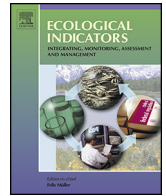




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Original Articles

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.

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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 commu-

nities 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, this special issue). 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. Smith's 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. (2007, this issue).

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 commu-

nity. 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", *Bilia columbiana* Planch. and Linden "pacche", *Elaeagia utilis* (Goudot) "lacre", *Guarea kunthiana* A. Juss "colorado", *Pochota squamigera* (Cuatrec.) "frutipan", *Sapium verum* Hems. "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-m² 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).

Table 1

Summary of manuscripts studying temporal changes of ant communities. For each study, I provide the approach (Chronosequence or Survey), time lapse, type of stressor, and type of response [Directional (D) vs. Non Directional (ND), Saltatory (S) vs. Gradual (G), Return (R) vs. No Return (NR)].

| Study | Type | Extent (yr) | Frequency Survey | Stressor | Type of response | Note |
|-----------------------------|----------------|-------------|------------------------------|-------------------------|------------------|-------------|
| Gosper et al., 2012 | Chronosequence | 300 | <12, 38–120, >140 | Fire | D, G, R | Interpreted |
| Jackson and Fox 1996 | Chronosequence | 18 | 1, 6, 12, 18 | Fire | ND, G, R | Interpreted |
| Jackson and Fox 1996 | Chronosequence | 18 | 1, 6, 12, 18 | Mine | ND, S, NR | Interpreted |
| Majer et al., 1984 | Chronosequence | 13 | various | Mine | D, G, NR | Interpreted |
| Patrick et al., 2012 | Chronosequence | 12 | 1–12, yearly | Gap | ND, G, NR | Interpreted |
| Jackson and Fox 1996 | Chronosequence | 18 | 1, 6, 12, 18 | Clearing | ND, S, NR | Interpreted |
| da Conceição et al., 2015 | Chronosequence | 33 | 1, 3, 4, 8, 15, 33 | Agriculture | Unknown | Interpreted |
| Lafleur et al., 2006 | Chronosequence | 79 | 1, 9, 23, 47, 79 | Fire | ND, S, R | Reanalysed |
| Barberena-Arias & Aide 2003 | Chronosequence | 60 | 5, 30, 60 | Secondary Succession | D, S, NR | Interpreted |
| Bihn et al., 2010 | Chronosequence | 60 | 4–6, 10–15, 35–50, >100 | Secondary Succession | D, S, NR | Interpreted |
| Vanderwoude et al., 2000 | Chronosequence | 40 | 1–5, 6–10, 11–20, 21–30, >30 | Timber harvesting | D, S, R | Interpreted |
| Majer 1981 | Survey | 2 | monthly | Mine | ND, G, NR | Interpreted |
| Majer and Nichols 1998 | Survey | 14 | 1–14 yearly | Mine | D, G, NR | Interpreted |
| Belcher et al., 2016 | Survey | 87 | 1, 87 | Land Conversion/Housing | ND | Interpreted |
| Donoso, 2017(This study) | Survey | 11 | 0, 3, 5, 6, 8, 10 | Secondary Succession | ND, G, NR | This study |

Directional (D) vs. Non Directional (ND)
Saltatory (S) vs. Gradual (G)
Return (R) vs. No Return (NR)

2.3. Statistical analyses

A dataset consisting of ant species present by trap (Winkler sacs and pitfall traps) and by year (6 censuses) was compiled. Singletons, defined here as species occurring once within the survey, and nomadic ant species, depicting the army ant syndrome (e.g., *Ceraphachys*, *Neivamyrmex*, *Labidus*) were removed from analyses. Removing singletons species lessen the influence of rare species in community analyses. Army ants do not permanently inhabit a patch of litter, and are usually trapped by these methods in large numbers, biasing the true, more permanent composition of the plots. Other species with special biology (such as *Atta cephalotes*, that build large long-term permanent nests, different to most other leaf-litter ants), and species with taxonomic uncertainties were also removed from analyses. In the Neotropics, species of the ant genus *Solenopsis* are difficult to sort apart, and thus all specimens/species of this genus were merged into a single category.

Temporal changes in ant diversity of the Otongachi ant community were characterized using three different temporal metrics; these metrics have been recently implemented in the R library “codyn” (Hallett et al., 2015, 2016). First, I investigated if the rate of change of community structure across the eleven-year interval shows a gradual or saltatory trajectory. For this, total species turnover (tST) in the community was calculated among consecutive censuses. The variable tST measures the proportion of total species richness lost and gained in the community from one year to the next, and ranges from 0 (no species are gained or lost) to 1 (all species are replaced). Communities may differ in species turnover even when total species richness remains constant over time. We can decompose tST further into two indices, such that all species appearing (aST) and disappearing (dST) over time are measured by calculating the proportion of species gained or lost with respect to that of the complete community. Large or unexpected values of ST from one year to the next surveyed year allow us to see if a saltatory (non-gradual or abrupt) change in community structure has occurred.

Second, mean shifts in species rank abundances (MRA; Collins et al., 2008) were calculated. MRA, an overall measure of changes of species abundances within the community, is the sum of species common to two sampling times weighted for the relative rank abundance change that the species displayed. Higher values of MRA indicate a higher amount of reshuffling in species ranks within a community. However, MRA values are a function of the total number of species in a community, as more species provide more room

for species reshuffling, and thus MRA should be higher in more speciose communities.

Finally, I measured the rate of directional change in community composition over time (Collins et al., 2000; Matthews et al., 2013). The rate of directional change was calculated from distance measures (here I used Euclidean distance) between time points. When these distances are regressed over time, the slope of the regression indicates the stability of the community over time. A slope of zero indicates that the community remains stable and that no change in structure occurs with time. Positive, linear and significant slopes indicate unstable communities with directional temporal trajectories. Negative, linear and significant slopes indicate unstable communities with convergent temporal trajectories (Collins et al., 2000).

3. Results

3.1. Ant sampling

The initial dataset coming from six censuses spanning eleven years shows a total of 12 342 ant specimens coming from 126 species and 52 genera (Table A1 in Appendix A). Of these, 20 singleton species were removed from further analyses. Sixteen additional species were also removed because they were army ants or taxonomic difficulties. In the final dataset, the five most common species found were *Nylanderia* EC004 (n = 650 specimens), *Pheidole* EC009 (n = 622), *Cyphomyrmex* EC003 (n = 531), *Hypoponera distinguenda* (n = 412) and *Octostruma* EC001 (n = 410). But, these species were not always the most abundant as the ranking was highly variable from year to year (Table 2). In total six species, which I call here the ‘core’ species, were in the top-five of species abundances in the 11-year interval. Ten additional species, which I call here the ‘occasional’ species, reached the top five only once in the 11-year interval (Table 2).

The mean number of species present each year was 58. The mean number of species present in Winkler traps (n = 50) broadly doubled the species in pitfall traps (n = 30). On average, in each sampling year I found 5 singletons. Ant species richness in the Otongachi forest remained constant with time (Fig. 1).

3.2. Changes in species turnover

The Otongachi ant community presented high levels of species turnover across the years, but the pattern shows mostly gradual

Table 2
The five most common ant species in the whole survey (Total) and in each year. Numbers represent the order of specimen abundance of each species (i.e. Nylanderia EC004 was the most abundant ant in the whole survey). Core species are defined here as species occurring 2 or more times in the top five. Occasional species are those who achieve high abundance only in one year.

| | Year | Total | 2003 | 2006 | 2008 | 2009 | 2011 | 2013 |
|--------------------|-------------------------|-------|------|------|------|------|------|------|
| Core Species | Nylanderia EC004 | 1 | 2 | | 1 | 2 | 1 | |
| | Pheidole EC009 | 2 | 3 | 1 | | 1 | 3 | |
| | Cyphomyrmex EC003 | 3 | | 3 | 2 | 4 | 2 | 4 |
| | Hypoponera distinguenda | 4 | | 2 | | | | 1 |
| | Octostruma EC001 | 5 | | | | 3 | | 3 |
| Occasional Species | Gnamptogenys bisulca | | 4 | 4 | 3 | | | |
| | Azteca EC001 | | 1 | | | | | |
| | Pheidole EC001 | | 5 | | | | | |
| | Pheidole EC003 | | | 5 | | | | |
| | Pheidole EC016 | | | | 4 | | | |
| | Pheidole EC002 | | | | 5 | | | |
| | Brachymyrmex EC001 | | | | | 5 | | |
| | Pheidole onyx | | | | | | 4 | |
| | Carebara urichi | | | | | | 5 | |
| | Octostruma EC002 | | | | | | | 2 |
| | Pheidole EC005 | | | | | | | 5 |

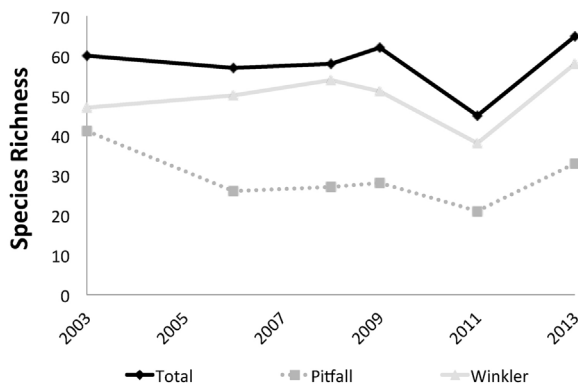


Fig. 1. Ant species richness in the Otongachi forest across eleven years. Total species richness, and species trapped by pitfall and Winkler traps are provided.

change (no abrupt difference in the rate of species turnover from year to the other, Fig. 1). The mean tST in Winkler traps was 0.51 (on average, 51% of the species sampled by Winkler traps in one year did not showed up in the year after) and mean tST in pitfall traps was 0.56. Winkler and pitfall traps showed a similar temporal pattern, where species turnover slightly decreased or was kept constant in time, but showed a spike in the last census interval (i.e. 2011–2013; Fig. 2). Species appearances and disappearances contributed equally to the pattern (mean Winkler aST=0.27, mean Winkler dST=0.24, mean pitfall aST=0.26, mean pitfall dST=0.30).

3.3. Changes in species abundance

Shifts in species rank abundances showed differences between Winkler and pitfall traps. On average, rank abundance changes in the ant community collected by Winkler traps doubled (Winkler MRA=6.63) that of pitfall traps (pitfall MRA=3.29). MRA values for both Winkler and pitfall traps also changed with time (Fig. 3). Winkler MRAs peaked at 2008, but then declined constantly. Pitfall MRAs peaked in 2006, after which it stabilized around a value of 3 (Fig. 3)

3.4. Changes in directionality

Across the 11-year census, neither directional change nor convergence was found in Winkler traps. The regression line of community similarity vs. census interval was positive, but it was not significant and explained little variation ($F=0.30$, $p=0.59$,

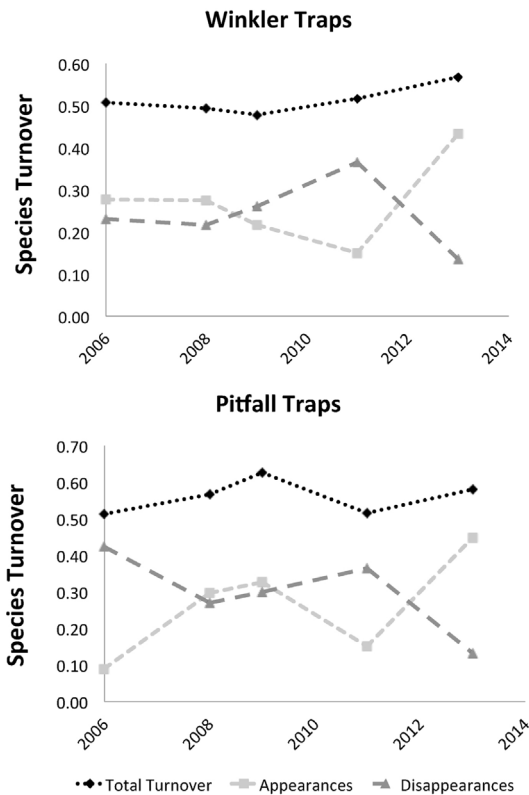


Fig. 2. Species turnover within the Otongachi ant community across eleven years, by trap type (Winkler vs. pitfall). Total species turnover (tST) is divided among those ant species appearing (aST), and those ant species disappearing (dST) with time.

$R^2=0.02$, Fig. 4A). However, for pitfall traps, I detected a significant positive change during the study interval ($F=5.41$, $p=0.036$, $R^2=0.29$, Fig. 4B).

4. Discussion

The Otongachi ant community was highly dynamic from one census to the other. However, over the course of the 11-year study there was not an apparent decrease of species richness either in Winkler traps or pitfall traps. More importantly, there was no long-term change in the community sampled by Winkler traps, and the pitfall community only weakly changed. The remarkably high tem-

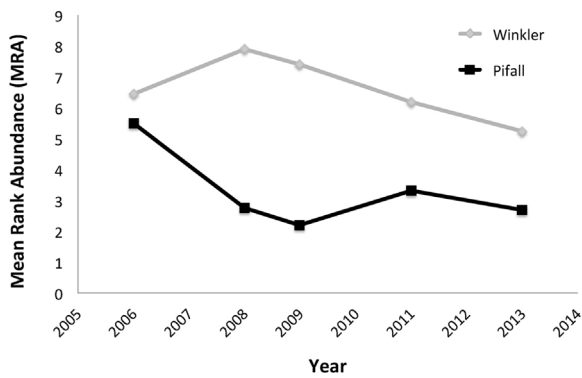


Fig. 3. Mean rank abundance (MRA) changes in the ant community over 11 years.

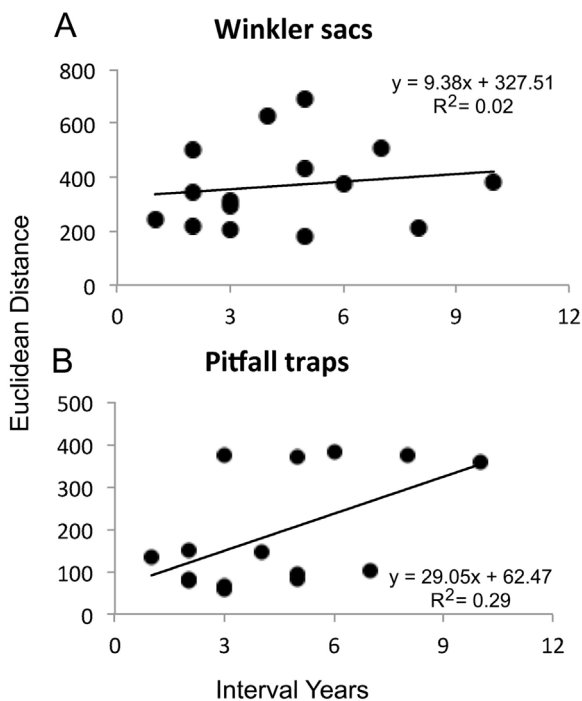


Fig. 4. Euclidean distances separating ant communities at increasing census intervals.

poral stability in species richness and community structure across the whole study period (2003–2011) presented by the Otongachi ant fauna is inconsistent with general expectations of effects of global stressors on local communities. For example, both habitat degradation and global warming are predicted to accelerate the loss of biodiversity (Gibb et al., 2015; Baez et al., 2016). Global warming (GW) is perhaps the major challenge facing natural communities nowadays and Andean forests like Otongachi have already experienced major increases in average yearly temperature (Mora et al., 2013). Generally, it is expected that due to global warming species distributions will shift, moving polewards in latitude and upwards in elevation, when possible (Parmesan and Yohe, 2003). For example, the Edith’s checkerspot butterfly (*Euphydryas editha*), which lives in the US and Canada’s East coast, may have moved up to two degrees northward in over a decade (Parmesan, 1996). Furthermore, species abundances of thermophilic taxa in Europe are known to increase under current global warming (Bowler et al., 2017). However, these scenarios of drastic shifts in species ranges in temperate regions contrast with the lack of predictions of species responses in tropical areas (Lenoir and Svenning, 2013). In fact, little theory is available forecasting the future of communities liv-

ing at the Equator (0° in latitude) and at sea level (0 m a.s.l.). In tropical forests, species adapted to narrow ranges in temperature (Janzen, 1967) may find it difficult to move polewards or upwards. Some studies have proposed that narrow temperature changes with latitude will make most distribution shifts to be upwards, not polewards (Bush, 2002). Yet extrapolation of these ideas to all taxa is difficult because not all taxa have shown the same response to altitude (Schuldt et al., 2015). This scenario led Colwell et al. (2008) to suggest that most tropical communities may be ‘between the devil and the deep blue sea’ and under danger of biological attrition. However, few documented examples currently exist in Andean ecosystems where little research has been done and it is strongly biased to certain taxa (i.e. plants and frogs) and observational (not experimental) studies (Baez et al., 2016). The study here presented found that the Otongachi ant community neither lost nor gained species in the last 11 years. The high temporal stability of the Otongachi ant community is thus in line with these studies, suggesting that dispersal capabilities of tropical ant species are limited and that distribution ranges in the tropics are narrow (Deutsch et al., 2008).

This study shows that tropical leaf-litter ant communities are highly dynamic in time, on average, only half of the ant species caught in one census were recovered in the following census. This pattern is supported by many natural history observations. For example, during the course of this study at least two species, *Stenamma alas* and *Lenomyrmex wardi* (two leaf litter ant species not recorded with our traps) were common in the reserve (Ramón et al., 2013), but attempts to find them in my survey were unsuccessful. Furthermore, as opposed to ants in Winkler traps, the ants in pitfall traps presented weak indication of directional change. Hence, the Otongachi leaf litter ant community can be divided in two compartments. The Winkler compartment contains the more diverse and cryptic fauna. The pitfall compartment contains less diversity, but is formed by larger and more mobile ants (Donoso and Ramoín, 2009). With the data at hand it is unclear why the trajectories of pitfall ants show directional change, the patterns of species appearances/disappearances, and that of MRA, are all too weak to articulate mechanisms behind these patterns. But I hypothesize that the stronger response of the pitfall fauna may depend on the higher dispersal abilities of larger and long-legged ants (Kaspari and Weiser, 2007). Importantly, these same characteristics (larger ants, with higher dispersal abilities) and their propensity to show directional change make the pitfall compartment the best subset of the ant community to indicate ecological perturbation. Thus, conclusions made by short-term studies should be revisited, as species appearing/disappearing from a site may be rather the rule, difficult to separate from responses to different sources of ecological stress. More studies are needed that quantify how strong fluctuations at the species-level impact the patterns gathered from complete ant communities.

Only six species, out of 126 leaf-litter species currently known in Otongachi, were constantly among the most abundant species. Instead, up to ten other species reached high abundance in one year, but failed to keep the pace in others. Magurran and Henderson (2003) found a similar pattern, splitting core and occasional species in a fish community. Studying a stuarine fish community for 21 years, they noticed that core fish species differ in their habitat preferences from occasional species. One explanation for such split suggest that core species are well adapted to the local environment, while occasional should not and their presence in the community is likely limited by dispersal (Tsang and Bonebrake, 2016).

There is an important caveat to this study. The pattern recovered for the Otongachi ant community may be partially explained by sampling artifacts, where the amount of traps used in a year (n = 20, per trap) was insufficient to thoroughly sample the whole ant community. This may not be the case in this study because the protocol

I used here (ALL Protocol, Agosti et al., 2000) has been shown elsewhere to be robust. However, long-term datasets may still contain outlier years, where either inadequate sampling or responses to singular weather events will bias community structure. One such case may be present in my dataset. For instance, the decrease in species richness in 2011 (Fig. 1) may have impacted the rate of species appearing and disappearing in that year (Fig. 2). Whereas stronger analyses, needed to identify these outlier communities and quantify their impacts on temporal patterns, are beyond the scope of this work, it is clear that long-term monitoring may help to correct for intrinsic biases of years inadequately sampled.

In conclusion, eleven years after the first census was made in the year 2003, the Otongachi ant community presents no indication of it undergoing significant structural change. This is significant because mountain forests near the equator are already facing significant global warming (Nogués-Bravo et al., 2007; Mora et al., 2013), and because the diversity of different animal and plant groups is already declining worldwide (Butchart et al., 2010). Clearly, more effort should be put in documenting responses of insect populations to GW, especially those in global biodiversity hotspots like Andean cloud forests (Baez et al., 2016). Furthermore, the analysis presented here suggests a minor effect of temporal fluctuations of individual species on overall community composition, with direct implications to monitoring schemes that generally focus on one

or a few species within the community. Finally, continuous monitoring of the Otongachi ant community as well as information on species physiological limits, and their altitudinal and latitudinal ranges (and how these ranges are changing with time) may be essential to forecast the response of this tropical ant community to local and global perturbations.

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Appendix A.

Table A1

Incidence and abundance of ant species found in the six censuses across the eleven years combined. Symbols in parenthesis denote species removed from analyses (S = Singletons, N = Nomadic, * = Other).

| SPECIES | INCIDENCE | | | ABUNDANCE | | |
|------------------------------------|-----------|---------|-------|-----------|---------|-------|
| | Pitfall | Winkler | Total | Pitfall | Winkler | Total |
| <i>Acanthognathus teledectus</i> | | 5 | 5 | | 38 | 38 |
| <i>Acanthoponera minor</i> | | 1 | 2 | 2 | 2 | 4 |
| <i>Acromyrmex</i> EC001 (S) | 1 | 1 | 1 | | 3 | 3 |
| <i>Acropyga</i> EC001 | | 3 | 3 | | 10 | 10 |
| <i>Adelomyrmex</i> EC001 | | 3 | 3 | | 3 | 3 |
| <i>Anochetus</i> EC001 | 2 | 1 | 3 | 3 | 21 | 24 |
| <i>Anochetus</i> EC002 | 1 | 3 | 4 | 7 | 11 | 18 |
| <i>Apterostigma</i> EC001 | | 3 | 3 | | 58 | 58 |
| <i>Apterostigma</i> EC002 | 5 | 5 | 10 | 10 | 45 | 55 |
| <i>Apterostigma</i> EC003 | 3 | 5 | 8 | 17 | 26 | 43 |
| <i>Apterostigma</i> EC004 | 1 | 1 | 2 | 1 | 3 | 4 |
| <i>Apterostigma</i> EC005 | 1 | 4 | 5 | 1 | 54 | 55 |
| <i>Atta</i> EC001 (*) | 3 | | 3 | 4 | | 4 |
| <i>Azteca</i> EC001 | 4 | 4 | 8 | 378 | 13 | 391 |
| <i>Azteca</i> EC002 | | 2 | 2 | | 2 | 2 |
| <i>Brachymyrmex</i> EC001 | 3 | 6 | 9 | 6 | 142 | 148 |
| <i>Brachymyrmex</i> EC002 | 1 | 1 | 2 | 7 | 3 | 10 |
| <i>Carebara urichi</i> | 3 | 4 | 7 | 19 | 61 | 80 |
| <i>Cerapachys nr. augustae</i> (N) | | 1 | 1 | | 1 | 1 |
| <i>Cerapachys nr. toltecus</i> (N) | | 2 | 2 | | 10 | 10 |
| <i>Cerapachys splendens</i> (N) | | 2 | 2 | | 3 | 3 |
| <i>Crematogaster</i> EC001 | 1 | 5 | 6 | 1 | 85 | 86 |
| <i>Crematogaster</i> EC003 (S) | | 1 | 1 | | 1 | 1 |
| <i>Crematogaster</i> EC004 | 1 | 2 | 3 | 1 | 12 | 13 |
| <i>Cyphomyrmex</i> EC001 | 3 | 2 | 5 | 4 | 3 | 7 |
| <i>Cyphomyrmex</i> EC003 | 6 | 6 | 12 | 23 | 508 | 531 |
| <i>Cyphomyrmex</i> EC004 | 2 | 2 | 4 | 2 | 4 | 6 |
| <i>Discothyrea</i> EC001 | | 2 | 2 | | 4 | 4 |
| <i>Dorymyrmex</i> EC001 (S) | 1 | | 1 | 1 | | 1 |
| <i>Ectatomma ruidum</i> | 2 | | 2 | 7 | | 7 |
| <i>Gnamptogenys annulata</i> (*) | 2 | | 2 | 2 | | 2 |
| <i>Gnamptogenys bisulca</i> | 6 | 6 | 12 | 92 | 315 | 407 |
| <i>Gnamptogenys continua</i> | | 4 | 4 | | 43 | 43 |
| <i>Gnamptogenys</i> EC002 (S) | 1 | | 1 | 1 | | 1 |
| <i>Gnamptogenys fernandezi</i> (S) | | 1 | 1 | | 1 | 1 |
| <i>Gnamptogenys minuta</i> | 1 | 1 | 2 | 1 | 1 | 2 |
| <i>Gnamptogenys perpica</i> (*) | 2 | | 2 | 2 | | 2 |
| <i>Hylomyrma</i> EC001 | 6 | 6 | 12 | 14 | 207 | 221 |
| <i>Hypoconera distinguenda</i> | 5 | 6 | 11 | 26 | 386 | 412 |
| <i>Hypoconera</i> EC001 | | 2 | 2 | | 7 | 7 |
| <i>Hypoconera</i> EC002 | 1 | 4 | 5 | 2 | 33 | 35 |
| <i>Hypoconera</i> EC003 (S) | | 1 | 1 | | 1 | 1 |

Table A1 (Continued)

| SPECIES | INCIDENCE | | | ABUNDANCE | | |
|------------------------------------|-----------|---------|-------|-----------|---------|-------|
| | Pitfall | Winkler | Total | Pitfall | Winkler | Total |
| <i>Hypoponera</i> EC004 | 1 | 3 | 4 | 2 | 22 | 24 |
| <i>Hypoponera</i> EC005 | | 2 | 2 | | 4 | 4 |
| <i>Hypoponera</i> EC006 | | 3 | 3 | | 6 | 6 |
| <i>Hypoponera</i> EC007 | 2 | 6 | 8 | 6 | 133 | 139 |
| <i>Labidus coecus</i> (N) | 1 | | 1 | 1 | | 1 |
| <i>Labidus praedator</i> (N) | 2 | | 2 | 412 | | 412 |
| <i>Labidus spininodis</i> (N) | 2 | 1 | 3 | 746 | 201 | 947 |
| <i>Lenomyrmex foveolatus</i> | 1 | 3 | 4 | 1 | 4 | 5 |
| <i>Leptogenys</i> EC001 | 1 | 2 | 3 | 1 | 2 | 3 |
| <i>Leptogenys famelica</i> (S) | 1 | | 1 | 1 | | 1 |
| <i>Megalomyrmex bidentatus</i> | 2 | | 2 | 3 | | 3 |
| <i>Megalomyrmex</i> EC002 | 6 | 2 | 8 | 51 | 14 | 65 |
| <i>Megalomyrmex incisus</i> | | 2 | 2 | | 27 | 27 |
| <i>Megalomyrmex mondabora</i> | | 2 | 2 | | 15 | 15 |
| <i>Megalomyrmex silvestrii</i> | | 4 | 4 | | 6 | 6 |
| <i>Myrmelachista</i> EC001 | 2 | | 2 | 2 | | 2 |
| <i>Myrmelachista</i> EC002 (*) | 3 | | 3 | 3 | | 3 |
| <i>Myrmicocrypta</i> EC001 | 2 | 3 | 5 | 3 | 9 | 12 |
| <i>Neivamyrmex</i> EC001 (N) | 1 | 1 | 2 | 80 | 2 | 82 |
| <i>Neivamyrmex</i> EC002 (N) | 2 | | 2 | 2 | | 2 |
| <i>Neoponera chyzeri</i> | 4 | 1 | 5 | 37 | 11 | 48 |
| <i>Neoponera unidentata</i> | 1 | 3 | 4 | 3 | 5 | 8 |
| <i>Neoponera verenae</i> | 3 | | 3 | 22 | | 22 |
| <i>Nylanderia</i> EC001 | | 2 | 2 | | 10 | 10 |
| <i>Nylanderia</i> EC002 | 1 | 4 | 5 | 1 | 166 | 167 |
| <i>Nylanderia</i> EC004 | 2 | 5 | 7 | 12 | 638 | 650 |
| <i>Ochetomyrmex</i> EC001 (S) | 1 | 1 | 1 | | 2 | 2 |
| <i>Octostruma</i> EC001 | 1 | 6 | 7 | 7 | 403 | 410 |
| <i>Octostruma</i> EC002 | 2 | 5 | 7 | 4 | 245 | 249 |
| <i>Odontomachus bauri</i> | 5 | 3 | 8 | 18 | 24 | 42 |
| <i>Odontomachus</i> EC001 | 1 | 3 | 4 | 2 | 9 | 11 |
| <i>Pachycondyla harpax</i> | 6 | 6 | 12 | 75 | 26 | 101 |
| <i>Pachycondyla impressa</i> | 6 | 4 | 10 | 49 | 7 | 56 |
| <i>Pheidole</i> EC001 | 4 | 3 | 7 | 84 | 74 | 158 |
| <i>Pheidole</i> EC002 | 6 | 6 | 12 | 80 | 77 | 157 |
| <i>Pheidole</i> EC003 | 5 | 5 | 10 | 41 | 152 | 193 |
| <i>Pheidole</i> EC004 | 5 | 3 | 8 | 28 | 5 | 33 |
| <i>Pheidole</i> EC005 | 3 | 6 | 9 | 25 | 134 | 159 |
| <i>Pheidole</i> EC006 | 6 | 4 | 10 | 60 | 8 | 68 |
| <i>Pheidole</i> EC007 | 1 | 2 | 3 | 64 | 5 | 69 |
| <i>Pheidole</i> EC008 | 2 | | 2 | 6 | | 6 |
| <i>Pheidole</i> EC009 | 6 | 5 | 11 | 445 | 177 | 622 |
| <i>Pheidole</i> EC010 | 1 | 6 | 7 | 2 | 144 | 146 |
| <i>Pheidole</i> EC012 | 5 | 3 | 8 | 23 | 17 | 40 |
| <i>Pheidole</i> EC013 | 1 | 1 | 2 | 2 | 1 | 3 |
| <i>Pheidole</i> EC015 (S) | 1 | | 1 | 1 | | 1 |
| <i>Pheidole</i> EC016 | 2 | 5 | 7 | 3 | 138 | 141 |
| <i>Pheidole</i> EC017 | 5 | 4 | 9 | 10 | 26 | 36 |
| <i>Pheidole</i> EC018 | 3 | | 3 | 3 | | 3 |
| <i>Pheidole</i> EC020 (S) | | 1 | 1 | | 2 | 2 |
| <i>Pheidole</i> EC021 | | 2 | 2 | | 8 | 8 |
| <i>Pheidole onyx</i> | | 3 | 3 | | 62 | 62 |
| <i>Pheidole</i> sp26 (*) | 2 | | 2 | 7 | | 7 |
| <i>Pheidole</i> sp27 (S) | | 1 | 1 | | 3 | 3 |
| <i>Prionopelta amabilis</i> (*) | | 2 | 2 | | 40 | 40 |
| <i>Prionopelta modesta</i> (*) | | 3 | 3 | | 18 | 18 |
| <i>Probolomyrmex</i> EC001 (N) | | 1 | 1 | | 1 | 1 |
| <i>Proceratium convexiceps</i> (S) | | 1 | 1 | | 1 | 1 |
| <i>Procryptocerus</i> EC001 (S) | 1 | | 1 | 2 | | 2 |
| <i>Protalaridris armata</i> | | 5 | 5 | | 29 | 29 |
| <i>Pseudoponera gilberti</i> | | 3 | 3 | | 13 | 13 |
| <i>Rasopone becculata</i> | 1 | 3 | 4 | 1 | 3 | 4 |
| <i>Rhopalothrix</i> EC002 | | 2 | 2 | | 8 | 8 |
| <i>Rogeria blanda</i> | | 6 | 6 | | 51 | 51 |
| <i>Rogeria</i> EC002 | | 3 | 3 | | 12 | 12 |
| <i>Solenopsis</i> spp | 6 | 6 | 12 | 157 | 3332 | 3489 |
| <i>Stigmatomma lurilabes</i> (S) | | 1 | 1 | | 2 | 2 |
| <i>Strumigenys</i> EC001 | | 6 | 6 | | 206 | 206 |
| <i>Strumigenys</i> EC002 | | 3 | 3 | | 6 | 6 |
| <i>Strumigenys</i> EC003 | | 4 | 4 | | 23 | 23 |
| <i>Strumigenys</i> EC004 | 1 | 5 | 6 | 1 | 22 | 23 |
| <i>Strumigenys</i> EC005 (S) | | 1 | 1 | | 11 | 11 |
| <i>Strumigenys</i> EC007 (S) | | 1 | 1 | | 1 | 1 |
| <i>Strumigenys</i> EC009 (S) | | 1 | 1 | | 9 | 9 |

Table A1 (Continued)

| SPECIES | INCIDENCE | | | ABUNDANCE | | |
|-------------------------------|-----------|---------|-------|-----------|---------|-------|
| | Pitfall | Winkler | Total | Pitfall | Winkler | Total |
| <i>Strumigenys</i> EC010 | | 3 | 3 | | 12 | 12 |
| <i>Strumigenys</i> EC013 | | 2 | 2 | | 15 | 15 |
| <i>Strumigenys</i> EC014 | | 2 | 2 | | 3 | 3 |
| <i>Tapinoma</i> EC001 | (S) | 1 | 1 | | 1 | 1 |
| <i>Tatuidris tatusia</i> | 1 | 3 | 4 | 7 | 8 | 15 |
| <i>Thaumatomyrmex zeteki</i> | | 2 | 2 | | 2 | 2 |
| <i>Trachymyrmex</i> EC001 | (S) | 1 | 1 | 1 | | 1 |
| <i>Trachymyrmex</i> EC002 | (S) | 1 | 1 | 1 | | 1 |
| <i>Typhlomyrmex pusillus</i> | | 3 | 3 | | 18 | 18 |
| <i>Wasmannia auropunctata</i> | | 7 | 11 | 16 | 103 | 119 |
| TOTAL | | 571 | 1251 | 3248 | 9094 | 12342 |

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