

The effect of swidden agriculture on ant communities in Madagascar

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ABSTRACT

Swidden agriculture is a widespread subsistence farming method in the tropics, which is being intensified as human populations grow. This study is the first to investigate the impacts of land degradation from swidden upon ant species (both native and introduced) across the full degradation gradient, from forest, to tree fallows, to shrub fallows, to exhausted land. Ant communities in closed canopy forests had higher species diversity and were taxonomically distinct, but as land became increasingly degraded, a significant reduction in overall and native species richness was detected, as were changes in overall community composition. Whilst native species decreased across the degradation gradient, introduced species increased. There was also a significant correlation in community compositional changes between native and introduced species which was independent from environmental factors. Co-occurrence analysis, however, suggested there was little evidence that introduced species were significantly impacting the communities of native species. This suggests these patterns are both separately driven by habitat degradation. Degraded fallow habitats were found to harbour unique and endemic species, including 22.4% of the species found in closed canopy forest. Together, our results highlight the potentially detrimental effects of further spread and increased intensification of swidden systems in tropical ecosystems. The conservation of existing closed canopy forests is of utmost importance but we also highlight that the fauna of degraded swidden habitats could still be important for biodiversity conservation in agricultural landscapes across the tropics.

1. Introduction

Currently, land for crop production accounts for approximately 38% of the earth's surface (FAO, 2020) but further expansion to accommodate an increasing human population is expected, particularly in the tropics (United Nations, 2019). Swidden agriculture is a widespread subsistence farming method in the tropics, and often drives deforestation and forest degradation (Rahman et al., 2017; Scales, 2014).

During swidden, forests are cleared and burned for cultivation. After harvesting, the land is left to fallow and native vegetation regrows. Repeated regeneration of forests is possible if cultivation periods are short and fallow periods are long (Rerkasem et al., 2009). However, in many countries, increasing population growth and the increased need for food have led to the lengthening of cultivation periods and

shortening of fallow periods. In Madagascar, fallow times have decreased from 8–15 years to 3–5 years over three decades (Styger et al., 2007). Successive rounds of cultivation and burning result in nutrient depletion, which leads to changes in the fallow vegetation structure; from early fallows dominated by trees, through later fallows dominated by shrubs, to the last fallows, which are unsuitable for agriculture, dominated by grasses and ferns (described here as exhausted land). As swidden systems are intensified, land is cycled through the swidden process at an increasing rate, and greater proportions of the land reaches the more degraded states, such as shrub fallows and exhausted land, faster.

Conversion of forest to agriculture has been shown to reduce ant species richness and a negative correlation between ant species richness and habitat degradation has been demonstrated (Solar et al., 2016).

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However, this is not always the case (Stork et al., 2017) and likely depends upon the extent that disturbance affects habitat structure; more structurally complex habitats provide more ecological niches, and a wider variety of food resources resulting in a higher species diversity than is found in less structurally complex habitats (Andersen, 1986). Changes to the habitat structure due to degradation is also likely to elicit changes in the ant community composition as different species will be favoured in different habitats (Andersen, 2019). Invasive ant species are often favoured within disturbed habitats (King and Porter, 2007), and can reduce the diversity and distributions of native ant species (Wittman, 2014). Thus, they are an important potential confounding factor when looking at habitat degradation, as they can present a threat to biological communities either solely, or in combination with habitat degradation.

Swidden has been shown to negatively affect the species diversity of amphibians and reptiles (Fulgence et al., 2021), although a loss of biodiversity is not always the case (Rerkasem et al., 2009). In Madagascar, it has been shown to reduce plant species richness and abundance (Klanderud et al., 2010) - an important predictor of ant species diversity (Roth et al., 1994). Thus, our prediction is that ant species diversity will be negatively impacted by swidden both directly and indirectly through simplification of vegetation structure. As swidden causes changes to the habitat structure, we would also expect ant community compositional changes to occur. These hypotheses are supported by previous studies on the immediate and short-term effects of swidden (Mackay et al., 1991; Castaño-Meneses & Palacios-Vargas, 2003), and the effect of fallow age on ant communities (Mathieu et al., 2005), as well as a study on the effect of swidden on army ants (Matsumoto et al., 2009). However, to date there has been no rigorous assessments which quantify how much, and what type of ant diversity may be lost or supported in the full range of habitats found across the swidden degradation gradient. Further, information about how swidden affects invasive species is lacking.

Ants are a practical taxonomic group to use for impact studies, as their rapid growth rates and relatively short generation times enable rapid responses to environmental change (Philpott et al., 2008). Ants play important ecological roles such as soil structuring, seed dispersal, decomposition, pollination, and help facilitate nutrient recycling (Diamé et al., 2017). Thus, understanding how they are impacted by land use change is important for assessing sustainability.

Here, we quantified the effect of swidden on ant communities in Madagascar by comparing ground dwelling ant species diversity and community composition among the four non-cultivated swidden habitats: closed canopy forests, tree fallows, shrub fallows, and exhausted land. As invasive species can be a confounding variable, we also analysed the patterns of diversity and community composition of native and introduced species separately. This allowed us to look for correlations in these patterns, which might suggest that invasive species were significantly impacting native species. We investigated this further by using a co-occurrence analysis to test if there were any significantly negative patterns of co-occurrence between native and introduced species.

2. Materials and methods

2.1. Study sites

We conducted sampling in three research areas located within and just outside the boundary of the Corridor Ankeniheny Zahamena (CAZ) in eastern Madagascar (Appendix A) (See Portela et al., 2012). Of the 35 sites sampled, 10 were in closed canopy forest, 6 in tree fallow, 10 in shrub fallow, and 9 in exhausted land (Appendix C). We determined habitat classifications by interviewing local people and systematic surveys for habitat indicator plant species (Styger et al., 2007). We collected samples during the wet seasons, between November and December of 2014, and January and April of 2014 and 2015. Each site was sampled once.

2.2. Data collection

Within each site, we set up 10 pitfall traps (9 cm diameter, 11 cm depth) at 10 m intervals along a 90 m transect. We buried the traps so that the rim was level with the ground, filled them with a water and unscented detergent mixture, and used lids to provide rain cover. After 5 days, we sieved and washed the trap contents, and preserved the biomass in 100% ethanol. Note that for some sites, data was not available for all pitfall traps. We identified all the ants in each sample to species using taxonomic keys provided to us by California Academy of Sciences, and the Antweb website (AntWeb, n.d.). We recorded the total count per species per sample. Undescribed species were matched to vouchers of morpho-species in the California Academy of Sciences collections that are awaiting formal description. Species were labelled as either native or introduced. Whilst the term introduced and invasive are not synonymous, not enough is known about the effects of introduced ant species in Madagascar to state whether or not they are invasive.

At each pitfall trap location, we measured a set of continuous environmental variables (Appendix B and C), including leaf litter depth and the percentage leaf litter cover. These were then averaged for each site.

2.3. Species diversity and community composition

We quantified ant taxonomic diversity at the species level using the first three integer Hill numbers, which express diversity in units of effective numbers of species (Hill, 1973). Hill numbers are characterised by their order q which influences their sensitivity to common species relative to rare species. When $q = 0$, the Hill number is the species richness, which has zero sensitivity to species relative abundances. When $q = 1$, the Hill number is $\exp(H)$ where H is the Shannon entropy. In this case, species are weighted according to their abundance. When $q = 2$, the Hill number is the inverse of Simpson's concentration, weighting common species more than rare species (Jost, 2006). Hill numbers thus act analogously to statistical moments with increasing emphasis on the dominance of the most abundant species. We quantified diversity by the Hill set ($q = 0, 1, 2$) to convey the intuitive concepts of species richness and evenness.

We pooled native and introduced ant species abundance data for the ten pitfall traps per site and estimated species diversity ($q = 0, 1, 2$) for the minimum sample coverage found within the individual sites (Chao and Jost, 2012) using the "iNEXT" R package (Hsieh et al., 2016). The minimum sample coverage in our study was estimated as 89%. We fitted linear mixed-effects models to examine the effect of habitat type on the different diversity indices (R package *nlme* (Pinheiro et al., 2013)). We included habitat type as a fixed effect and research area as a random effect, and accounted for heterogeneity of variances within the models (Zuur et al., 2009). Furthermore, because spatial heterogeneity affects biodiversity (Brockhoff et al., 2008), we accounted for spatial autocorrelation within the models using semivariograms fitted with an exponential model (R packages *PBSmapping* and *nlme* (Schnute et al., 2015; Pinheiro et al., 2013)). We used an analysis of variance (ANOVA) to assess the overall effect of habitat type. We then followed up with a Tukey post hoc test to look for significant differences between the different habitats (R packages *emmeans* and *multcomp* (Hothorn et al., 2008; Lenth, 2020)).

We also calculated, for each individual species and genus, the proportion of sites within each habitat at which the species/genus was present. This enabled us to identify the species and genera which were most affected by swidden.

We pooled native and introduced ant species data for all traps for each site, and calculated the proportional incidences for each species, that is the proportion of the traps at each site which contained the respective species. These data were Hellinger transformed and then a Principal Component Analysis (PCA) was used to summarise the effect of habitat type on ant community composition. We tested the effect of habitat type on species composition using a permutational multivariate

analysis of variance (PERMANOVA) (Anderson, 2001) based on Bray–Curtis dissimilarity matrices and 999 permutations. These analyses were all conducted using the *vegan* R package (Oksanen et al., 2015).

2.4. Introduced and native species

We calculated species richness ($q = 0$) and abundance (the total count of all individual ants) separately for both introduced and native ant species for each site. We fitted linear mixed-effects models to test the effect of habitat type on these four indices using the methods described above (R package *nlme* (Pinheiro et al., 2013)). Due to non-normal residuals of the model looking at habitat type effect on introduced ant abundance, we added one and carried out a log transformation on the independent variable. Further, we carried out correlations between the abundances of native and introduced species per site, as well as the species richness ($q = 0$) of native and introduced species for each site using Spearman's rank correlation tests.

We used Redundancy Analysis (RDA) to quantify the relative power of introduced ant species assemblages and environmental variables in determining native ant species community structure. We calculated the proportional incidences for both the introduced species and native species data which were then individually Hellinger-transformed. We then further transformed introduced species abundances by PCA, and selected the first two axes (labelled IntSp.Axis1 and IntSp.Axis2). We used these axes as the constraining variables for RDA conducted on the (Hellinger-transformed) native ant species proportional incidence data (the response variable matrix) and tested for significance using an ANOVA. We also performed a PCA on the continuous environmental variables taken from each site, and selected the first axis of the PCA (Env.Axis1) for use in further analysis. We then used IntSp.Axis1 IntSp.Axis2 as explanatory variables in a multivariate regression approach based on Redundancy Analysis and multivariate variance partitioning to model the response of the native ant communities to introduced ant species. We accounted for any possible covariation between the environmental conditions and introduced species composition by including Env.Axis1 into the RDA as a conditioning variable. We then used an ANOVA to test the significance of the effect of introduced ant assemblages on native ant assemblages. Finally, to test the effect of habitat type on native community composition independently of the effect that introduced species has on native community composition, we used a second RDA model with Env.Axis1 as the explanatory variable and IntSp.Axis1 and IntSp.Axis1 as the conditioning variables (Appendix D). These analyses were carried out using the R package *vegan* (Oksanen et al., 2015).

Finally, we used a probabilistic model of species co-occurrence (R package *cooccur* (Griffith et al., 2016) based on work by Veech, 2013) to test if there were any significantly negative patterns of co-occurrence between native and introduced ant species (compared to the frequency of co-occurrence patterns expected if the distribution of each species were random and independent of the other species). This analysis was run on site presence-absence species data for each habitat individually. All possible species pairs were analysed but we focused on pairs which consisted of one introduced species and one native species.

All these analyses were carried out using R version 3.2.2 (Team, 2013). For all linear models, we checked the assumptions of linearity, normality of the residuals, and homogeneity of residual variance. This was done by plotting the residuals against the response variable, the standardised residuals against the quantiles of standard normal for each level of the random effects, and the residuals against the fitted values. As some transects reported less than 10 pitfall traps, sensitivity analyses excluding these transects were run for every analysis listed above to confirm that they did not drive any of the following reported findings.

3. Results

3.1. Species diversity

In total, 10,324 worker ants were recorded, belonging to 195 species from 33 genera across the 35 sites (Appendix E). Of the 195 species, 177 species are thought to be endemic and there were 18 introduced ant species. Fifty-one species and seven genera were found only in closed canopy forests (Table 1). Sexuates were not included in this analysis as due to their ability to fly, their presence in a habitat does not necessarily indicate colonial establishment.

Habitat significantly affected species richness (ANOVA: $F_{3,29} = 6.0$, $p < 0.005$). Closed canopy forests had significantly higher species richness (Hill $q = 0$) than shrub fallows (Tukey HSD: $t(29) = 3.9$, $p < 0.005$), and exhausted lands (Tukey HSD: $t(29) = 4.0$, $p < 0.005$; Fig. 1a). There were no other significant differences between the habitats (Fig. 1a). When native species were analysed separately, species richness also generally decreased as land becomes more degraded (Fig. 3d). Habitat also significantly affected the exponential of Shannon diversity ($q = 1$) (ANOVA: $F_{3,29} = 5.41$, $p < 0.005$). However, the only significant difference was that shrub fallows had significantly lower diversity than closed canopy forests (Tukey HSD: $t(29) = 3.9$, $p < 0.05$; Fig. 1b). There were no significant differences between any of the other habitats. Furthermore, whilst habitat significantly affected the inverse of Simpson diversity ($q = 2$) (ANOVA: $F_{3,29} = 4.9$, $p < 0.01$), there were no significant differences between any of the habitats (Fig. 1c).

Of the five species that were most negatively affected by swidden, three of them are considered predatory species, one of them is considered as omnivorous or a seed-harvester, whilst the other two are currently unclassified. Of the most negatively affected genera, all are considered as predatory. Further, of the five species that were most positively affected by swidden, all were omnivores, except one which was unclassified. All of the five most positively affected genera are considered as omnivorous.

3.2. Community composition

Habitat had a significant effect on species composition (PERMANOVA: $F_{3,31} = 2.27$, $p = 0.001$). Axis one of the PCA (Fig. 2) showed a transition in ant community composition among habitats: from exhausted land and shrub fallows, to tree fallows, to closed canopy forests, although this axis only described 14.2% of the variation. The loadings of each individual study site on axis one were significantly correlated with the following environmental variables: mean canopy cover, mean leaf litter depth, mean leaf litter coverage, mean height of nearest tree and mean shrub cover (Appendix F). Closed canopy forest sites were separated from the three categories of degraded sites along

Table 1

Numbers of native species, and unique species and genera, found in the different habitats.

Habitat	Species richness of native species	Number of unique native species	Species richness of introduced species	Number of unique introduced species	Number of unique genera
Closed canopy forest ($n = 10$)	115	51	4	0	7
Tree fallow ($n = 6$)	74	13	4	0	0
Shrub fallow ($n = 10$)	91	19	12	2	1
Exhausted land ($n = 9$)	81	17	14	5	2

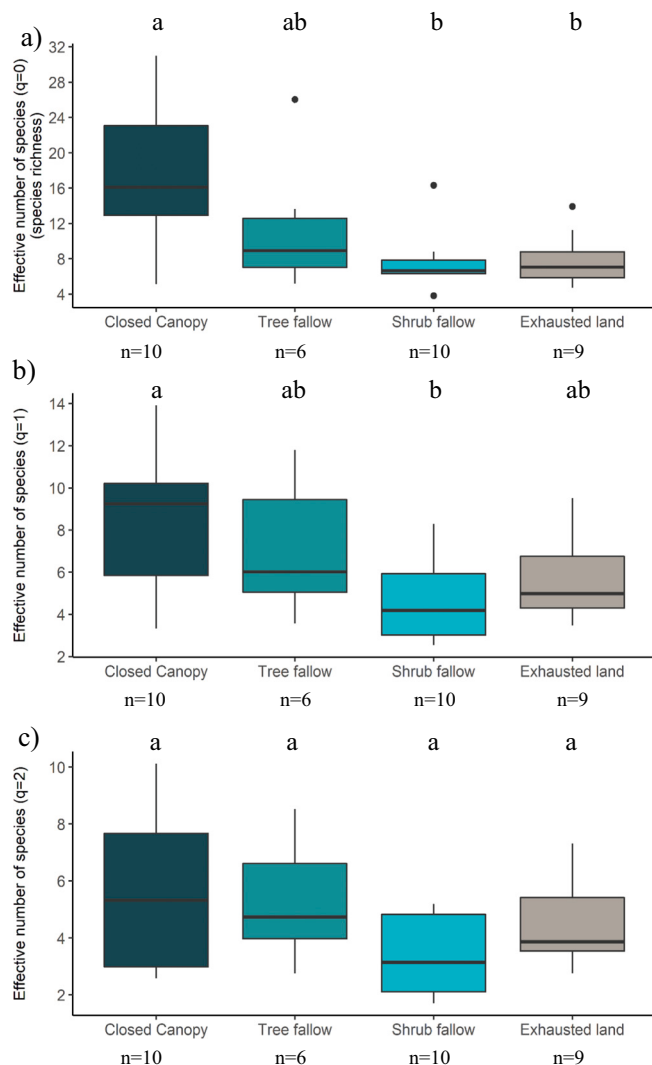


Fig. 1. Effective number of species calculated using a) $q = 0$ b) $q = 1$ and c) $q = 2$ for each sampled habitat type when rarefied to minimum sample completeness following Chao and Jost (2012). In the box plots, the boundary of the box closest to zero indicates the 25th percentile, a black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points above and below the whiskers indicate outliers outside the 10th and 90th percentiles. Bars with different letters are significantly different as tested using a Tukey HSD approach.

Axis one. Axis two, which explained 11.6% of the variation, shows a directional change in ant community composition among those habitats associated with swidden (from tree fallows, through shrub fallows, to exhausted lands). The loadings of each individual study site on axis two were significantly correlated with mean canopy cover; mean leaf litter depth; mean leaf litter coverage; mean height of nearest tree, and mean grass cover (Appendix F).

3.3. Introduced and native ant species

Habitat type did not have a significant effect on the abundance of introduced species (ANOVA: $F_{3,29} = 2.8$, $p = 0.06$; Fig. 3a), or the abundance of native species (ANOVA: $F_{3,29} = 2.3$, $p = 0.09$; Fig. 3c). Further there was no significant correlation between the abundances of introduced species and native species (Appendix G). Habitat type did have a significant effect on introduced species richness (ANOVA: $F_{3,29} = 10.8$, $p < 0.005$; Fig. 3b). Introduced species richness increased

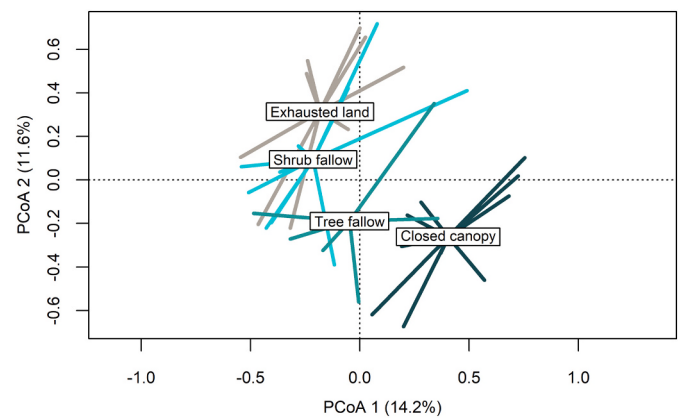


Fig. 2. Ordination plots of the Principal Component Analysis on the total ant community (native and introduced) matrix. Each line on the diagram represents a site for the corresponding habitat type whilst boxes are the habitat centroids. The effect of habitat type was significant.

gradually with habitat degradation; closed canopy forests had significantly lower introduced species richness than shrub fallows (Tukey HSD: $t(29) = -5.0$, $p < 0.001$ and exhausted land (Tukey HSD: $t(29) = -3.5$, $p < 0.001$). However, there was no significant difference in introduced species richness between any of the other habitats (Fig. 3b). This was the opposite to the pattern seen in native species richness; habitat type had a significant effect on native ant species richness (ANOVA: $F_{3,29} = 11.7$, $p < 0.001$; Fig. 3d) with native species richness decreasing gradually with habitat degradation; closed canopy forests had significantly higher native species richness than shrub fallows (Tukey HSD: $t(29) = 5.4$, $p < 0.001$ and exhausted land (Tukey HSD: $t(29) = 5.5$, $p < 0.001$). There was a significant negative correlation between native species richness and introduced species richness (Spearman's rank correlation: $r(33) = -0.51$, $p = 0.002$), but there was no visible pattern in the distributions of the different habitats within the correlation (Appendix G).

Changes in introduced ant species community composition were significantly correlated with changes in native ant species community composition; the first and second axes from the PCA of introduced species explained 15% of the variation and were significantly correlated with changes in native ant community composition, even when environmental variables were controlled for (ANOVA: $F_{1,26} = 2.08$, $p = 0.001$ and $F_{1,26} = 2.29$, $p = 0.001$, respectively). Furthermore, redundancy analysis showed that the major pattern in native ant community compositional change was along the first axis, with exhausted land, shrub fallow, and tree fallow sites ordered along this axis (Fig. 4). This was correlated with the first axis of the introduced species PCA. The other major pattern in native ant community compositional change was along the second axis with a transition across the degradation gradient: from closed canopy forest, to tree fallows, to shrub fallows, to exhausted land. This correlated with the second axis of the introduced species PCA. Furthermore, when the effect of introduced community composition was accounted for, environmental conditions still had a significant effect on the native species community composition (ANOVA: $F_{1,26} = 2.06$, $p = 0.002$).

3.4. Co-occurrence between introduced and native species

There were significant negative co-occurrence between three pairs of introduced and native species; two of these pairs were found in closed canopy forest and one pair was found in shrub fallow (all $p < 0.05$). All these negative interactions involved the introduced species *Pheidole megacephala*.

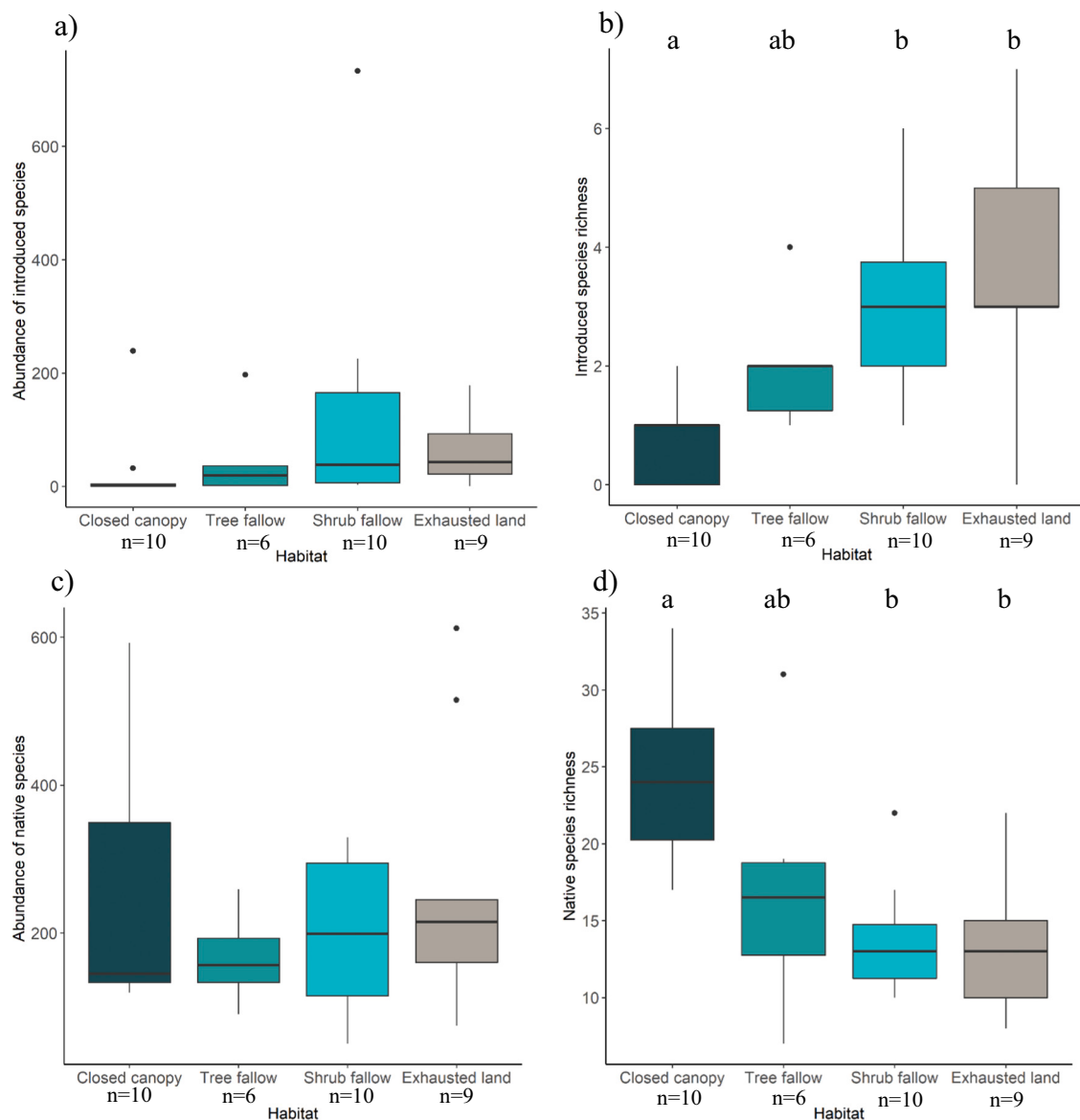


Fig. 3. For each sampled habitat: a) abundance of introduced ant species, b) introduced ant species richness ($q = 0$) c) abundance of native ant species and d) native ant species richness ($q = 0$). In the box plots, the boundary of the box closest to zero indicates the 25th percentile, a black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points above and below the whiskers indicate outliers outside the 10th and 90th percentiles. Bars with different letters are significantly different as tested using a Tukey HSD approach.

4. Discussion

4.1. Total ant species diversity and community composition

Tropical forests are the world's most diverse terrestrial ecosystem (Myers et al., 2000) and our analysis accordingly demonstrates that closed canopy forests in Madagascar have the highest ant species richness among all the examined habitats. The observed decline in ant species richness (Fig. 1a, Fig. 3.d) in response to degradation by swidden is consistent with the general observation that increased anthropogenic disturbance reduces biodiversity (Alroy, 2017). Importantly, the greater ant species richness of closed canopy forest comes from rarer species (comparing $q = 0$ (Fig. 1a) with $q = 2$ (Fig. 1c)), which are more vulnerable due to their smaller populations yet potentially critical to ecosystem functioning (Leitão et al., 2016). However, it is important to note that the diversity indices ($q = 1$ and $q = 2$), which were the only analyses for which we used abundance data, could be biased by inter-specific difference related to foraging strategies (recruitment vs

solitary). This could confound the observed patterns in diversity related to the habitat degradation.

We observed a gradient of change in ant community composition through the successive swidden habitats (Fig. 2). Analysis of the species and genera most affected by swidden, suggests that generally predatory species, such as *Bothroponera cambouei* and *Leptogenys angusta* are the most likely to be negatively affected by swidden, whilst generally omnivorous species, such as *Brachymyrmex cordemoyi* and *Cardiocondyla emeryi*, are the most likely to benefit from this form of agriculture. This is supported by previous research which suggests that predator species are associated with more heterogenous environments than omnivorous species, and are also more sensitive to environmental change (Dias et al., 2013). We also observed that each habitat contained unique species, and in some cases unique genera, relative to the other habitats (Table 1), possibly reflecting habitat-specific differences (Bihn et al., 2010; del Toro et al., 2012) and changes in ecological services (Bihn et al., 2010).

Overall, the highest number of unique native species (fifty-one) and genera (seven) were found in closed canopy forest, which is clear

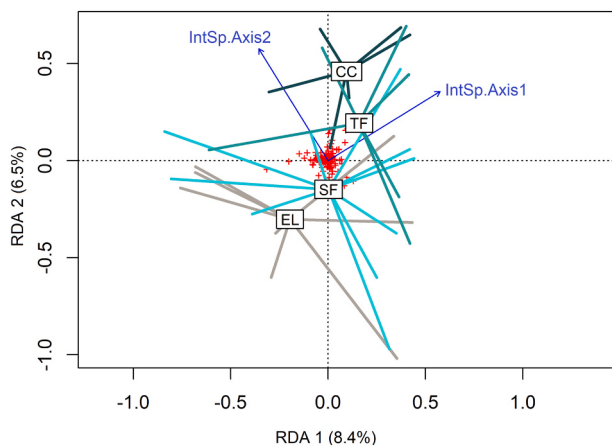


Fig. 4. Ordination plots of the redundancy analysis on the native ant community matrix as dependent on habitat type. Each line on the diagram represents a site for the corresponding habitat whilst boxes are the habitat centroids. Also shown are the first two axes from the principal component analysis on the introduced ant species community matrix (IntSp.Axis1 and IntSp.Axis2). Crosses represent individual species. CC = Closed canopy forest, TF = Tree fallow, SF = Shrub fallow and EL = Exhausted land.

evidence for the importance of conserving this habitat. Of these unique genera to closed canopy forest, five were predacious, whilst two were omnivorous. However, the more degraded habitats, such as tree fallow and shrub fallow, are not devoid of species (Fig. 1) and contain native species and, in the case of shrub fallows, genera which are found in no other habitat (Table 1), suggesting that also these habitats also need to be carefully considered in future conservation plans.

Ant diversity has been shown to decline when agricultural activities lead to the simplification of vegetation structure (Roth et al., 1994). In Madagascar, swidden has been shown to reduce plant species richness and plant species abundance (Klanderud et al., 2010). These findings could explain our observed differences in species richness between the investigated habitats because the species richer closed canopy forests are structurally more complex, and complexity reduces along the degradation gradient to exhausted lands (Fig. 1a). The mechanism may be that more structurally complex habitats provide more nest sites, ecological niches and a wider variety of food resources (Andersen, 1986). This complexity is expected to better support rare species than structurally simpler habitats (Byrne, 1994). Our results support this theory because successive swidden habitats had declining coverage and depth of leaf litter (Appendix H), which was significantly correlated with ant species richness (Appendix I) and changes in community composition (leaf litter depth and cover were significantly correlated with Axis 1 and Axis 2 in Fig. 2) (Appendix F).

Tree fallows can arise either from few swidden cycles, having recently been forest, or from longer term natural regeneration of shrub fallows (Styger et al., 2007). We were unable to discriminate between these processes given the information available for our study sites. The variance in diversity indices and community composition of tree and shrub fallows was, however, similar to that seen in the other habitats, so does not currently support splitting the fallow habitats into sub-categories.

4.2. Introduced species

The observed increase in the richness of introduced species as land became increasingly disturbed due to swidden (Fig. 3) is consistent with a previous study on the effects of anthropogenic disturbance on introduced ant species (King and Porter, 2007). It is also consistent with another study, which suggests that disturbed habitats are more favourable for the persistence of invasive ant species than undisturbed habitats

(Tschinkel and King, 2013).

Some studies suggest that introduced ants reduce native ant species diversity (Walker, 2006; Sarty et al., 2007), whilst others indicate little effect on co-occurring native ants (King and Tschinkel, 2013). The observed increase in introduced species richness was significantly correlated with the reduction in native species richness across the same disturbance gradient. However, results from the co-occurrence analysis show that there were only three pairs of introduced and native species which showed a pattern of negative occurrence, suggesting that antagonistic pairings, and thus introduced species, did not lead to the decline in total species richness between the different habitats. Instead, the changes in land use arising from swidden simultaneously, but independently, affected both introduced and native ant species, with a positive effect on the former and a negative effect on the latter. This is in accordance with King and Tschinkel (2013) findings on disturbance and invasive fire ants.

We observed a significant correlation between changes in species composition of introduced and native assemblages, which did not depend on changes in environmental conditions (Fig. 4). One possible explanation for this correlation is that changes in introduced species caused the shift in native ant community composition through competition and/or aggression. Results from the co-occurrence analysis show that all significant co-occurrence patterns involved *P. megacephala*, an invasive species which has been shown to have physically aggressive workers and soldiers (Fluker and Beardsley, 1970). However, this species was highly abundant in closed canopy forests and had the lowest abundance in exhausted land, suggesting that competition and/or aggression between introduced and native species is not the driving factor in compositional changes between the different habitats. Interestingly, this pattern of abundance may be related to the habitat preference of *P. megacephala*; this species prefers shaded habitats with higher humidity and lower temperatures (Greenslade, 1972). Alternatively, the correlation between changes in species composition of introduced and native assemblages could have resulted from environmental variables which were not included in our analysis. This is particularly true for environmental factors which are related to specific functional traits. For example, many authors have found a significant relationship between heat tolerance and body size in ants (Kaspari, 1993). Changes in these environmental conditions, such as temperature, could therefore correlate with community compositional changes as a result of the traits required to inhabit specific areas. Further research including behavioural studies and more extensive habitat assessment would be needed to explain these patterns.

4.3. Conservation implications

Given the growing population in the tropics, it is critical to find a way to increase swidden productivity whilst also protecting biodiversity. One widely discussed management option is land sparing (Green et al., 2005), which involves intensifying existing agricultural land to reduce pressure on natural habitats. Currently intensification of swidden is achieved through shortening of the fallow stages, and lengthening of the growing periods (e.g. Styger et al., 2007). Thus in recent years, land has been cycled through the swidden process faster, reaching the shrub fallow, and ultimately the exhausted land stage, faster. Our study demonstrates, for the first time, the potential detrimental effects that this intensified swidden cycle can have on native ant communities, and how it likely facilitates the increased prevalence of introduced ant species. Furthermore, intensification of swidden in this way seems self-defeating in the long run, as it hastens land degradation, bringing forward the need to move into and degrade new areas of closed canopy forest.

Another strategy, land sharing, involves low-yield farming and enables biodiversity to be maintained within agricultural landscapes (Green et al., 2005). In order to not compromise on food production, more land is often needed for cultivation. In swidden systems, this would

likely result in further degradation of forests into fallows, unless exhausted land can be restored and brought back into the swidden cycle. Our results highlight the importance of conserving the remaining forests, as their ant communities have greater species diversity and are taxonomically distinct from those found in the other swidden habitats. Our results suggest that in addition to increasing its potential agricultural productivity, restoring exhausted land to tree and shrub fallow habitats could provide connectivity between remnant forest patches for some ant species; as 22.4% of the species in closed canopy forests were found in these other habitats.

No single measure is likely to produce the required increase in crop yields to relieve pressure sufficiently so that longer, sustainable, fallows may be achieved. “Slash and char” swidden, where the cleared vegetation is burned to produce bio-char, which is then spread on the land, has been demonstrated to increase soil fertility and crop production (Barrow, 2012). Further to this, more research into improved cropping materials and methods could prove useful (Pretty et al., 2011). Combining such measures would i) reduce the frequency of fallow clearance, thus allowing more regeneration time, and ii) reduce the rate at which forest are deforested to bring new land into the swidden system. Both of these outcomes would both benefit ant communities and the ecological functions they provide. As swidden systems have demonstrated capacity to maintain and even enhance carbon stocks (Fox et al., 2014), REDD+, a framework that aims to curb climate change by stopping the deforestation, could potentially bridge the economic gap that is critical to ensure the sustainable implementation of such measures.

5. Conclusions

Across the full range of swidden habitats, closed canopy forests have the highest ant species diversity, are taxonomically distinct, and therefore should remain a conservation priority. When these habitats are cut down, and land becomes degraded due to swidden, species richness declines, the community composition changes, and there is an increased prevalence of introduced species. However, tree and shrub fallows habitats harbour unique species as well as 22.4% of the species found in closed canopy forest. We thus recommend that if these habitats are used sustainably, with long fallows to avoid the degradation spiral, these could still play an important role in biodiversity conservation in swidden landscapes across the tropics.

CRediT authorship contribution statement

Elizabeth A. Finch: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Eric T. Rajoelison:** Investigation, Data curation. **Matthew T. Hamer:** Investigation, Data curation. **Tancredi Caruso:** Conceptualization, Methodology, Software, Formal analysis, Writing – review & editing, Resources, Supervision. **Keith D. Farnsworth:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Brian L. Fisher:** Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition. **Alison Cameron:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Data curation, Validation, Resources, Funding acquisition.

Data archiving

Site, environmental and ant data from pitfall samples are archived at The Environmental Information Data Centre (<https://catalogue.ceh.ac.uk/documents/9461f9d7-f7a5-4328-a395-50a3b25da190>).

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary materials to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109400>.

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