Impact of habitat shift driven by humans on ants biodiversity and foraging strategies

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Abstract

Ants are ecologically successful animals present in most ecosystems. Despite a strong competition for such dominant taxa, communities of ants can be extremely rich in terms of species number in a same habitat. Here we explore how foraging strategies can promote such coexistence in two contrasted habitats: well preserved forests, and slash and burn crops in the coastal area of French Guiana. Four types of baits were used to emulate major foraging strategies described for ants in the literature. Our results indicate a richness three times lower in ant slash-and-burn communities than in forest communities. The equitability is also lower in crops. Human activities have therefore a negative impact on ant communities biodiversity. Ants have a complex relationship with biotic and abiotic environment. So, we observed a difference of species composition in forest and between forest and crops. Ant communities present a niche partitioning, through stress tolerance, trophic levels, and time activity. Habitat conversion (from forest to crops) seems to increase ant activity. We observed a reduction of specialization in ant slash-and-burn communities. Foraging strategies have been studied according to different trade-offs. In this study trade-offs cannot explain the coexistence of many species according to niche theory.

Keywords: ants, antropic activities, biodiversity, functional characteristics, foraging strategies

1. Introduction

Ants are one of the most abundant animals in the world. Their ecological success is due to their important roles in ecosystem functions and in environment, for example in soil nutrient dynamics, and through the community management of other organisms. They have also an highly biodiversity (high number of species), particularly in tropics. For example, in West Indies, Mexico, Central and South America, 2233 species have been listed and more than 2500 in Africa (sub-Saharan) (Folgarait, 1998). Niche theory predicts that the number of species cannot be greater than the different resource available, because of interspecific competition. However, in ant communities three coexistence ways are possible. In the first one, many species can coexist with overlapping niches, exploiting the same type of food (Andersen et al., 2000). In the second one, species can coexist with overlapping niches, but using different favourite resources or size of prey (Morrison et al., 2000). In the third case species have no overlapping niche as predicted by the niche theory. So, in the first case, niche theory does not match reality. Consequently, the limiting similarity results in niche partitioning, through stress tolerance, different trophic levels (majority of ant are predators, scavengers, or generalists), and through difference in seasonal and daily activities (MacArthur and Levins, 1967; Andersen, 2008). In spite of that, more than one hundred species can forage at the same time, and the same season.

1.1. Mechanisms related to foraging strategies

Many articles have described several aspects of ant community ecology, describing their communities ecology, such as to their trophic levels, habitat or foraging strategies. These strategies have been studied through different trade-offs, described in the literature. Most of leaf litter ants in tropical forests are omnivorous and opportunists. In the same way as autotrophic plants need water, light, and specific nutrients, these ant functional groups have the ability to exploit a various kinds of food, immediately available. So, they have often high overlapping resource requirements (Andersen, 1991). We focused on the foraging strategies and on ant biodiversity between two habitats. Ants adopt different strategies to find, monopolize and collect a food resource. Several mechanisms have been proposed for ants to avoid competition related to their foraging strategies, such as the trade-off dominance-discovery. Adler et al. (2007) research in Arizona, shows the model dominance-discovery trade-off predicts the coexistence of five of the six most abundant members of the Chiricahua Mountains communities. In this model, a direct conflict leads ants best discovering, and collecting food to colonize new sites, and specialize in low-resource sites (Pearce-Duvet and Feener, 2010). During discovery phase, competitive performance depends of colony size, because the number of foraging workers will increase the probability of finding a food resource (f). According to Gause (1964) law on the competitive exclusion, two ecologically similar species are not likely to coexist due to a high competitive pressure. As a consequence, the less well adapted competitor is sometimes excluded. For example, Solenopidines use mass recruitment of foragers to defend aggressively their food, and exclude other ant species (Perfecto and Vandermeer, 2011). Other factors influence the effectiveness of discovery, and harvest of resource. Indeed, the speed of discovery change according
and richness increase in ant communities Bihn et al. (2010). The quantity variation of resource has not impact on the discovery activity, but regulates the recruitment. If a scout finds a food source larger than the expected quantity, it put down a recruitment trail towards the nest. On the contrary, if the source is smaller, the scout stays on the foraging area to search additional food sources (Mailloux et al., 2000). In mutualism foraging strategy, such as aphid-tending ants, a low quantity of honeydew emitted by aphid (per individual) leads ants to discover neighbouring aphid population, or adopt predation behaviour (Mailloux et al., 2000). In addition, the variation of the habitat complexity, for example resulting from litter deposition, can also modify the number of ants recruited. (Karban et al., 2013) shows that the effect of litter depth is negative on recruitment in wet habitats. Predation rate is also influenced negatively by thick litter. So, the ant ability to locate and consume prey is altered. In wet sites, deep litter is athermal refuges for the prey.

1.2. Effects of habitat conversion on ant communities

Each ant species has a complex interrelationship with their physical and biological environment, and it is very sensitive to the environmental stress (Vasconcelos et al., 2006; Crist, 2009). Indeed, human activities such as agriculture have a significant effect on soil properties, shade, and resource availability, strongly influencing species diversity, abundance, composition, and organization of soil ant communities (Lindenmayer et al., 2008; Crist, 2009). At local, regional and global scales, loss of their initial habitat brings to decrease of species diversity, whereas the effects of fragmentation are more variable. These two phenomena are enhanced according to land-use intensity, and the degree of change in the abiotic and biotic conditions (Crist, 2009).

Consequently, the ecosystem function is altered (Folgarait, 1998; Bihn et al., 2010). The habitat conversion also results in modification of the food available, of possible nest sites and abundance of mutualists or competitors. Indeed, in slash-and-burn, loss of canopy covers leads to high solar radiation, which is conducive to dominant species, whereas opportunists and generalist species are lost (Andersen and Majer, 2004). Competitive exclusion can also explain a negative effect on species richness. Example in Australian ant communities, high species richness is related positively with high levels of dominance, such as habitat disturbance (Andersen, 1997; Hoffmann and Andersen, 2003). Density of functional groups and variety of foraging strategies can also be modified by changing land. In addition, decreased diversity and higher dominance in ant assemblages can be related to a reduction of habitat complexity (Scott et al., 2004; Sarty et al., 2006). Contrarily, another study shows that a high level of species diversity and richness can be restored in tropical secondary forests and in parallel, functional diversity and richness increase in ant communities Bihn et al. (2010).

1.3. Objective of the study

In this study, we explored some major foraging strategies that leaf litter ant communities use to exploit resources, in order to understand how they manage to coexist in two contrasted habitats. First, we explained how land changes influence species richness, and composition in ant assemblages. Secondly, how forest conversion into crops affects ant foraging strategies, through a comparison between forests and slash-and-burn.

2. Materials and methods

2.1. Study site and sampling design

The sampling design consisted on baiting trials, carried in a set of plots situated both on forest and slash-and-burn crops at “La Montagne des Singes” area (Fig. 1) in French Guiana next by Kourou (N 5° 4’ 26.69”, W-52° 42’ 2.95”). In these area relatively well preserved forests and crops can be found in a close range, allowing comparison of human driven habitat shifts within a same area.

Each plot consisted on a rectangular grid of 20 sampling points. A distance of 10 m was left between points. This distance is supposed to be enough in most of the cases to find ants coming from different ant nests at each point (Pearce-Duvet and Feener, 2010). Four people participated on sampling sessions, each controlling and surveying 20 baits on 5 sampling points. Baiting boxes were closed, and ants were brought to the laboratory and killed by freezing them at -20°C. Identifications to genera were carried following Bolton (2003), and then sorted to morphospecies by Alex Salas-Lopez. Morphospecies generally do not have species name. So, in this study morphospecies are given with a number to distinguish the different ants.

The sampling was carried on a total of 120 sampling points in forest and 100 sampling points in slash-and-burn. Sampling was carried only in absence of rain, and in dry soil conditions to avoid any bias linked to field conditions (Andersen (1997))

The sample number 1 in forest was performed twice. The first time the site was sampled, a low activity of ants was found. Plot seemed to present low level of richness and evenness. Further discovery of army ant raids close to the plot was suggested as a possible bias. Therefore the plot was resampled a week later. Both sampling trials were included in the analysis to provide sets of two habitat replicates, eventhough we are aware of the problem of pseudoreplication this suppose.

We counted all ants in each box. The number of ants is not an indicator of biodiversity. Number of ants is mainly depending on ant recruitment capacity, strategies, and behaviour, as well as colony size. Rare species with a great capacities to recruit workers could overpass in number all the other abundant species by looking on the number of ants.

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That is the reason why we transform the numeric information into a binary information with only a presence/absence data. Then we counted the occurrences of observation for each species.

2.2. Sampling strategy

The sampling aimed to capture a large proportion of ants foraging on the ground.

The baits were plastic boxes where dead mealworms were presented in four different ways (Fig. 2), each of which represented a possible resource acquisition strategy. Dead mealworms is an attractive resource for most ants, and by ensuring large quantities, dominant ants were expected to recruit in large numbers. The explored strategies corresponded to the abilities of different ant species to discover and/or dominate the items, the preferences depending on the food quantities provided, and the ability to forage being in relation to habitat complexity.

To capture ants rapidly discovering food items previews to monopolization by a single dominant species, one of the devices consisted on a plastic cap where mealworms were deposited on the cover. The baits were surveyed frequently (5-10 minutes), and closed when some ant activity was detected. To capture the ants foraging on litter and likely to dominate resources, a Petri dish of 5 cm diameter covered with para-film, was set with a large quantity of meal-worms.

To identify differences between species foraging for different food quantities, ants were also offered small food particles on a plastic cap. A piece of cooking paper stuck with fixing paste to the cover, and spread with mealworm powder obtained from the same meal-worms used in the rest of the experience. The amount contained on this device was extremely small in comparison to the others (for example the mean weight of mealworms on Petri dishes was 2.5g) while on these items was lower than 0.1 g. The idea was to capture ants consuming resources even in small quantities, or particles that may be found spread in the forest.

Finally, to emulate intertidal foraging (ants searching resources inside the litter) an eppendorf tube containing dead mealworms was set in a plastic cup, with 4 holes perforated at the base filled with paper slices of different sizes and shapes.

2.3. Statistical analysis

2.3.1. Measures of biodiversity

Biodiversity have been evaluated based on generalized entropy model (Tsallis, 1988) by computing the biodiversity profile ($\alpha$-diversity vs. diversity order). The Tsallis’ model is sensitive to bias, because of the rare species not found, despite high sampling effort. Richness is particularly sensitive to bias. We calculated the $\alpha$-diversity with two non-biased estimators of the entropy. The first non-biased estimator is given by Chao and Shen (2003) and the second...
one is given by Grassberger (1988). The two estimators cannot correct the biodiversity by the same way. Chao & Shen provide a correction for not found species. Grassberger provides a correction for non linearity. The best correction given by Marcon and Herault (in prep.) is the maximum of the two estimations. These methods are implemented in R into the `entropart` package developed by Marcon and Herault (in prep.).

To delimit a confidence interval for the biodiversity indexes we proceeded to a bootstrap like re-sampling method. 1000 communities have been re-sampled by sorting ants in a multinominal distribution from the original one. Confidence intervals are given with 95% reliability.

2.3.2. Comparison between sample sites composition

To evaluate if sample sites are similar or different in composition, we proceeded to a non metric multidimensional scaling (MDS) by computing dissimilarities matrix between sample sites, using the Bray-Curtis distance. Bray-Curtis distance was used, because this distance is helpfull to understand general community structure due to double standardization of the samples, which ensures that neither rare or highly frequent species bias the results. MDS allows to define main groups of sample sites. Groups could be defined with clustering method (k-mean clustering, hierarchical clustering...), but in our study the groups were visually obvious. To determine the pertinence of the visually grouping method, we proceed to an analysis of similarities (ANOSIM) (Clarke, 1993; Warton et al., 2012) from vegan R package (Oksanen et al., 2013). Analyse of similarities can confirm statistically the significance of defined groups.

To understand ant functional activity on each plot, the percentage of consumption of each item was obtained. We considered that an item was exploited when at least one ant was found retrieving food.

2.3.3. Evaluation of functional characteristics

In order to explore the distribution of ant communities in the different boxes FCA was used. It allowed to cluster ant species in relation to their foraging characteristics in a two dimensions space. Only ants occurring at least 10 times were used for the analysis. Further analysis of their foraging specialization was calculated using a test of proportions for each species. A species is considered as non-specialist if there is a uniform distribution in all boxes, whereas ant specialists are expected with a non uniform distribution. An FCA was made for ant species in forest and for ant species in slash-and-burn. For FCA we kept only ant species which were found at least ten times because species which are not enough observed could bias the estimation (in the critical case, a species which was seen only once is necessarily completely described by the box where it has been found, representing a foraging strategy).

Then, we realized a test of equal or given proportions (prop.test) for each species, to know if they are statistically specialized. Species are not specialized if the probability to find a species in a box (each represents a foraging strategy) is 0.25. In the same test, small p-value indicates that the probability of finding the observed distribution from a uniform distribution is very low. So, small p-value reflects more specialized species. Basically, if p-value is 1 the species is equi-distributed in all boxes, and it is completely not specialized. If p-value is 0 the species is always observed in the same box, so it is completely specialized in only one foraging strategy. Between 0 and 1, there is a gradient of specialization. Consequently, p-value could be used as an index of specialization.

With this index, we compared the specialization rate between forest and slash-and-burn. For each species, we computed a rate of specialization, and those which have a p-value < s in the test are considered as specialized. We compared this rate between forest and slashed and burned for different values of s.

Finally, to understand how ant communities are partitioned between the foraging strategies we tested the effect of foraging strategies on niche partitioning. This analysis aimed to understand if foraging strategies are factors which can describe a part of the niche hypervolume according to the niche theory. We carried a principal component analysis to test the composition dissimilarities between each foraging strategies for both forest and slash-and-burn. Then we tested the significance of result with an ANOSIM test.
All statistics previously described have been carried out with R software (R Development Core Team, 2009).

3. Results

3.1. Impact of anthropization on biodiversity

Fig. 3 presents the $\alpha$-diversity (Hill number defined by Hill (1973)) for forest system and slash-and-burn system. The specific richness, Shannon index and Simpson index could be extracted from these functions (see table 1).

![Figure 3: $\alpha$-diversity (Hill number) profiles obtained for the different diversity orders using the numbers of Hill. The lines represent the mean value of diversity, and the colored area the 95% confidence interval](image)

Table 1: Biodiversity index for forest and slash-and-burn crops: specific richness, equivalent species number for Shannon index and equivalent species number for Simpson index. Intervals are given with 95% confidence

<table>
<thead>
<tr>
<th></th>
<th>richness</th>
<th>Shannon</th>
<th>Simpson</th>
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<tbody>
<tr>
<td>Forest</td>
<td>86.5 ± 6.4</td>
<td>52.6 ± 4.3</td>
<td>38.3 ± 7.7</td>
</tr>
<tr>
<td>Slash &amp; burn</td>
<td>29.8 ± 4.1</td>
<td>8.9 ± 1.0</td>
<td>5.3 ± 0.7</td>
</tr>
</tbody>
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![Figure 3: $\alpha$-diversity (Hill number) profiles obtained for the different diversity orders using the numbers of Hill. The lines represent the mean value of diversity, and the colored area the 95% confidence interval](image)

3.2. Comparison between sample sites

On the multidimensional scaling plot fig. 4 three clusters can be distinguished. Two groups of forest and the group of slash-and-burn. The group I was composed of the slash-and-burn sites. The group II on the bottom left was composed of the first (for1) and the second (for2) sample from forest and the third group (III) was composed of the 3rd, 4th and 5th (for3, for4 and for5) sample from forest. With these three groups, ANOSIM indicated a R index of 0.97 and a p-value of 0.001. The two groups of forest were at the same distance to the group of slash-and-burn crops. Distance between forest groups were approximately 0% an 60% on coordinate 1 and 2 respectively.

![Figure 4: Non-Metric Dimensional Scaling using the Bray-Curtis similarity index, for the 10 sampled plots](image)

3.3. Impact of anthropization on functional characteristics

Fig. 5 is the projection of forest data on the first factorial plane. Factorial plane explains the trade-off between the four foraging strategies. Strategies axis have opposite directions so, they seem not to be correlated. Horizontal line explains the trade-off dominance - few quantities preference, and the trade-off discovering ability - intertidal foraging strategy. Vertical line represents the trade-off dominance - discovery, and the trade-off few quantities preference - intertidal foraging strategy. By the same way, we can add diagonal lines to explain other combinations of trade-off. Species on the center are without any specialization, whereby species close to the strategy points are the most specialized.

First FCA axis explains 53% of variance and second axis explains 37% of variance. Variance unexplained is 10%.

Fig. 6 is the projection of slash-and-burn crops data on the first factorial plane. Strategies axis do not have completely opposite directions so, they seem to be correlated. It is more difficult to describe the first FCA factorial plane with trade-off behaviours. FCA of slash-and-burn crops data shows it is difficult to interpret the
Figure 5: First FCA factorial plane analysis for forest graph with trade-off opposition. We analyse these results as a clue of a global loss of specialization.

First FCA axis explains 79% of variance and second axis explains 18% of variance. Variance unexplained is 3%.

Figure 6: First AFC factorial plane analysis for slashes-and-burn

Fig. 7 is the rate of species from forest and slashes-and-burn-crops which have a smaller specialization index (more specialized) than the index in abscissae. For any index of specialization, the percentage of ants coming from the forest with an index smaller or equal to $i$, is always higher than the percentage of ants coming from the slash-and-burn, using the same index $i$. For example, for an index of 0.4, 90% of forest species are more specialized than 0.4, against only 30% of ants from crops.

Figure 7: Comparison between specialization of ant from forest and slash-and-burn, using specialization index previously described

About activity level, percentage of boxes with ants are different between groups: in forest we found at least one ant in 71% of boxes, against in 90% of slash-and-burn crops boxes. By comparing activities between groups I, II and III previously defined, in group I we found ant in 90% of boxes, in group II 66%, and in group III 77%. These results are discussed in part 4.3 after the description of the three groups.

Fig. 8 is a Principal Coordinates Analysis applied to foraging strategies using Bray-Curtis distance. Fig. 8 show a shift between forest and slash-and-burn due to completely different composition. Coordinate 1 is an axe describing habitat change. Coordinate 2 describe composition divergence with foraging strategies. Ants compositions in slash-and-burn seem to be very close for each foraging strategies. Ants compositions in forest seem to be more divergent for each foraging strategies and let think about niche partitioning. ANOSIM analysis indicate a R-value of -0.17 and p-value of 0.97 for slash-and-burn. ANOSIM analysis indicate a R-value of 0.04 and p-value of 0.44 for forest.
4. Discussion

4.1. Impact of anthropization on biodiversity

The richness of slash-and-burn crops is three times lower than the richness of forest. This result show that the antropization induce a large lost of species diversity. Furthermore the equitability of slash-and-burn crops system is also lower than equitabilty of forest system. This result mean that slashes-and-burn crops present few dominant species and a larger percentage of rare species.

We can conclude that antropic transformation of forest induce a large lost of richness but also a lost of equitability according to Scott et al. (2004); Sarty et al. (2006).

4.2. Comparison between sample sites

The sample strategy defined two types of habitat with two gradient factors (slash-and-burn and forest). The MDS showed that we can distinguish three groups.

Forest II and forest III have the same diversity (specific richness and evenness) but not the same composition. That explain dissimilarities. Forest I was rather composed of Pheidole5 (13.3%), Azteca3 (9.6%), Azteca2 (9.1%), Oxyepoecus1 (6.4%), Diplorhoptrum1 (5.9 %) and Pheidole2 (5.0 %) whereas forest III was rather composed of Odetomyrmex1 (22.8 %), Wasmannia1 (11.4 %), Pheidole8 (10.4 %), Oxyepoecus1 (6.7 %), Diplorhoptrum3 (6.3 %) and Crematogaster2 (5.7 %).

Samples from forest II group are close to the road (50m) whereas samples from forest III group are deeper in the forest and higher on the hill. Two hypothesis can be advanced to explain these results:

1. **Edge effect**: we could distinguish three types of gradient. Anthropized land, seminatural land and natural land. Forest II (close to the road) could be considered as seminatural land. Not anthropized but not completely wild. More light enter which accelerates organic matter decomposition of often induce higher tree-fall rate. In this hypothesis we expect to see group II between group I and group III. In fact group II is not between group I and group III but they are all together at the same distance.

2. **Shallow area effect**: group II is on the bottom on the hill whereas group III is on the mid hill or on the top of the hill. This place is wetter and more subject to flood risk. So ant composition could differ from group III because of soil condition without impacting diversity.

4.3. Impact of anthropization on functional characteristics

Results of specialization analyse confirm the hypothesis of a loss of specialization in slash-and-burn. Results seemed to confirm niche partitioning by showing that coexistence of a large number of species (forest) is permitted by a divergence of functional traits. On the contrary, when the number of species is low (slash-and-burn), the dominance is established by generalist ants which use all strategies and all food types. These results are in opposition with Andersen and Majer (2004). These differences are associated with a variation of exploitation level. The four strategies are better used in slash-and-burn (only 10% of empty box against 30% in forest). This observation could be linked to the simplification of the habitat. Habitat simplicity induces a lower forage surface and a better probability for ants to find the food. But the observation in group II (bottom of forest) is in opposition with this hypothesis. Litter is simplified in the bottom of the hill probably due to hydric phenomena. We observed a litter 75% less thick in the bottom than in the middle of the slope. With the previous hypothesis we expect a greater level of exploitation. We probably charge this observation to the hydric stress due to regularly overflowed soil which could affect ants activities. Furthermore we could link the greater biodiversity richness and evenness see in part 3.1 to the hydric phenomena according to intermediate perturbation theory (Cordonnier, 2004).

We could not conclude about the effect of anthropization on functional characteristics. The samples did not contain the same species in forest and in slash-and-burn. Our approach is not neutral with species. If ants from forest seem to be more specialized in their foraging strategies we could not link this phenomena to the human activities and the land transformations. This also could be the effect of the species composition. We probably could charge this observation to the land changes and therefore to human activities according to Karban et al. (2013); Scott et al. (2004); Sarty et al. (2006).
but this study can't allow to answer the question.

To finish, it seemed that there was a greater community structuring in forest with regard to the ant composition in foraging strategies. These results are not statically significant and we must conclude to two non structured communities. These results indicate that the niche could not be defined by foraging strategies. Each ant niche must be described with other abiotic and biotic factors. Niches are probably better described through stress tolerance, different trophic level or daily activities according to (MacArthur and Levins, 1967; Andersen, 2008).

5. Conclusion

We studied the impact of habitat shift driven by humans on ants comparing natural forest and slash-and-burn. We compared five points: (i) the change in community biodiversity (ii) the change in community composition (iii) the change in level of activity, (iv) the change in foraging strategies and (v) the role of foraging strategies on niche partitioning.

This study showed that impact of habitat shift driven by humans induces a large loss of ants biodiversity. Especially we found a lost of 66% of specific richness by comparing natural forest and slash-and-burn. Furthermore we showed a shift between ants composition in forest and slash-and-burn. First there is a shift into the forest sample probably due to change of litter type. Secondly there is a change of composition between forest and slash-and-burn.

Concerning the level of foraging activity we found the higher activity in slash-and-burn. We charged this observation to habitat simplification. The second higher activity level was for overfloodable forest on the bottom of the hill. We charged this observation to intermediate perturbation theory which can justify differences between the two forest types.

About ant foraging strategies, we showed a loss of specialization between ants from forest and ant from slash-and-burn. Foraging strategies seemed to be simpler in slash-and-burn probably due to habitat simplification. But the hypothesis of a shift in foraging strategies due to species composition could not be rejected. To finish, despite graphical appearance, we refute the hypothesis of a niche partitioning based on foraging strategies.

References


