Rainforest conversion to monocultures favors generalist ants with large colonies

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Abstract. The conversion of natural ecosystems to agricultural land is one of the most important drivers of biodiversity decline worldwide, particularly in the tropics. Species loss is typically trait-associated, leading to filtering of disturbance-resistant species during community assembly, which affects ecosystem functioning and evolutionary potential of communities. To understand the ecological and phylogenetic impact of rainforest conversion to agricultural systems, we combine analysis of nesting habit, feeding habit, colony size, and body size of canopy ants (Formicidae) with a phylogenetic analysis of species collected in four land-use systems in Sumatra, Indonesia: (1) lowland tropical rainforest, (2) jungle rubber (extensive rubber agroforest), and smallholder plantations of (3) rubber and (4) oil palm. Canopy ant communities in these land-use systems differed in trait composition, with a larger proportion of generalist nesting and generalist-omnivore feeding species in oil palm compared to rainforest and a larger proportion of generalist nesters and species with large colonies (>1000 individuals) in rubber than in rainforest. Traits of canopy ant communities in jungle rubber were more similar to those in rainforest than to those in rubber and oil palm plantations. In rainforest, mean pairwise phylogenetic distance was lower than expected for random community assembly, but did not differ from random in the other land-use systems. Of the traits nesting habit, feeding habit, and colony size, only feeding habit exhibited phylogenetic signal. Our results show that rainforest conversion to agricultural systems is accompanied by shifts in trait composition of canopy ant communities. Further, our results argue against environmental filtering of closely related canopy ant species as the major community assembly mechanism in plantation systems, but suggest that the Sumatran lowland rainforests harbor recently diverged endemic ant species that are particularly vulnerable to rainforest conversion to agricultural systems. Given the importance of ants for tropical ecosystems, the ecological differences among ant communities along the land-use gradient might have important consequences for ecosystem functioning and services in plantation systems.

Key words: agroforest; ant community; canopy ants; ecological traits; Indonesia; jungle rubber; land-use change; oil palm; phylogenetic relatedness; rainforest; rubber; Southeast Asia.

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INTRODUCTION

Land-use change threatens natural ecosystems worldwide (Gibbs et al. 2010, Gibson et al. 2011, Newbold et al. 2015). This includes tropical lowland rainforests, which are among the most biodiverse ecosystems on our planet. For decades, agricultural intensification in South America and Southeast Asia has come at the expense of the highly diverse rainforests in Amazonia and Sundaland (Hansen et al. 2009, Hansen 2013, Turubanova et al. 2018). Large areas of those rainforests are within the boundaries of Brazil and Indonesia, recently experiencing exceptionally high rates of deforestation (Hansen et al. 2009, Margono et al. 2012, 2014). It is well established that the conversion of rainforest into agricultural systems reduces abundance and species diversity of most animals, plants, and microbes (Böhnert et al. 2016, Drescher et al. 2016, Prabowo et al. 2016, Barnes et al. 2017, Rembold et al. 2017, Brinkmann et al. 2019, Berkelmann et al. 2020, Grass et al. 2020). Moreover, rainforest conversion to agricultural land also heavily affects ecosystem services (Foley 2005, Cardinale et al. 2012, Barnes et al. 2014, Dislich et al. 2017), such as decomposition (Krashevska et al. 2018), soil nutrient cycling (Kurniawan et al. 2018), and carbon storage (Guillaume et al. 2015, 2018).

Forest canopies rank among the most species-rich terrestrial habitats, especially in tropical rainforests (Lowman and Nadkarni 1995, Lowman and Rinker 2004). Consequently, rainforest conversion to cash-crop monocultures in Sumatra has been shown to result in the loss of hundreds of species of arthropods, including ants, beetles, butterflies (adults and larvae), flies, parasitoid wasps, salticid spiders, springtails, and true bugs (EFForTS Newsletter 2018, 2020, Nazarreta et al. 2020, Panjaitan et al. 2020, Junggebauer et al. 2021, Rizqulloh et al. 2021). Ants (Formicidae) are among the most conspicuous taxa in tropical rainforests and often contribute more than half of all arthropods in the canopy, in both abundance and biomass (Tobin 1995, Davidson 2003, Dial et al. 2006). Based on canopy fogging, it has been estimated that about half of all tropical ant species are at least partially associated with the canopy (Floren et al. 2014).

Ants display a wide variety of feeding strategies, ranging from opportunistic scavenging for live or dead animals, fruit, fungi, excrements, or human waste to more specialized strategies, such as obligate predation on live prey or foraging for plant-derived food, like extrafloral nectar, fat bodies, and honeydew, to highly species-specific fungus cultivation on processed plant material (Hölldobler and Wilson 1990, 2011). With the exception of nomadic species, for example, army ants (Kronauer 2020), ants rear their brood in nests varying widely in size, from cubic centimeters to square kilometers, made from a large variety of materials, and are socially organized in colonies, ranging from a few dozen to millions of largely sterile workers with one to several thousand reproductive queens (Gößwald 1985, Hölldobler and Wilson 2009, Keller and Gordon 2009, Lach et al. 2010). Due to their high abundance and biomass, as well as their wide range of strategies in feeding, nesting, and colony size, ants are essential for the maintenance and functioning of many terrestrial ecosystems and provide a variety of ecosystem services and disservices (Wilson 1987, Del Torro et al. 2012).

Here, we analyzed the phylogenetic relatedness and trait composition of canopy ant communities along a rainforest transformation gradient from lowland rainforest via extensive rubber agroforestry to monoculture plantations of rubber (*Hevea brasiliensis*) or oil palm (*Elaeis guineensis*) in Jambi Province, Sumatra, Indonesia. We compared community composition with respect to nesting habit, feeding habit, colony size, and body size and the phylogenetic relatedness of communities to understand how trait community composition shifts with land-use change and which community assembly processes operate after rainforest conversion to agricultural systems. We targeted the traits nesting habit (soil, arboreal, generalist, nomadic, leaf litter, rotten wood), feeding habit (predator, trophobiosis associated, seed harvester, myrmecophyte associated, omnivore-generalist), and colony size (<100 individuals, 100–1000 individuals, >1000 individuals) because they reflect fundamental components of ant biology (Kaspari 2000, Lach et al. 2010). We compared body size of the ant species in the different land-use systems because body size is often considered a "master trait" in

biological interactions which determines the trophic position of organisms in food chains (Brose et al. 2006, Moretti et al. 2017). A phylogenetic comparison between communities in the different land-use systems can provide insight on community assembly processes, that is, distantly related communities suggest a role of competition and closely related communities a role of environmental filtering during community assembly, given that process-related traits are phylogenetically conserved (Emerson and Gillespie 2008).

As generalist species are more resilient to land-use change and habitat disturbance than specialists (Börschig et al. 2013, Carrara et al. 2015, Mueller et al. 2016), we expected a shift from more specialist nesting and feeding species in lowland rainforest to more generalist species in monoculture plantations. Due to reduced structural complexity in the monocultures (Ehbrecht et al. 2017, Zemp et al. 2019), ecological dominance might play a more important role in rubber and oil palm plantations than in rainforest and therefore we expected more ant species with large colonies in the monocultures (Palmer 2004, Helanterä et al. 2009, Boulay et al. 2014). Phylogenetic analyses of anthropogenically disturbed ecosystems indicate that such communities often consist of closely related species that are filtered from the species pool (Ding et al. 2012, Chapman et al. 2018). Therefore, in the phylogenetic analysis, we expected that communities in the agricultural systems consist of closely related species, indicating environmental filtering as a community assembly process after rainforest conversion to agricultural systems.

MATERIALS AND METHODS

Sampling and species occurrence

This study took place within the replicated plot design of the EFForTS project (Drescher et al. 2016). We collected ants by canopy fogging eight research plots in each of four land-use systems in the lowlands of Jambi Province, Sumatra, Indonesia: (1) degraded primary lowland rainforest (sensu Margono et al. 2014), (2) jungle rubber (extensively cultivated rubber in mixed stands with lowland rainforest tree species; Gouyon et al. 1993, Rembold et al. 2017), and smallholder-owned monoculture plantations of

(3) rubber and (4) oil palm. We fogged each of the 32 50 m × 50 m research plots twice, once in dry season 2013 (May–Sep) and again during the rainy season 2013–14 (Nov–Mar). Using the Swingfog SN50 fogger (Swingtec GmbH, Germany), we targeted three canopies per plot per sampling date with a mixture of 50 mL DECIS 25 EC (Bayer Crop Science, active ingredient deltamethrin, conc. = 25 g/L) dissolved in four liters of petroleum. Target canopies were chosen by visually identifying three areas with dense, interlocking canopies representative of the typical canopy in the plot; gaps and damaged trees were avoided. Beneath each target canopy, we suspended 16 1 m × 1 m square collection funnels, each fitted with a 250 mL wide neck PE bottle containing 100 mL 99% analytical grade EtOH. We removed the traps two hours after the application of the insecticide, cleaned the samples from debris and plant material, and stored them at −20°C in 100% EtOH.

We identified worker ants to genera using a widely known key to Bornean ants (Fayle et al. 2014), updated with Sumatran ant genera (Nazarreta et al. 2021). Whenever possible, workers were determined to species using online keys and resources available at AntWiki (https://www.antwiki.org) and AntWeb (https://www.antweb.org). Otherwise, we assigned worker ants to morphospecies as documented in "A Guide to the Ants of Jambi" (Nazarreta et al. 2021) and online in the Ecotaxonomy.org database (Potapov et al. 2019a). In total, we assigned 130,607 worker ants to 226 canopy ant morphospecies from 60 genera. Almost a third (31.9%) of the morphospecies could be assigned full Linnaean names, and an additional quarter (24.7%) were determined to taxonomic levels beyond genus, such as subgenus, species complex/group or resembling described species (confer, "cf"). The remaining morphospecies could so far only be determined to genus, despite involvement of taxonomic experts (for details, see Nazarreta et al. 2021). Preliminary, unrevised data on 2013 dry season species richness were published in Drescher et al. (2016) and a detailed community ecology analysis of taxonomically checked species-abundance data of dry season 2013 canopy ants was published in Nazarreta et al. (2020). For the present analysis, we merged dry and rainy season canopy ant data from the same

plots. All subsequent statistics were performed using R 3.5.0 (R Core Team 2015).

Trait assembly

We compiled information on three key traits for the members of the canopy ant community: (1) nesting habit, (2) feeding habit, and (3) maximum colony size. Because information on many aspects of ant biology is severely limited even in described species, and less than one-third of the morphospecies in our collection could be attributed to species, we compiled traits on the genus level and assigned those states to all descendant morphospecies of a genus. Nesting habit was defined as a discrete trait with six states, that is, "arboreal," "leaf litter," "nomadic," "soil," "rotten wood," and "generalist." Similarly, feeding habit was defined with five discrete states, that is, "myrmecophyte associated," "predator," "trophobiosis associated," "seed harvester," and "omnivore-generalist." Trait states for nesting habit and feeding habit were inspired by Brown Jr. (2000), but refined and expanded by using information from AntWiki. For each species, species group, subgenus, and genus, we browsed the introductory section and the biology section of the respective AntWiki page for information on nesting and feeding habits and assigned one of the above trait states to a genus if warranted by the available information. "Generalist" (nesting habit) and "omnivore-generalist" (feeding habit) were used for a genus if none of the alternatives could reasonably be assigned or if the genus was specifically described as such. Maximum colony size was derived from Blanchard and Moreau (2017) in three discrete states: "<100 individuals," "100–1000 individuals," and ">1000 individuals." Additionally, we measured body length and width of a maximum of five worker ants per species to calculate mean body length and mean body width. For a link to the full data set, including character states, see the data availability statement.

Based on species occurrences in the plots, we calculated mean proportions of the discrete trait states for nesting habit, feeding habit, and maximum colony size, and mean values of body length and width for each land-use system using the *functcomp* function from the R package "FD" (Laliberté and Legendre 2010, Laliberté et al. 2014). Although discrete traits were identical for all members of a genus, we calculated proportions based on species occurrence data to account for differences in within-genus species richness between plots. All proportion data were logit-transformed before statistical analyses. We performed principal component analysis (PCA) separately for nesting habit and feeding habit of the ant communities using the *rda* function from the R package "vegan" (Oksanen et al. 2019). We compared the proportions of species exhibiting each discrete trait state, body length, and body width of species between the land-use systems in separate analyses of variance (ANOVA) followed by Tukey's post hoc multiple comparison test.

Sequencing

For DNA extraction, we pulverized 1–10 worker ants of the same species in a TissueLyser (Qiagen, Hilden, Germany). DNA was extracted with the DNA Purification Mini Spin Column Kit (Genaxxon Bioscience, Ulm, Germany) according to the manufacturer's recommendations. PCR-amplified fragments of 28S rDNA (1112-1271 bp) and cytochrome c oxidase I (COI) mtDNA (331bp) were purified in Millipore MultiScreen PCRμ96 Filter Plates (Merck Chemicals, Darmstadt, Germany) and sequenced by Microsynth Seqlab (Microsynth Seqlab, Göttingen, Germany). Detailed PCR conditions are given in Appendix S1: Table S1.

Phylogeny

Of 226 collected morphospecies, we recovered sequences of both markers for 141 species which had a total abundance of >10 individuals over all plots. One such species could not be successfully sequenced and was added to the phylogeny based on its taxonomy (see below). Due to sequencing failure, we inferred the first part of the 28S fragment for 12 species and the entire 28S fragment for one species based on consensus sequences from the members from the same taxonomic group, that is, the genus or the species complex. Partial sequences for 8 species were completed using sequences from GenBank. Additionally, 13 rare species (abundance ≤10) were included with sequences from GenBank (for details, see Appendix S1: Table S2).

We edited and assembled Sanger-sequencing output in Geneious 11.0.4 (https://www.geneious.com). Sequences were aligned using MAFFT

version 7 (Katoh and Standley 2013) and masked in GUIDANCE2 with standard settings (Sela et al. 2015). Alignments of 28S and COI were concatenated with FASconCAT-G (Kück and Longo 2014). We calculated phylogenies in IQ-TREE with partitioned models and 10,000 bootstraps to infer branching support (Nguyen et al. 2015, Chernomor et al. 2016, Kalyaanamoorthy et al. 2017, Hoang et al. 2018).

We transformed the phylogenetic tree comprising 154 species (Appendix S1: Fig. S1) to an ultrametric tree using the strict clock model with the function *chronos* implemented in the R package "ape" (Paradis and Schliep 2018) and calibrated it with branching times from Moreau and Bell (2013) (Appendix S1: Fig. S2, Table S3). Species for which we had no sequence data were added to the phylogenetic tree according to taxonomy and assigned a random position within their species group, subgenus, genus, or to the root of their family (for details, see Appendix S1: Table S2) using the function *add.species.to.genus* implemented in the R package "phytools" (Revell 2012).

Mean pairwise phylogenetic distance

Using the function *ses.mpd* implemented in the R package "picante" (Kembel et al. 2010), we calculated mean pairwise phylogenetic distances (MPD) for each land-use system with pooled species presence data from all its plots, as well as random MPD with the same species number as each land-use system, each based on 4999 random communities drawn from the total species pool. We report the standardized effect size (z) and P value of each land-use MPD compared to its corresponding random MPD.

Phylogenetic signal of traits

As we assigned the discrete traits to all descendent species of the same genus, we explored phylogenetic signal of these traits using a genus-level phylogeny, which excluded genera without sequences and genera for which trait data were incomplete. We calculated Pagel's lambda with the function *fitDiscrete* implemented in the R package "geiger" (Harmon et al. 2008). We estimated the optimal lambda value of tree transformation and set two transition rate models: equal-rate (ER) and all-rate-different (ARD). We compared support of the lambda = 0 model, lambda optimal models (ER or ARD) and lambda = 1 models (ER or ARD) using the corrected Akaike information criterion (AIC_c) and report the AIC_c of the lambda = 0 model and the transition rate model with the better fit.

RESULTS

Nesting habit

Rainforest (F), jungle rubber (JR), rubber (R), and oil palm (O) communities were composed of species with different nesting habits (Fig. 1a). Rubber had 1.26 times and oil palm 1.35 times greater proportions of generalist-nesting ant species than rainforest (ANOVA: $F_{3,28} = 4.63$, $P = 0.009$; Fig. 2a). Oil palm differed from all other land-use systems in having a greater proportion of soil nesters, 1.9 times that of rainforest (ANOVA: $F_{3,28} = 6.39$, $P = 0.002$; Fig. 2b), and a lower proportion of arboreal nesters, 0.8 times that of rainforest (ANOVA: $F_{3,28} = 6.11$, $P = 0.002$; Fig. 2c). The proportion of species nesting in rotten wood was a factor of 0.5 lower in oil palm than in rainforest and rubber (ANOVA: $F_{3,28} = 5.06$, $P = 0.006$; Fig. 2d), but oil palm had a larger proportion of ant species nesting in leaf litter than did rubber (ANOVA: $F_{3,28} = 3.48$, $P = 0.029$; Fig. 2e). The land-use systems did not differ significantly in the proportion of nomadic species (ANOVA: $F_{3,28} = 0.96$, $P = 0.427$; Appendix S1: Fig. S3a).

Feeding habit

Different feeding habits predominated in the four land-use systems (Fig. 1b). Oil palm was inhabited by a larger proportion of omnivore-generalist species than rainforest and jungle rubber. The proportion of omnivore-generalist species in oil palm was 1.13 times that of rainforest. Rubber also had a larger proportion of omnivore-generalist species than jungle rubber ($F_{3,28} = 8.72$, $P < 0.001$; Fig. 2f). Myrmecophyte-associated ants made up a greater proportion of the community in rubber and a lower proportion in oil palm compared to rainforest and jungle rubber; compared to rainforest, proportions differed by a factor of 2.7 in rubber and 0.17 in oil palm ($F_{3,28} = 43.87$, $P < 0.001$; Fig. 2g). Rainforest and oil palm communities had proportionally more predators than rubber, which had 0.5 times the proportion of predators as rainforest (ANOVA: $F_{3,28} = 3.68$, $P = 0.024$; Fig. 2h). Oil
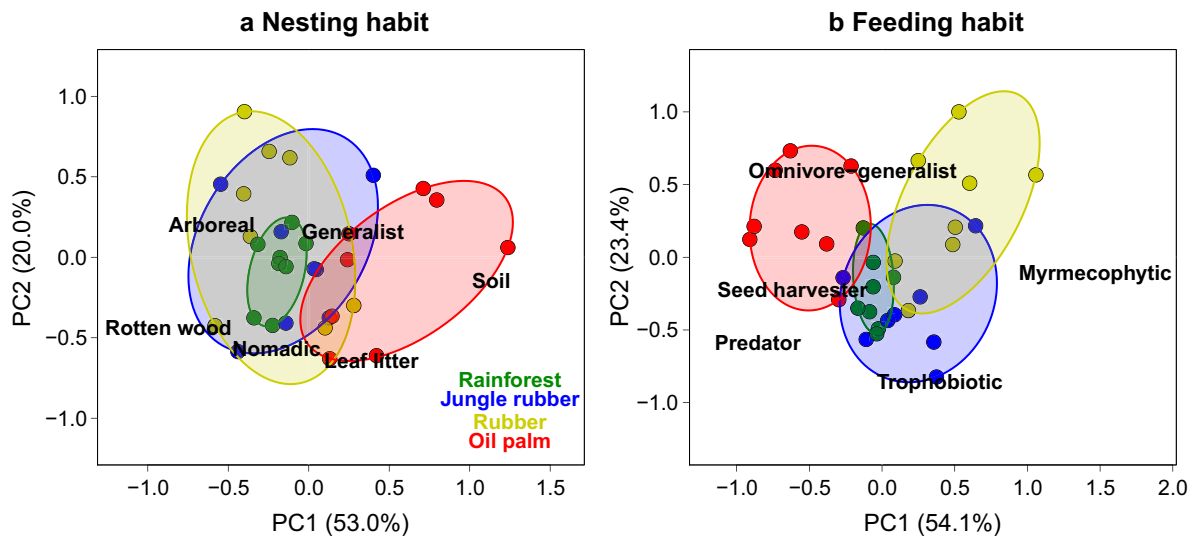
Fig. 1. Principal component analysis (PCA) of Sumatran canopy ant nesting (a) and feeding habits (b) by land-use system. Dots represent plots in which ants were sampled and ellipses enclose all plots: green = rainforest, blue = jungle rubber, yellow = rubber, and red = oil palm. Nesting and feeding trait states are positioned according to their PCA loadings.

palm was inhabited by proportionally fewer trophobiotic ants than rainforest and jungle rubber, by a factor of 0.34 compared to rainforest, while rubber had a lower proportion of trophobiotic ants than jungle rubber ($F_{3,28} = 8.96$, $P < 0.001$; Fig. 2i). The land-use systems differed marginally in their proportions of seed-harvesting species (ANOVA: $F_{3,28} = 2.89$, $P = 0.053$; Appendix S1: Fig. S3b).

Colony size

Rubber had a greater proportion of species with large colonies (>1000 individuals) than rainforest and jungle rubber, with 1.12 times the proportion of species with large colonies in rainforest (ANOVA: $F_{3,28} = 5.56$, $P = 0.004$; Fig. 2j). The land-use systems did not differ in the proportion of species with small colonies (<100 individuals; ANOVA: $F_{3,28} = 1.21$, $P = 0.324$; Appendix S1: Fig. S3c) and differed marginally in the proportion of medium-sized colonies (100–1000 individuals; ANOVA: $F_{3,28} = 2.38$, $P = 0.091$; Appendix S1: Fig. S3d).

Body size

Body length of canopy ant species ranged from 1.34 to 20.46 mm and body width from 0.16 to 2.9 mm. Neither mean body length (ANOVA:

$F_{3,28} = 1.70$, $P = 0.191$; Appendix S1: Fig. S4a) nor mean body width (ANOVA: $F_{3,28} = 2.26$, $P = 0.103$; Appendix S1: Fig. S4b) of canopy ant species differed between the land-use systems.

Mean pairwise phylogenetic distance

Species occurring in rainforest but absent in the other land-use systems were distributed over the ant phylogeny (Fig. 3). In rainforest, mean pairwise phylogenetic distance (MPD) of canopy ant species was significantly lower than expected for random assembly ($MPD_F = 82.48$ my, $MPD_{random} = 84.34$ my $\pm$ 0.62 SD, $z = -2.98$, $P = 0.007$). In jungle rubber, rubber, and oil palm, mean pairwise phylogenetic distances of canopy ant species did not differ from random ($MPD_{JR} = 84.71$ my, $MPD_{random} = 84.38$ my $\pm$ 1.04 SD, $z = 0.32$, $P = 0.776$; $MPD_R = 85.56$ my, $MPD_{random} = 84.40$ my $\pm$ 1.55 SD, $z = 0.75$, $P = 0.451$; $MPD_O = 83.89$ my, $MPD_{random} = 84.37$ my $\pm$ 1.63 SD, $z = -0.29$, $P = 0.745$).

Phylogenetic signal of traits

Of the three discrete traits, only feeding habit exhibited phylogenetic signal (lambda 1; ER, $AIC_c = 98.8$; lambda optimal = 0.65; ER, $AIC_c = 99.9$; lambda 0, $AIC_c = 102.5$). Nesting habit
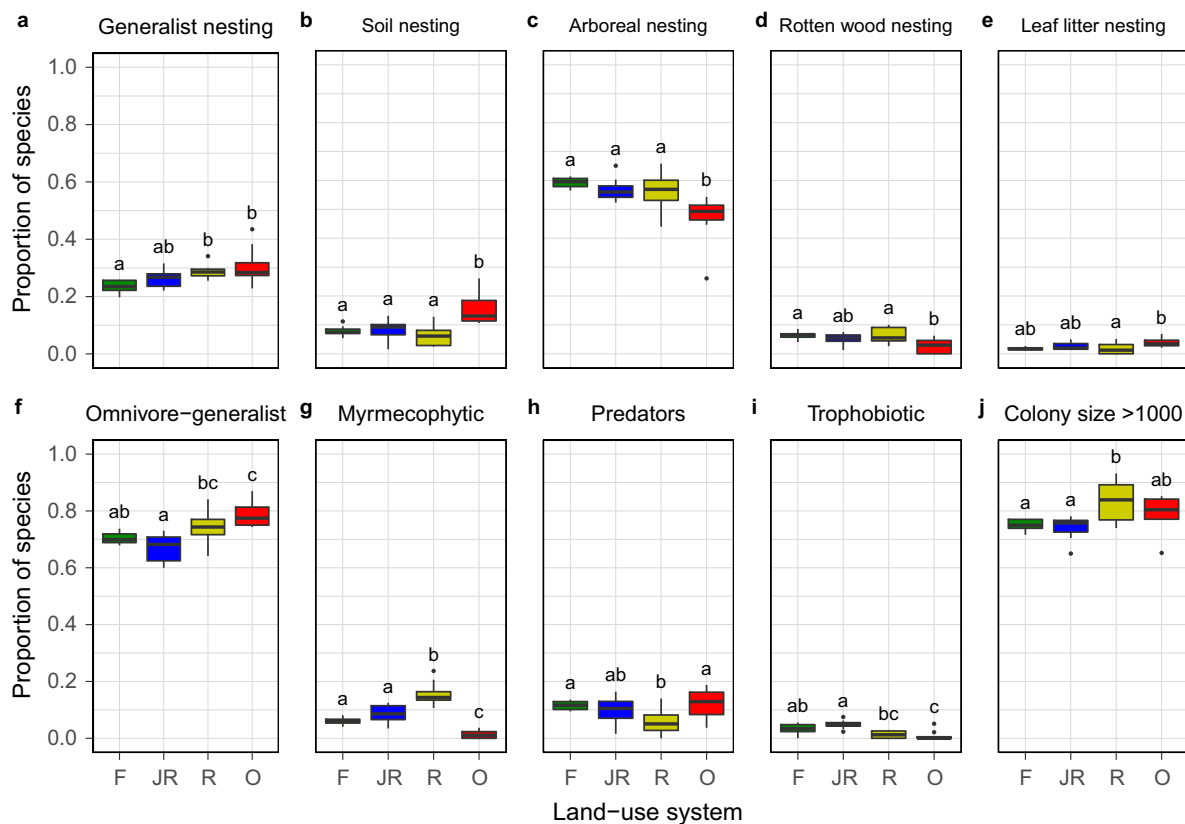
Fig. 2. Proportion of Sumatran canopy ant species exhibiting the selected trait states by land-use system. F = rainforest (green), JR = jungle rubber (blue), R = rubber (yellow), and O = oil palm (red). Letters indicate significant differences between land-use systems (Tukey's post hoc multiple comparisons, α = 0.05). For trait states without significant differences between land-use systems, see Appendix S1: Fig. S3. Summary tables for all trait states in Appendix S1: Tables S4, S5.

(lambda 1; ER, AIC_c = 162.6; lambda optimal = 0.52; ER, AIC_c = 163.8; lambda 0, AIC_c = 156.7) and colony size had no phylogenetic signal (lambda 1; ARD, AIC_c = 93.4; lambda optimal = 0.00; ER, AIC_c = 95.0; lambda 0, AIC_c = 85.3; Fig. 4).

DISCUSSION

The results indicate that rainforest conversion to plantation systems is accompanied by changes in the trait composition of canopy ant communities. The more central position of rainforest in the PCA biplots compared to the other land-use systems shows that communities in the plantation systems are more variable and tend to be dominated by particular trait states compared to rainforest. Specifically, generalist and soil-nesting ant species are more prevalent in oil palm than in rainforest canopies, but rotten wood and arboreal nesters are less prevalent. The relative abundance of soil nesters in oil palm canopies may be explained, in part, by canopy height. Oil palm canopies in our study sites were less than 7 m high, but rainforest canopies averaged around 45 m (Kotowska et al. 2015). Hence, oil palm canopies were more likely utilized by foragers of soil-living ants than rainforest canopies. Moreover, oil palms feature large amounts of suspended soils along their trunks, which are mainly occupied by ants known to build belowground nests (Potapov et al. 2020). In rainforest, suspended soils in epiphytes also provide ample nesting space for ants (Ellwood et al. 2002,
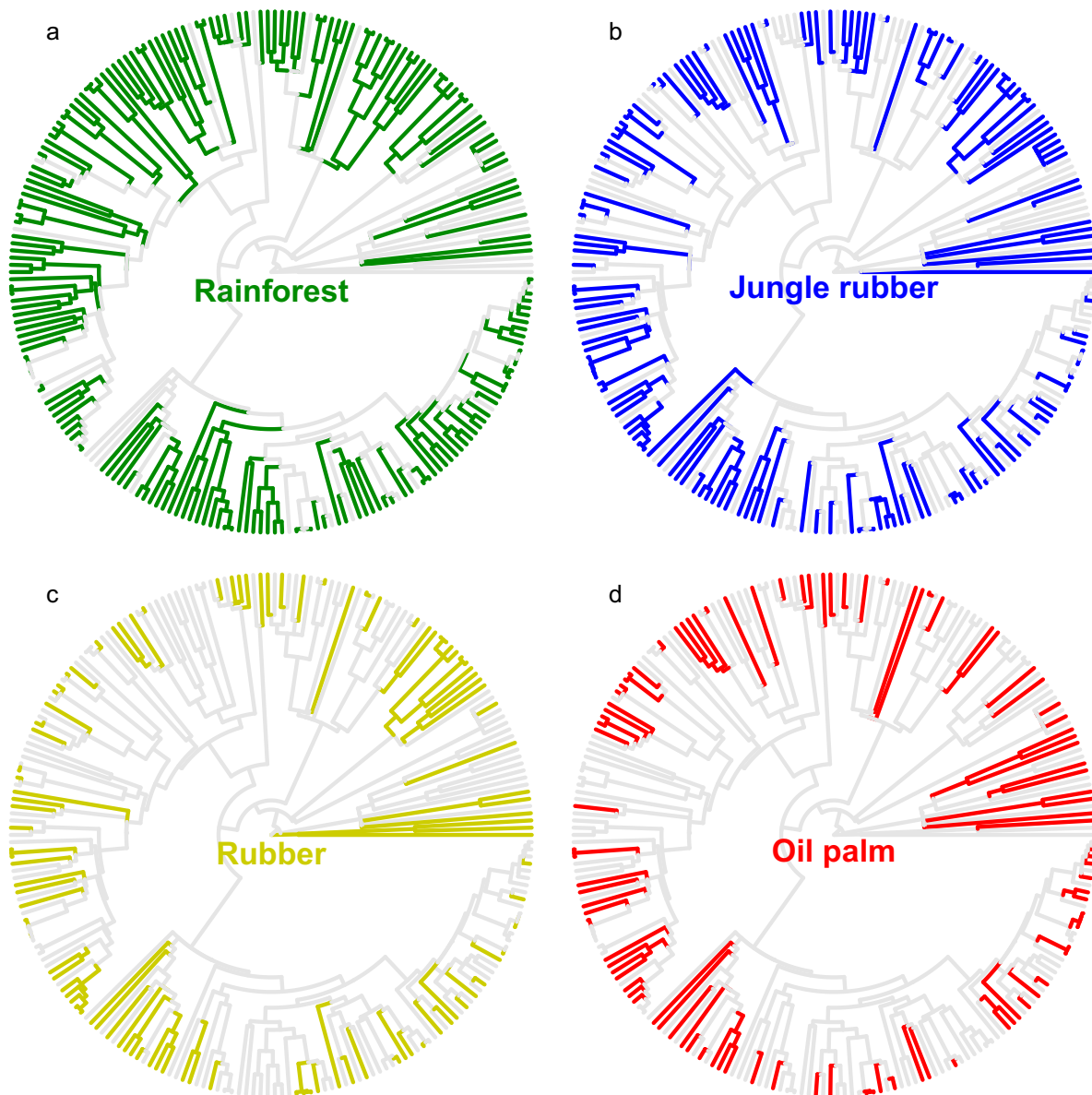
Fig. 3. Phylogenetic distribution of Sumatran canopy ants in rainforest (a), jungle rubber (b), rubber (c), and oil palm (d). Colored branches indicate species presence in the respective land-use system. Coloring extends to the last common ancestor of species occurring in the same land-use system.

Ellwood and Foster 2004); however, these tend to be colonized by different species, categorized as arboreal nesters. The lack of arboreal nesters in oil palm may be due to the combination of unsuitable abiotic conditions and the prevalence of highly abundant, dominant tramp ants (see below; Nazarreta et al. 2020). The low proportion of ants nesting in rotten wood in oil palm is

due to the lack of this resource. Although rotten wood is abundant in rainforest, ants nesting in it seldom venture high into the canopy, as indicated by the low proportion of those ants in our rainforest canopy samples.

We also found that lowland rainforest conversion to rubber or oil palm monocultures had a mixed effect on ants associated with myrmecophytes
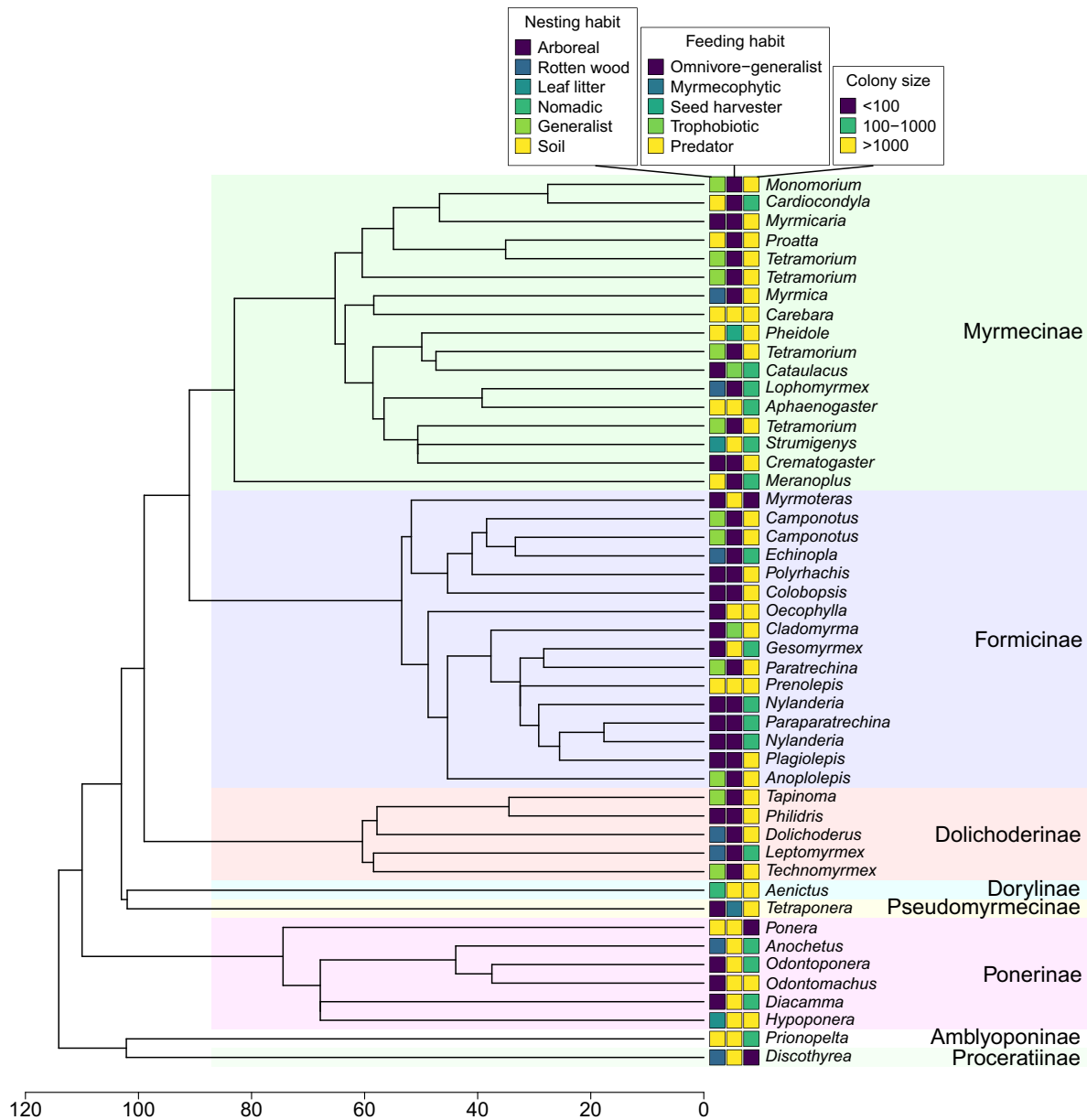
Fig. 4. Genus-level phylogeny of Sumatran canopy ants and phylogenetic distribution of nesting habit, feeding habit, and colony size. Phylogeny excludes genera identified in the study for which sequence and/or trait data was incomplete. Scale represents age in millions of years.

(increased proportion in rubber, reduced in oil palm), predators (reduced proportion in rubber, unchanged in oil palm), and ants conspicuously relying on trophobioses (unchanged in rubber, reduced in oil palm). It is important to note that our data are skewed to the trait state "omnivore-generalist," which comprised almost 70% of all species. Similarly, the trait state "myrmecophytic" was ascribed only to the genus *Tetraponera*, which was rarely encountered in oil palm. There are obviously ant species from other genera that are associated with myrmecophytes in Southeast Asia, including some *Crematogaster* (Fiala et al. 1999, Feldhaar et al. 2003). Because

we worked on genus level to cope with the large proportion of unknown ant species in our samples, those species were categorized as "omnivore-generalist" to reflect the heterogeneity of feeding habits within the genus. In contrast, the trait states "predators" and "trophobiotic" were assigned to several genera, possibly providing a more realistic image of canopy ant feeding habits in response to land-use change. Similar patterns were reported by Luke et al. (2014), who found more opportunist ants in oil palm than in rainforest and a tendency toward more specialist predators in rainforest than in oil palm.

In contrast to nesting habit, feeding habit, and colony size, body size of canopy ant species did not differ significantly between the land-use systems. This indicates that, on the microhabitat scale, the four land-use systems offer niche space to a similar spectrum of ant sizes, despite the fact that stand structural complexity of lowland rainforest plots was almost twice that of oil palm plantations (Zemp et al. 2019, Junggebauer et al. 2021). Additionally, the recent review by Potapov et al. (2019b) suggests that, in terrestrial ecosystems, body size may scale poorly with trophic position; this may apply to ants in particular because large resources, such as large prey, can be overwhelmed by multiple cooperating workers.

For this study, we assigned trait states to species based on genus affiliation, meaning that all member species of a genus had the same trait state. This approach was necessitated by the fact that more than two-thirds of the species in our collection could not be assigned to described species, and natural history information was sparse even for described species. As a consequence, our data are of low resolution, as exemplified by "nesting habit" comprising around 54% "arboreal" nesters or "feeding habit" being dominated by almost 70% "omnivore-generalist" feeders. Nevertheless, we detected significant differences in ant community trait composition between the land-use systems. We expect this to approximate species-level reality and that including higher resolution intra-genus variability of traits would recover more pronounced differences among the land-use systems.

In addition to the trait comparison of canopy ants in the different land-use systems, we compared phylogenetic relatedness of the communities in order to gain insight into the community assembly processes acting after rainforest conversion to agricultural systems. In contrast to our expectation, mean pairwise phylogenetic distance in the agricultural systems did not differ from random, arguing against environmental filtering as the major assembly mechanism of canopy ant communities in plantation systems. A similar result has been obtained by Liu et al. (2016), who also found trait filtering in ant communities in rubber plantations but no indication of phylogenetic filtering. This might be due to phylogenetic lability of the traits associated with community assembly, of which only feeding habit exhibited phylogenetic signal. In contrast to the agricultural systems, rainforest was inhabited by more closely related canopy ant species than expected by random. This might be due to high levels of canopy ant endemism in the Sumatran lowland rainforests. As Sumatra has a long history of uninterrupted rainforest coverage, recently diverged species adapted to rainforest habitats may be filtered out during community assembly of plantation systems. Additionally, the prevalence of six "tramp species" (ants known to form invasive populations elsewhere, but whose invasion status is unclear in the study area), namely *Anoplolepis gracilipes*, *Cardiocondyla wroughtonii*, *Monomorium floricola*, *Paratrechina longicornis*, *Tapinoma melanocephalum*, and *Technomyrmex albipes* (Nazarreta et al. 2020), in the monocultures might increase mean pairwise phylogenetic distance. Similarly, invasions by alien species contribute to phylogenetic overdispersion of plant communities in agricultural systems (Kusuma et al. 2018).

In conclusion, our study shows that lowland rainforest conversion to jungle rubber agroforestry or rubber and oil palm monoculture plantations is accompanied by shifts in canopy ant community trait composition, favoring generalist nesters and feeders, and species with large colonies of >1000 individuals. The results of our study argue against environmental filtering of closely related canopy ant species as the major community assembly mechanism in plantation systems after rainforest conversion, but instead suggest that recently evolved, probably endemic, ant species are particularly threatened by rainforest conversion to agricultural systems. Given the importance of ants for tropical

ecosystems, and the differences in trait composition we detected among the studied land-use systems, our results suggest severe ramifications for ecosystem functioning and ecosystem services in monoculture plantations of rubber and oil palm.

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DATA AVAILABILITY STATEMENT

Sequence data are available on GenBank under accession numbers MT903472–MT903611 and MT904514–MT904653. Species-abundance data, trait data, and the data analysis script are available from Figshare: https://doi.org/10.6084/m9.figshare.12821624

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3717/full