stable trajectories in this ant community with time? I answered these questions by looking at the responses of two compartments of the leaf litter ant community. Previously, Donoso and Ramoín (2009) have shown that pitfall and Winkler traps capture different subsets of the ant community. In the Otongachi forest, the ant fauna caught by Winkler traps was more diverse and cryptic than the larger and long-legged (more mobile) ant species captured by pitfall traps (Donoso and Ramoín, 2009).

2. Materials and methods

2.1. Study area

This study was conducted within the Otongachi forest (00° 08′49′′s; 078°57′15′′W, 850-m), Pichincha Province, a 20-ha forest patch in the lowest-most part of the Bosque Integral Otonga (BIO Reserve). The forest is located on the western slopes of the Ecuadorian Andes, near La-Unión-del-Toachi town. Otongachi is a secondary wet pre-montane forest (Can˜adas (1983)) that was modified until the year 2000 by low-intensity selective timber harvesting [timber of *Cedrela odorata* L. (Cedro), *Nectandra* sp. (Canelo), and *Guadua* sp. (Caña guadua) was logged down from the site; G. Onore, personal communication]. The average annual temperature is 18–24 °C, and the annual rainfall is between 1000 and 2000 mm. Forest leaf litter was composed of plant species from sub-tropical, cloud and Andean forests, including *Cedrela odorata* L. "cedro", *Billia columbiana* Planch. and Linden "pacche", *Elaegia utilis* (Goudot) "lacre", *Guarea kunthiana* A. Juss "colorado", *Pochota squamigera* (Cuatrec.) "frutipan", *Sapium verum* Hemsl. "lechero" and *Nectandra acutifolia* (Ruiz and Pav) "Gigua" (Jaramillo, 2001).

2.2. Ant sampling

The Otongachi forest was surveyed in six censuses spanning eleven years. In years 2003, 2006, 2008, 2009, 2011, and 2013, ant communities were sampled using the Ants of the Leaf Litter (ALL) protocol as described in Agosti et al. (2000). In each year, ant assemblages were sampled using a complete replicate of the ALL protocol, in August-September, during a period of low rain. Each transect consisted of 20 sampling points separated by 10 m for a total extent of 200 m. Because litter removal is destructive and may influence ant community structure (Donoso et al., 2013), the starting sampling point and direction of the transect was chosen every year in a haphazardly way, always starting near the research station. At each sampling point, a randomly placed pitfall trap partially filled with 70% alcohol for 48 h was used alongside leaf litter from a nearby 1-m^2 plot that was placed in a Winkler extractor. The 2003 census, measuring ant community structure at the Otongachi forest, was reported by Donoso and Ramoín (2009). Further sampling methodology details are available there.

Samples were processed in the laboratory. From every sample, at least one individual of each morphospecies was mounted and labeled, and the abundance of the morphospecies was recorded. Specimens were identified to species with the use of taxonomic keys and local reference collections. Where specific identifications were not possible, specimens were assigned to a morphospecies. I compared specimens with those deposited at the Ecuadorian Ant Reference Collection (ARCE), housed in the EPN Museum (Museo de Historia Natural Gustavo Orcés V.) at the Instituto de Ciencias Biológicas of the Escuela Politécnica Nacional (Quito, Ecuador), and curated by DAD. Ants identified to morphospecies bear an ARCE morphospecies number (EC###). ARCE serves as a national reference collection for ant species of Ecuador. Additional voucher specimens of all species and morphospecies have been deposited in the MUTPL Museum at the Universidad Técnica Particular de Loja (Loja, Ecuador).