Ground-dwelling ant assemblages severely degrade in oil-palm plantations – a case study from the Golfo Dulce region, SW Costa Rica

Martin Falk, Christian H. Schulze & Konrad Fiedler

Due to the rising demand for bio-fuels and plant oils, and fostered by high economic benefits, the area of oil palm cultivation is tremendously increasing all over the tropics. This development has spilled over to Costa Rica during the past 20 years, with manifold potentially negative effects on biodiversity. We surveyed ground-dwelling ants in 5 oil palm plantations, in comparison to 5 old-growth and 5 secondary forest sites in the Golfo Dulce region (SW Costa Rica), to assess the magnitude of faunal impoverishment in these agro-ecosystems. By combining hand sampling with pitfall traps and the Winkler method, we observed 136 ant species from 44 genera and 9 subfamilies during two months in the year 2015: 34 species in oil palm plantations, 76 species in secondary forest, and 90 species in old-growth forest. On average, individual old-growth forest sites harbored more than twice as many ant species as plantations, with secondary forest taking an intermediate position. Litter samples from Winkler bags contributed a far lower proportion of ant species in plantations, compared to secondary and especially old-growth forest. Hence, the litter fauna is particularly severely hit by converting forest into plantations. Secondary forest showed the largest variation in species composition between individual sites, whereas ant assemblages of oil palm plantations were the most uniform. Our data show that assemblages of ground-dwelling ants are severely impoverished in oil palm plantations (ca 50 % reduction in species). Young regenerating secondary forest harbored distinctly fewer ant species than old-growth stands, but was far less impoverished than plantations and thus of substantial conservation value.

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Aufgrund ihrer hohen Rendite nimmt die Kultivierung der Ölpalme in allen Tropenregionen der Erde massiv zu. In den letzten 20 Jahren hat diese Entwicklung auch Costa Rica erreicht, mit vielfachen negativen Folgen für die Biodiversität. Wir haben die bodenlebenden Ameisen in 5 Ölpalmplantagen, 5 jungen Sekundärwäldern und an 5 Standorten im weitgehend naturnahen Tieflandregenwald in der Golfo-Dulce-Region (SW Costa Rica) erfasst, um das Ausmaß der Faunenveränderungen zu quantifizieren. Mittels Handaufsammlungen, Bodenfallen und Winkler-Extraktion wiesen wir in 2 Monaten 136 Ameisenarten aus 44 Gattungen und 9 Unterfamilien nach: 34 Arten in Plantagen, 76 Arten im Sekundärwald und 90 Arten im Regenwald. Im Mittel beherbergten Regenwaldstandorte etwa doppelt so viele Arten wie Plantagen, während Sekundärwälder intermediären Reichtum aufwiesen. Streuproben lieferten in den Plantagen einen besonders geringen Beitrag zur Artenvielfalt. Standorte im Sekundärwald zeigten die größte Variabilität in der Zusammensetzung ihrer Ameisenfauna, während in Ölpalmplantagen die Ameisengemeinschaften besonders einförmig waren. Unsere Studie bestätigt damit den enormen Biodiversitätsverlust in Ölpalmplantagen am Beispiel von Ameisen (Rückgang der Artenzahl um ca. 50 %). Junge Sekundärwälder wiesen hingegen eine deutlich weniger verarmte Fauna auf, was ihren naturschutzfachlichen Wert (etwa im Kontext der Waldregeneration) unterstreicht.

Keywords: *Elaeis guineensis*, Formicidae, land use, secondary forest, tropical biodiversity loss.

Introduction

Ants are among the most dominant terrestrial animals on Earth, with a high diversity and prevalence especially in tropical regions (Hölldobler & Wilson 1990, Lach et al. 2010). Besides humans and their livestock, ants are the main heterotrophic land organisms in terms of biomass. Ants play essential roles in soil perturbation and in energy and nutrient flow through ecosystems (Lobry de Bruyn & Conacher 1990, Hölldobler & Wilson 1990, Nkem et al. 2000). They are the leading predators of other insects and small invertebrates (Blüthgen & Feldhaar 2010), and they are key to many mutualistic interactions with plants, fungi or other animals (Rico-Gray & Oliveira 2007, Voglmayr et al. 2011, del Toro et al. 2012). In the Neotropical realm, leaf-cutting ants are the most destructive insect herbivores (Wirth et al. 2003). Hence, changes in ant communities may trigger massive effects on ecosystem services and functions.

Habitat loss through the ever growing demand for agricultural production areas is one of the major drivers of global biodiversity loss (Newbold et al. 2015). In humid tropical regions, the increasing cultivation of oil palms (*Elaeis guineensis*) poses a severe threat to biodiversity (Fitzherbert et al. 2008, Turner et al. 2008, Wilcove & Koh 2010, Prescott et al. 2015, Pardo et al. 2018a, 2018b). In Costa Rica, cultivation of oil palm has massively grown during the last 20 years, particularly in the Southern Pacific region, where 64 % of the current plantations and more than 50 % of the area identified as being suitable for establishing new plantations are located (Beggs & Moore 2013). The cultivation of oil palms did not necessitate forest clear-cutting (Vijay et al. 2016), as especially large tracts of areas on plain ground that had formerly been stocked with other cultivated plants or used as pastures were converted into oil palm plantations (Carlson et al. 2012, Höbinger et al. 2012). As a consequence, most old-growth lowland forest nowadays persisting in Costa Rica is situated on more or less steep slopes (Weissenhofer et al. 2008).

Multiple studies have shown that animal assemblages in oil palm plantations are dominated by only a few species, though some of these may reach very high abundance (Danielsen et al. 2008). In particular, the fate of ants in oil palm plantations has received considerable attention by scientists, though mostly in SE Asia (Brühl & Eltz 2010, Fayle et al. 2010, Pfeiffer et al. 2008). Lowest ant species richness was found in oil palm plantations relative to other forested habitats (Brühl & Eltz 2010). As oil palm plantations are structurally more homogeneous than forests, they may also have a lower beta diversity due to an increased importance of widespread generalists and a reduced number of rare species depending on specific food sources or nesting sites (Fayle et al. 2010, Wang & Foster 2015).

One reason for the dominance of just a few ant species in oil palm plantations is the massive reduction of possible nesting sites and foraging grounds in the litter layer, due to the near complete absence of leaf litter (Brühl & Eltz 2010, Fayle et al. 2010). Furthermore, the establishment and survival of shade adapted ant species is constrained by hot and dry conditions that may transiently occur in plantations during the dry season (Brühl & Eltz 2010). Also the abundance of arboreal ant species is much higher in forest than in oil palm plantations (Pfeiffer et al. 2008, Fayle et al. 2010). Thus, species as well as functional diversity of ants massively degrades when converting tropical forest into oil palm plantations. For example, Fayle et al. (2010) observed in Malaysia that total ant species richness decreased from 309 to 110 (64 % loss), and leaf-litter ant species richness even from 216 to 56 (74 % loss), between primary forest and oil palm plantations.

Spontaneously regenerating secondary forest (e.g. after agricultural or forestry use of a site has been abandoned) can be understood as a successional transition back to a more natural rainforest ecosystem. Multiple studies have shown that the fauna of tropical secondary forest has a higher species diversity than plantations, but a lower diversity than old-growth forest (for ants: Schonberg et al. 2004, Bihn et al. 2010, Brühl & Eltz 2010, Klimes et al. 2012; for other wildlife: Gibson et al. 2011). Case studies in the Golfo Dulce region in SW Costa Rica revealed that bird species diversity at forest margin sites was even higher than inside old-growth forest (Mollik 2013) and no significant differences of amphibian and reptile species diversity were observed between old-growth forest interior and forest margin sites (Gallmetzer & Schulze 2015). Similarly, moth species diversity was drastically reduced in oil palm plantations, but no substantial differences were found between old-growth forest interior, forest margin sites, and secondary forest (Alonso et al. 2017). Other taxa, such as amphibians, appear to recover even more rapidly, reaching not only similar species richness, but also a similar species composition in Costa Rican young secondary forests (10–16 years) in comparison to old-growth forests (Hilje & Aide 2012). Secondary forests are attaining ever higher importance for biodiversity conservation as well as from a functional perspective, given that remnants of near-natural forest areas are under severe pressure everywhere (Chazdon 2014).

Even though biodiversity in oil palm plantations has almost invariably turned out to be lower than in forest ecosystems, the magnitude of biodiversity loss varies across biogeographical regions and between focal taxa, and depends on the wider landscape context (e.g. Pardo et al. 2018a, 2018b). Hence, it is important to empirically assess the response of animals to conversion of forest into oil palm plantations, as well as to spontaneous forest regeneration on land that had previously been deforested, in every region where oil palm expansion is of environmental concern (Turner et al. 2008, Foster et al. 2011). Along these lines, we studied ground-layer ant assemblages in old-growth and secondary forest and compared these communities to oil palm plantations in a tropical lowland area of SW Costa Rica. Specifically, we tested the following hypotheses:

(1) Ant species richness is very substantially reduced in oil palm plantations, intermediate in secondary forest, and highest in old-growth forest. Especially leaf litter ants are underrepresented in plantations because of the near-complete absence of a litter layer.

(2) Species composition of ant assemblages differs between all three habitat types, with oil palm plantations showing the most distinct and least variable communities through the homogenizing effects of recurrent interventions during plantation management.

(3) Ant communities of oil palm assemblages are impoverished nested subsets of those found in old-growth forest.

Material and methods

Study area and study sites

Study sites were selected within marginal areas of the Piedras Blancas National Park (Puntarenas province) and in its surroundings, near the Research Station La Gamba (8°42′3″N, 83°12′6″W). The area is characterized by oil palm plantations, pasture areas and a tropical rural landscape mosaic on plain ground, while old-growth forest persists on slopes (Höbinger et al. 2012). Tracts of secondary forest are either found at the border of the

national park, or occur interspersed in cultivated areas. The average annual precipitation is about 6,000 mm and the annual mean temperature is 28.5° C (Weissenhofer & Huber 2008).

We sampled ground-dwelling ants in old-growth forest, secondary regenerating forest and oil palm plantations at elevations between 70–250 m (Fig. 1). While old-growth forest and secondary forest sites were located on hilly terrain, all oil palm plantations were situated on the relatively plain valley floor. In each habitat type, five replicate plots were chosen, all 40 m × 40 m = 1600 m² in size. Neighboring study sites were separated by a minimum distance of 400 m.

Oil palm plantations are simply structured and even aged, with sparse ground cover and almost free of leaf litter (Brühl & Eltz 2010; Weissenhofer et al. 2008). They are cleared and replanted on a 25–30 year rotation (Fitzherbert et al 2008). All selected oil palm plantations in our study area were at least 2 ha in size, with palms of more than 10 m in height. The understory vegetation was free of woody shrubs and only consisted of a sparse herb layer covering less than 50 % of the ground due to frequent herbicide application. In contrast, our old-growth forest sites were strongly heterogeneous with regard to tree size and age, tall trees reaching up to 50 m in height. This forest type is characterized by a high species diversity of trees and other vascular plants and harbors a thick leaf litter layer (Weissenhofer et al. 2008). We use the term old-growth forest here to emphasize that we cannot exclude the possibility that single trees were selectively cut in the past.

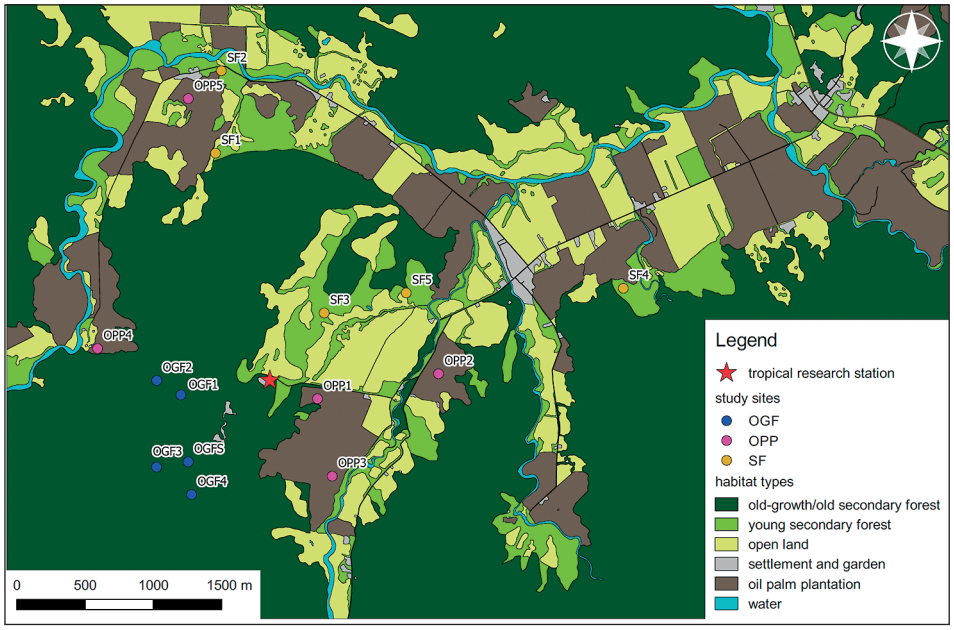


Fig. 1: Schematic map of the study area in the surroundings of the Research Station La Gamba (8°42′3″N, 83°12′6″W; red asterisk). Location of study sites in the three habitat types indicated by colored circles: old-growth forest (OGF, blue), secondary forest (SF, orange) and oil palm plantation (OPP, purple). – Abb. 1: Lage der Sammelstandorte in der Umgebung der Tropenstation La Gamba (8°42′3″N, 83°12′6″W; roter Stern). OGF: alter Regenwald (blau); SF: Sekundärwald (orange); OPP: Ölpalmplantage (violett).

However, during the last 80–100 years, these forest tracts remained largely undisturbed and their vegetation structure closely resembles natural lowland forests of the Golfo Dulce region. All old-growth forest sites were located near or on ridges (see Hofhansl 2014 for ecosystem differences between old-growth forest types in the region relative to topography). Finally, stretches of secondary forest exist on areas that had been cleared, but are now undergoing spontaneous forest regeneration for the past 10–15 years. Secondary forests show a less heterogeneous three-dimensional structure, rather dense ground cover, lower tree species diversity and also a smaller number of tree individuals per unit area than old-growth forest (Weissenhofer et al. 2008; see Alonso Rodríguez 2014 for data on stand structure from the study region). All selected secondary forest stands were larger than 1 ha.

Sampling of ants

Field work was conducted during the rainy season in June and July 2015. To representatively cover the ground-dwelling ant fauna, it is important to apply more than one method of collecting (Agosti et al. 2000, Bestelmeyer et al. 2000). Therefore, we used pitfall trapping, hand sampling and the Winkler method in combination. A schematic example for the spatial arrangement of the application of the three sampling methods per site is shown in Fig. 2.

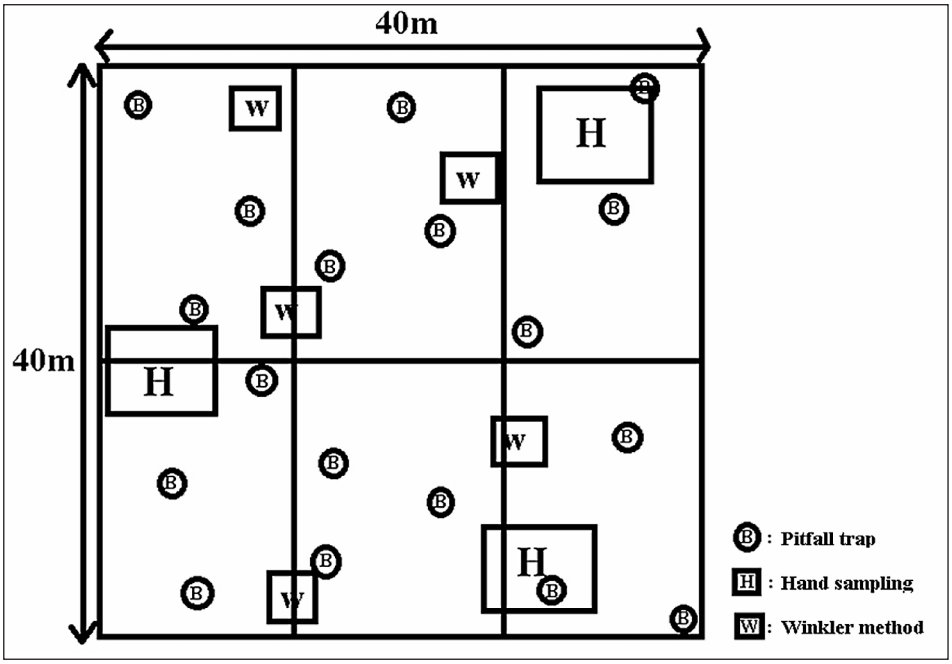


Fig. 2: Schematic representation of the locations of pitfall traps, Winkler sampling and hand sampling within each study site. In order to avoid spatial clustering of sampling micro-sites within the plot, the area was subdivided into 6 subareas for better orientation during field work. – Abb. 2: Schema der räumlichen Anordnung der verschiedenen Probennahmen (Bodenfallen, Handaufsammlung, Streuproben zur Winkler-Extraktion) auf den Probeflächen. Um eine räumliche Klumpung der Probennahmen innerhalb der Fläche zu vermeiden, wurde diese zur besseren Orientierung bei der Feldarbeit in 6 Teilflächen unterteilt.

Pitfall trapping

Pitfall traps capture surface-active ants that fall into a container placed in the ground (Agosti et al. 2000). As containers, we used 200 ml plastic drinking cups (diameter: 6.5 cm), filled with propylene glycol mixed with ethanol as preservation liquid. Pitfall traps were first left for two days in the ground, before filling them with preservation liquid. Then, traps were kept active for two more days. To prevent sample loss by inundation from rainfall a plastic soup plate (diameter: 15 cm) was placed as a roof over every trap. We distributed 18 pitfall traps randomly across every plot. After retrieval, samples were transferred into 70 % ethanol.

Hand sampling

This is a suitable method to collect ants foraging on the ground and in lower vegetation layers, thereby covering different microhabitats within an area (Agosti et al. 2000). In addition, by hand sampling one can collect larger leaf litter and slow moving ants which are not always reliably surveyed with pitfall traps. At each site, three randomly selected subplots (5 m × 6 m = 30 m² in size) were searched for foraging ants, each over a time span of 30 min during daylight hours. Hence, ants were sampled by hand on the entire plot for a total duration of 90 min. We caught all ants which moved about on the soil, litter or lower herb vegetation with forceps or an aspirator (Agosti et al. 2000, Tista & Fiedler 2011). We also turned stones, twigs, palm leaves or other ground material (Brühl & Eltz 2010). All sampled ants were preserved on site in 70 % ethanol.

Winkler method

Winkler extraction is an efficient method to record leaf-litter ants (Agosti et al. 2000). For this purpose, all litter from 1 m² of ground was removed and manually sifted with a sieve with a wire mesh of 1 cm (Tista & Fiedler 2011). The litter was then filled into the inner bag of a Winkler sack which consisted of nets with a mesh width of 6 mm. After closing the upper end of the Winkler sack, throughout the next three days ants were allowed to fall into a jar filled with 70 % ethanol at the lower end (Tista & Fiedler 2011). At each study site we randomly chose five replicate subplots for litter removal, resulting in a total area sampled of 5 m^2 per plot. Also all ants extracted from the leaf litter were preserved in 70 % ethanol.

All ant vouchers are deposited in the collections of the Natural History Museum, Vienna.

Ant identification and species' ecological traits

Worker ants were identified under a stereomicroscope to genus level and were further segregated within each genus into morpho-species, mainly using the internet data-base www.antweb.org (v7.34.4, last accessed 10/07/2018). Morpho-species of the same ant genus were differentiated from one another on the basis of multiple character differences, for example with regard to body size, color, presence or absence of spines, hairiness, cuticle sculpture, etc. In genera known for worker polymorphism, vouchers showing only slight morphological differences were treated as one species, when collected at the same place, especially if one morpho-type occurred much more often than the second. The few alate females and males obtained in pitfall or hand samples were discarded, since it is unknown whether these originated from colonies living at the sampling sites. Information on ecological traits of ants was mainly retrieved from the data-base www.antwiki.org (last accessed: 11/07/2018) and from Brandão et al. (2012).

Data analysis

For statistical analyses of ant biodiversity, we only used presence-absence coding, since ants as eusocial insects often show a highly clumped representation in ecological field samples. Accordingly, worker numbers will often be higher in samples drawn near nest sites or ant trails. After morpho-species sorting, data were entered into a spread-sheet program for subsequent management and retrieval. Primarily, we extracted two types of tabulated data: (1) the numbers of ant species and the proportions of various ant groups (subfamilies or ecologically important groups such as army ants and leaf-cutter ants) per site; and (2) a species × site × sample type matrix for analyses of species composition on habitat level.

Using the software packages PAST 3.26 (Hammer et al. 2001), box-whisker plots and one-way analyses of variance by ranks (Kruskal-Wallis ANOVA) served to analyze differences in species richness per site and for the comparison of sampling methods between habitat types. We further compared overall ant richness of the three habitat types by means of species accumulation analysis (calculated with iNext Online; Chao et al. 2016), treating each sample type from every site as a replicate unit of analysis and extrapolating (two-fold) to 30 sample units per habitat type.

Species composition was analyzed based on a Soerensen similarity matrix. We visualized sample composition by means of unconstrained ordination (non-metric MDS) and tested for possible differences between habitat types and sampling methods by a two-way permutational analysis of variance (PERMANOVA, 9999 permutations) using the software packages PRIMER 7.0.13 (Clarke & Gorley 2006) and PERMANOVA+ for PRIMER (Anderson et al. 2008), respectively. Faunal nestedness was assessed using a program developed by Strona (2015) with 100 replicates in null model analysis.

Results

Species richness

Altogether, 4752 worker ants were collected, belonging to 136 morpho-species out of 44 genera in 9 subfamilies. In total, 36 species were found in the oil palm plantations, 76 species in secondary forest, and 90 species in old growth forest. Species accumulation analysis (Fig. 3) indicated that, while the ants to be expected in oil palm plantations were already largely covered by sampling (coverage: 0.913), many more ant species awaited discovery in secondary (coverage: 0.805) and old-growth forest (coverage: 0.834). Overall, ant species richness in both forest types was significantly higher than in oil palm plantations, as indicated by the non-overlapping 95 % confidence intervals of the species accumulation curves for oil palm plantations versus the two forest types (Fig. 3).

Ant species numbers were unevenly distributed across the subfamilies (Fig. 4). Representatives of Myrmicinae were present in all three habitat types in high species numbers. Ponerinae ants were substantially more prevalent in old-growth forest than in secondary forest or plantations. Richness of Formicinae was greatly reduced in oil palm plantations compared to secondary and old-growth forest, whereas the subfamilies Heteroponerinae and Proceratiinae were only found in old-growth forest. Overall, gross taxonomic composition of ant assemblages was most complex in old-growth forest and most simplified in oil palm plantations.

Differences between habitat types in species numbers recorded per site were highly significant (Fig. 5). Oil palm plantations (mean 17.6 species/site) showed the lowest richness, old-growth forest (mean 36.4 species/site) the highest, and secondary forest (mean 26.9 species/site) an intermediate richness. On average, oil palm plantation sites reached 48.4 %

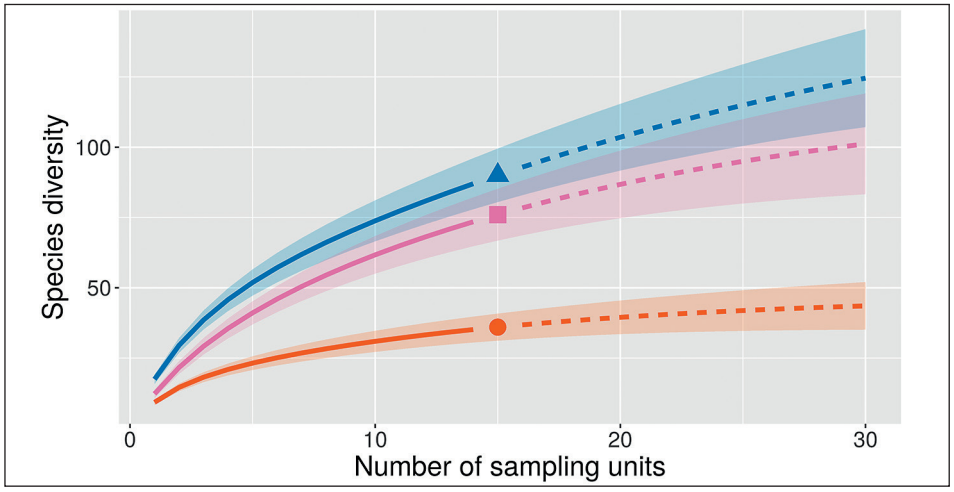


Fig. 3: Rarefaction (solid) and extrapolation curves (dashed) for ant species in oil palm plantations (brown), secondary forest (purplish) and old-growth forest (blue). Symbols: observed species richness. Shaded areas around curves are 95 % confidence limits. – Abb. 3: Interpolation (durchgezogene Kurven) und Extrapolation (gestrichelt) des Artenreichtums von Ameisen in Ölpalmplantagen (braun), Sekundärwald (violett) und Regenwald (blau). Symbole geben beobachteten Artenreichtum an, die schattierten Bereiche die 95 %-Vertrauensbereiche der Kurven.

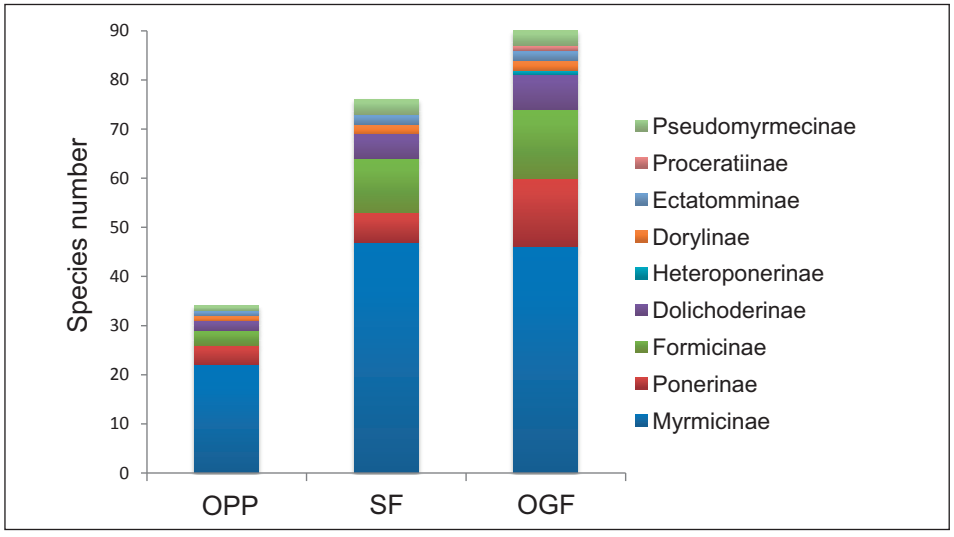


Fig. 4: Subfamily composition of ground-dwelling ant assemblages in the three studied habitat types. OPP: oil palm plantations; SF: secondary forest; OGF: old-growth forest. – Abb. 4: Zusammensetzung der Ameisen-Gemeinschaften auf Unterfamilien-Ebene. OPP: Ölpalmplantagen; SF: Sekundärwald; OGF: Regenwald.

and secondary forest 73.9 % of the mean ant species richness observed at old-growth forest sites. Interestingly, when using the combined number of worker ants recorded by the three sampling methods per site as a proxy of overall ant abundance, no consistent difference between the three habitat types was apparent (H_{2df} = 2.94; p = 0.23).

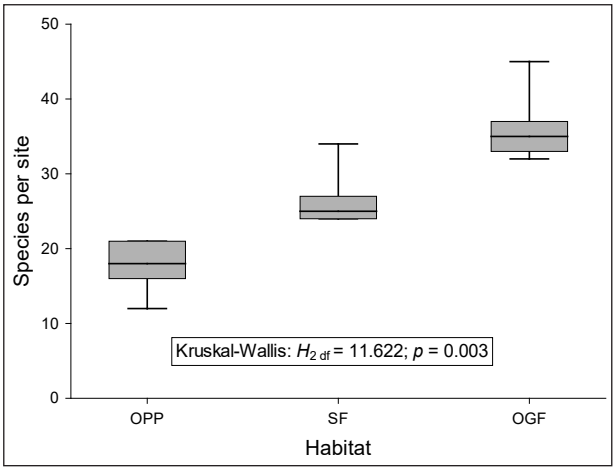


Fig. 5: Ant species richness per site compared across oil palm plantations (OPP), secondary (SF) and old-growth forest (OGF). Line: median; box: inter quartile range, whiskers: range of observed values. – Abb. 5: Artenreichtum der Ameisen pro Standort, im Vergleich von Ölpalmplantagen (OPP), Sekundärwäldern (SF) und Regenwaldstandorten (OGF). Querlinie: Median, Kasten: Interquartilbereich; Streuungsbalken: Spannweite der Werte.

Contribution of specific ant groups

In total, 64 (of 136) ant species were retrieved at least once from a leaf-litter sample by the Winkler method. These ants contributed 2–8 species per site in oil palm plantations, 9–18 species in secondary forest, and 14–28 species in old-growth forest. The proportion of ant species recorded in Winkler samples relative to the total species number per site was lowest in oil palm plantations and highest in old-growth forest (Fig. 6).

We observed three species of army ants (two species of *Labidus*, one of *Eciton*) at the 15 study sites. Army ants were observed in four plantations and at four secondary forest sites, but only in two old-growth forest sites. Hence, army ants tended to be slightly less prevalent in old-growth forest (Kruskal-Wallis ANOVA: H_{2df} = 5.579; p = 0.061).

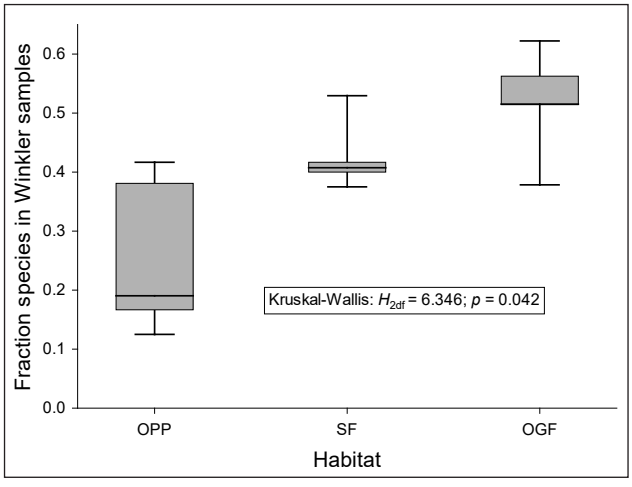


Fig. 6: Proportion of ant species retrieved from litter samples relative to total ant species number per site, across oil palm plantations (OPP), secondary (SF) and old-growth forest (OGF). – Abb. 6: Artenanteil der Ameisen aus Laubstreu-Extraktionen, im Vergleich von Ölpalmplantagen (OPP), Sekundärwäldern (SF) und Regenwaldstandorten (OGF). Querlinie: Median, Kasten: Interquartilbereich; Streuungsbalken: Spannweite der Werte.

Three species of leaf-cutter ants (two species of *Acromyrmex*, one of *Atta*) plus a range of other fungus-growing ants (in the genera *Apterostigma*, *Cyphomyrmex*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*) showed up during our surveys. However, the relative contribution of these fungus growers to local ant species richness did not differ consistently between the three habitat types (H_{2df} = 1.580; p = 0.454).

Species composition

A representation of the species × site matrix by means of an unconstrained ordination (non-metric MDS, stress = 0.22, Fig. 7) revealed clear differences in ant species composition between all three habitat types, but with little overlap. Along the first ordination axis, ant assemblages differentiated from old-growth forest (to the left) towards oil palm plantations (to the right). The second ordination axis reflected sampling methodology, with hand samples attaining high values, pitfall samples intermediate values, and Winkler samples lowest axis scores. These differences were all significant (two-way PERMANOVA; habitat type: F = 7.822, sample type: F = 3.315; both p < 0.001; habitat × sample interaction: F = 1.325, p = 0.044).

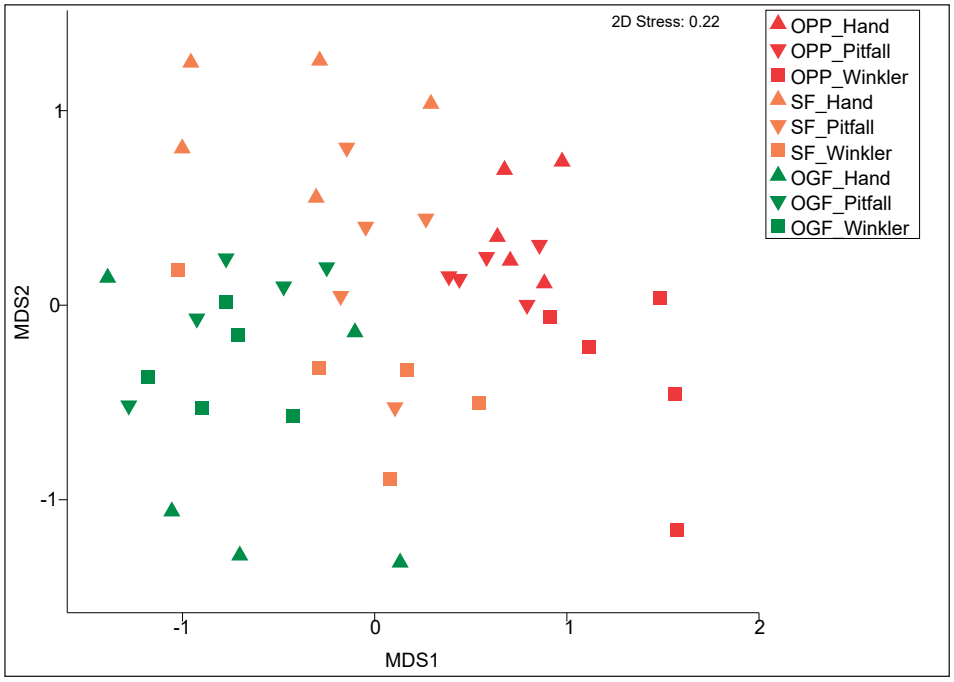


Fig. 7: Non-metric MDS ordination plot of the ant assemblages of the 15 study sites, further segregated according to the sampling method, based on species incidence data. OPP = oil palm plantations (red), SF = secondary forest (orange), OGF = old-growth forest (dark-green). Upright triangles – hand samples; inverse triangles – pitfall trap samples; squares: Winkler litter samples. – Abb. 7: Ordinationsdiagramm der Ameisen-Aufsammlungen, gegliedert nach Standorttyp und Methodik der Erfassung. OPP: Ölpalmplantagen (rot); SF: Sekundärwald (orange); OGF: Regenwald (grün). Aufrechte Dreiecke: Handaufsammlungen; umgekehrte Dreiecke: Bodenfallen; Quadrate: Winkler-Extraktionen.

Inspection of the ordination plot suggested that ant assemblages of oil palm plantations were the most homogeneous and those from secondary forest sites the most heterogeneous. An index of multivariate dispersion (MVDISP routine in PRIMER7) confirmed that notion. Here, index values below 1.00 indicate relative clumping, and those larger than 1.00 indicate high dispersion of samples. This index was 0.697 for ants in plantations, 1.005 for old-growth forest, and 1.298 for secondary forest samples.

A total of 35.3 % (48 species) of all observed ant species were only collected in old-growth forest, 21.3 % (29 species) in secondary forest, while only 4.4 % (6 species) were unique to oil palm plantations (Fig. 8). On the genus level, nine ant taxa were only found in old-growth forest (*Acanthoponera, Acropyga, Anochetus, Ectatomma, Hylomyrma, Leptogenys, Myrmecocrypta, Probolomyrmex, Tapinoma*), and six only in secondary forest (*Adelomyrmex, Cephalotes, Eciton, Linepithema, Nesomyrmex, Rogeria*), but no single ant genus only showed up exclusively in oil palm plantations. Some ant species were collected in 12 or more of the 15 study sites (for example certain representatives of *Odontomachus, Pachycondyla*, and *Nylanderia*), while others were collected in four or more study sites of one habitat type but nearly never in one of the other two habitat types (for example in plantations: *Acromyrmex* and some *Pheidole* species; in old-growth forest: *Brachymyrmex* and *Trachymyrmex*). 34 unique species (i.e. species only collected at one of the 15 study sites) were found in old-growth forest, 22 in secondary forest and only three in oil palm plantations.

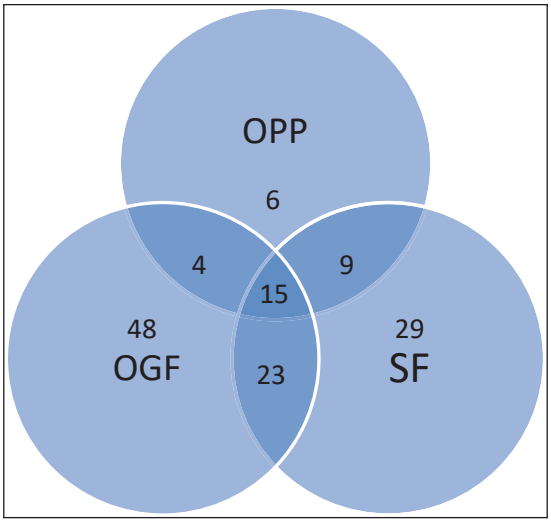


Fig. 8: Venn diagram showing numbers of exclusive and shared ant species across the three habitat types. – Abb. 8: Venn-Diagramm der Ameisen-Artenzahlen in den drei Habitattypen.

The results above indicate that species richness of local ground-dwelling ant assemblages decreases severely from old-growth across secondary forest to oil palm plantations. Yet it remains to be addressed whether the concomitant shift in ant species composition primarily reflects a pauperization of the communities or whether true species turnover also plays a role. We therefore analyzed the ant assemblages of the 15 sites for the strength of nestedness in community patterns. If communities were fully nested, all assemblages of lower richness should represent subsets of the richer communities. Our analyses indeed revealed that the local ant assemblages along the gradient from old-growth forest to oil palm plantations were highly and significantly nested ($NODF_{sites}$ = 40.671, matrix

temperature T = 33.376; for the null model of proportional row and column totals: z = –6.634 and z = 14.319, respectively; p<0.001). The maximally ordered species × site matrix is shown in Figure 9.

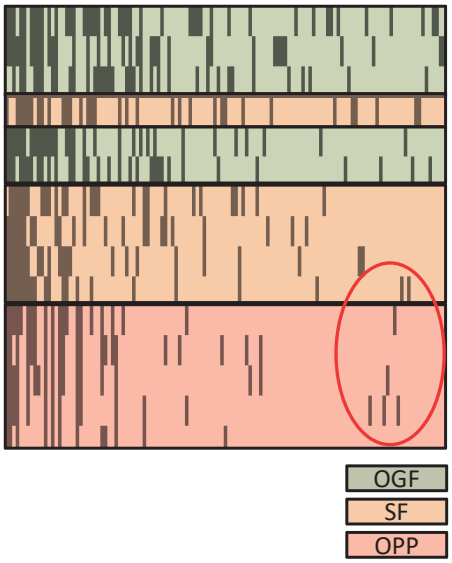


Fig. 9: Visual representation of the maximally ordered species × site matrix of ground-dwelling ants. Rows: sites; columns: ant species. Species-poor assemblages are subsets of richer ones, indicating a gradient of faunal impoverishment from old-growth forest (OGF) towards oil palm plantations (OPP). Only few ant species (marked with red ellipse) deviate from that pattern and can thus be interpreted as beneficiaries of land-use. – Abb. 9: Visualisierung der maximal geordneten Arten-Standorts-Matrix. Zeilen: Standorte; Spalten: Arten. Artenarme Gemeinschaften sind Teilmengen der artenreicheren, was einen Gradienten der Verarmung vom Regenwald (OGF) hin zu den Ölpalmplantagen (OPP) anzeigt. Nur wenige Ameisenarten (markiert mit roter Ellipse) können als Nutznießer der Plantagen angesehen werden.

Discussion

Species richness

Oil palm plantations harbored by far the lowest richness of ground-dwelling ants (36 species), i.e. about one third of the total species number observed in old-growth forest (90 species) and only a quarter of the total ant species richness observed near La Gamba in this study (136 species). This corresponds well with other studies in which species richness of ants was found to be up to five times higher in primary forest than in plantations (Brühl & Eltz 2010, Fayle et al. 2010, Pfeiffer et al. 2008). One important reason for these massive differences is the almost complete absence of leaf litter in plantations which reduces availability of nest sites and foraging opportunities (Carvelho & Vasconcelos 1999). This affects in particular those 'cryptic' ant species which predominantly forage in soil and litter and rarely show up above ground. Cryptic leaf litter ants are a hallmark of tropical rainforest ant assemblages (King et al. 1998). The distribution of a substantial litter stratum explains the higher species number of Ponerinae in old-growth forest as well as the total absence of the ant subfamilies Proceratiinae and Heteroponerinae in secondary forest and plantations. The far lower contribution of ants sampled by the Winkler method in oil palm plantations underpins the impoverishment of the litter fauna in this agro-ecosystem.

Moreover, the temporarily hot and dry microclimatic conditions in plantations, compared to primary and secondary forest (Turner & Forest 2006), may prevent colony establishment of shade-adapted forest ants in plantations. Food availability might also be critical for ant species with specialized diets, whose resources might be lacking in plantations (Andersen 2000). Surprisingly, however, we did not observe a lower representation for

army ants and fungus growers in oil palm plantations relative to the forest. Nevertheless, our data confirm that the ecological conditions in oil palm plantations act as a severe filter which prevents a large fraction of ants from the regional species pool to colonize such sites.

Secondary forests harbored far more ant species than oil palm plantations, but fewer species than old-growth forest. This reflects, on the one hand, the lower complexity and thus lower number of niches in regenerating forest, compared to old-growth forest. For example, Dunn (2004) showed that ants re-colonize regenerating areas after disturbance, which leads to an increasing number of ant species during secondary forest succession. Accordingly, the recovery of ant species richness in tropical forests could be complete after 20–40 years of succession, provided that re-colonization is possible from the surrounding landscape (Hethcoat et al. 2019). On the other hand, the relatively high ant species numbers observed at our young secondary forest study sites underpins the potential of areas left to spontaneous regeneration for biodiversity conservation. Already after 10–15 years, these habitats had accumulated a substantial fraction of the ant fauna seen in old-growth forest.

The increase of ground-dwelling ant species richness from oil palm plantations across secondary towards old-growth is also explicable with the different vegetation structure of these habitat types (Philpott et al. 2008). Ant biodiversity is often very closely related to heterogeneity and structural complexity of habitats (e.g. Bestelmeyer & Wiens 2001). Plantations have the simplest, secondary forests a more strongly differentiated, and primary forests a particularly complex vegetation structure (Chazdon 2014). Alonso Rodríguez (2014) confirmed for the region around La Gamba that oil palm plantations have lowest plant species richness, vegetation density and complexity, whereas these attributes attain much higher values in secondary and especially in old-growth forest. In ants, anthropo-

Tab. 1: Species richness of ants, butterflies (Wiemers & Fiedler 2008), understory birds (Mollik 2013), bats (Freudmann et al. 2015), amphibians and reptiles (Gallmetzer & Schulze 2015) and two moth subfamilies (Alonso Rodríguez et al. 2017, figures amended by personal communications of D. Rabl and G. Brehm) in oil palm plantations around La Gamba, compared with old-growth and secondary (or disturbed) forest. – Tab. 1: Artenreichtum von Ameisen, Tagfaltern (Wiemers & Fiedler 2008), Unterwuchsvögeln (Mollik 2013), Fledermäusen (Freudmann et al. 2015), Amphibien und Reptilien (Gallmetzer & Schulze 2015) und zwei Nachtfalter Unterfamilien (Alonso Rodríguez et al. 2017, Zahlen durch persönl. Mitteilungen von D. Rabl and G. Brehm ergänzt) in Ölpalmplantagen um La Gamba, verglichen mit Regenwald und Sekundärwald (bzw. gestörtem Wald).

Group	Total	Number of recorded species (% of species total)		
		Oil-palm plantation	Secondary forest (incl. forest margins)	Old-growth forest
Ants	136	34 (25.0)	76 (55.9)	90 (66.2)
Birds	77	23 (29.9)	54 (70.1)	47 (61.0)
Bats	36	20 (55.6)	22 (63.9)	28 (75.0)
Amphibians	28	11 (39.3)	20 (71.4)	22 (78.6)
Reptiles	19	7 (36.8)	12 (63.1)	13 (68.4)
Butterflies	118	47 (39.8)	59 (50.0)	70 (59.3)
Arctiinae moths	132	34 (25.8)	78 (59.1)	111 (72.1)
Geometridae moths	154	31 (20.1)	119 (77.3)	107 (69.5)

genic simplification of vegetation structures leads to an even heavier loss of species richness than in other animal groups (Philpott et al. 2008).

A comparison of studies on various animal groups like ants, butterflies (Wiemers & Fiedler 2008), understory birds (Mollik 2013), bats (Freudmann et al. 2015), amphibians and reptiles (Gallmetzer & Schulze 2015) and two moth (sub-)families (Alonso Rodríguez et al. 2017), which were all carried out around La Gamba, invariably showed a substantial loss of species richness in oil palm plantations relative to old growth forests (Tab. 1).

Ground-dwelling ants and moths suffered the highest loss of local species richness in oil palm plantations in the Golfo Dulce region. Only about one fourth to one fifth of total species richness known to occur in the landscape from targeted surveys of those two insect taxa was also recorded in these agro-ecosystems. For birds, amphibians, reptiles and butterflies 30–40 % of the total species list also occurred in plantations, and in bats even over 55 % of the regional species at least occasionally showed up in plantations (Tab. 1). These substantial losses of biodiversity are all the more remarkable as all oil palm plantations surveyed around La Gamba were situated close to old-growth forest in the Piedras Blancas National Park. With distances to near-natural forest of less than 1 km, spill-over of animals from source areas situated in the reserve likely contributed a substantial fraction of species recorded in plantations, especially in mobile organisms such as bats, birds or butterflies. For ants, however, the species recorded in oil palm plantations were indeed an integral part of the agro-ecosystems since we only considered wingless worker ants. Hence, the presence of workers clearly indicates the existence of established ant colonies nearby.

The above compilation also sheds further light on the conservation value of secondary forests or disturbed forest habitats in the Golfo Dulce region. Species numbers known from old-growth forest were not invariably the highest. Rather, for certain groups of organisms, forest sites under not too severe human influence supported even higher local biodiversity. Therefore, secondary forest as well as disturbed forest allowed to regenerate may have a substantial conservation value, for example as buffer zones at the margins of large reserves (Chazdon et al. 2009, Chazdon 2014). Generally speaking, with the progress of succession, regenerating tropical forest communities will eventually converge to near-natural situations similar to "pristine" forest, even though this might not allow every single species to recover (Bihn et al. 2010, e.g. for plants in Mesoamerica: Dent 2013).

Species composition

Ant species composition of the three habitat types differed highly significantly from each other. Just 15 of all 136 collected morpho-species were common to all habitat types and can therefore be regarded as opportunistic habitat generalists (one species each in the genera *Crematogaster, Dolichoderus, Labidus, Monomorium, Nylanderia, Odontomachus, Pachycondyla, Pheidole, Pseudomyrmex, Sericomyrmex, Strumigenys, Wasmannia* and three species of *Solenopsis*). In these genera there are some well-known generalist and 'weedy' invasive ants (for example *Monomorium, Nylanderia, Pheidole, Solenopsis* and *Wasmannia*; Bertelsmeier et al. 2015). Otherwise, oil palm plantations shared only 4 additional species with old-growth forest and 9 species with secondary forest. In contrast, faunal overlap between secondary and old-growth forest was much larger, with 23 ant species in common in addition to the generalists. This highly nested community pattern is best explained by an impoverishment of ant assemblages, from species-rich old-growth forest characterized by a high number of available niches, across secondary regenerating forest (where niche di-

versity becomes successively restored), to oil palm plantations. Very few weedy ant species could be recognized as beneficiaries of land-use in oil palm plantations. Moreover, the ant assemblages of the five investigated plantations were remarkably similar to one another. Hence, faunal impoverishment of ground-dwelling ants in these agro-ecosystems was accompanied by strong homogenization.

Among ant guilds, leaf-litter ants experienced by far the strongest loss in oil palm plantations (see above). In contrast, another spectacular guild of ground-dwelling ants, viz. army ants (genera *Labidus* and *Eciton*: O'Donnell et al. 2007), showed no clear difference in their incidence across habitat types. If anything, army ants were slightly less apparent in old-growth forest, but a more extensive survey effort might well also have resulted in more frequent encounters with raid swarms there. Elsewhere in the Neotropics, army ants are well known to forage in plantations and other agro-ecosystems as long as these are situated close to near-natural forest (Monteiro et al. 2008, Roberts et al. 2000).

In summary, our study corroborated the severe negative effects that oil palm cultivation has on biodiversity (Foster et al. 2011), using ground-dwelling ants in Costa Rican lowlands as an example. Ants are important predators of other arthropods including agricultural pests. Therefore, substantial shifts in ant species richness or community composition could interfere with the ecosystem services that ants usually provide (Philpott & Armbrecht 2006). Yet, a recent study (Denmead et al. 2017) found no effect of the manipulation of ant densities on important ecosystem processes in oil palm plantations in Sumatra, even though ants turned out once more to be the most important invertebrate predators there. Hence, while the detrimental influence of oil palm cultivation on biodiversity becomes ever better documented, the potential effects that this biodiversity loss may have on the functioning of ecosystems deserves further scrutiny.

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