Competition can lead to unexpected patterns in tropical ant communities

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19   Running head: Pairwise interactions in tropical ant communities

20   Type of article: Standard Article

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22   Statement of authorship:

23   MDFE designed research and performed experiments; NB & FM designed analytical tools;

24   FM implemented analytical tools and analysed the data; FM & MDFE wrote the paper; TMF

25   identified ants; all authors contributed to data interpretation and manuscript revision.

26

Abstract

Ecological communities are structured by competitive, predatory, mutualistic and parasitic interactions combined with chance events. Separating deterministic from stochastic processes is possible, but finding statistical evidence for specific biological interactions is challenging. We attempt to solve this problem for ant communities nesting in epiphytic bird's nest ferns (*Asplenium nidus*) in Borneo's lowland rainforest. By recording the frequencies with which each and every single ant species occurred together, we were able to test statistically for patterns associated with interspecific competition. We found evidence for competition, but the resulting co-occurrence pattern was the opposite of what we expected. Rather than detecting species segregation—the classical hallmark of competition—we found species aggregation. Moreover, our approach of testing individual pairwise interactions mostly revealed spatially positive rather than negative associations. Significant negative interactions were only detected among large ants, and among species of the subfamily Ponerinae. Remarkably, the results from this study, and from a corroborating analysis of ant communities known to be structured by competition, suggest that competition within the ants leads to species aggregation rather than segregation. We believe this unexpected result is linked with the displacement of species following asymmetric competition. We conclude that analysing co-occurrence frequencies across complete species assemblages, separately for each species, and for each unique pairwise combination of species, represents a subtle yet powerful way of detecting structure and compartmentalisation in ecological communities.

Keywords: ant mosaics, assembly rules, competitive exclusion, community assembly, co-occurrence patterns, limiting similarity

1 Introduction

2 The question of whether rules do or do not govern the coexistence of species has interested

3 ecologists for decades (Bell, 2001; Chesson, 2000; Connor and Simberloff, 1979; Diamond,

4 1975; Hubbell, 2001; Leibold, 1995; Matthews and Whittaker, 2014). All species interact,

5 both with their environment, and with each other. These interactions can be negative, as in the

6 case of interspecific competition or predation, or the interactions can be positive, as in the

7 case of mutualism or facilitation. The importance of positive interactions to the composition

8 and stability of ecological communities is becoming increasingly acknowledged. Indeed, the

9 overall balance between positive and negative interactions may be fundamental to the

10 maintenance of biodiversity (Mougi and Kondoh, 2012; Wang et al., 2012). For example,

11 parasitic species can only establish if their hosts are present (we define this as a positive

12 interaction, since parasite and host usually occur together), and mutualists can face extinction

13 if the partner species dies out (Koh et al., 2004). Interspecific interactions, whether positive or

14 negative, cause shifts in the abundance of species, and generate communities with predictable

15 composition (Hejda et al., 2009; Parr and Gibb, 2010).

16

17 Species segregation, the result of negative interspecific interactions, is traditionally associated

18 with competition. However, species segregation in ecological communities may also result

19 from environmental filtering (Kraft et al., 2015) and dispersal limitation (Hubbell, 2001). By

20 controlling for these effects, a previous study revealed the importance of interspecific

21 competition relative to stochastic processes in structuring arthropod decomposer communities

22 (Ellwood et al., 2009). However, given that the physical tolerances and dispersal abilities of

23 species are difficult to quantify, it is challenging to define the contributions of particular

24 species, and of particular pairs of species, to the overall levels of competition within a

25 community.

26

1 Here we suggest a way around such problems, using ants in a tropical rainforest to

2 demonstrate our technique of analysing each potential interaction between species. Our

3 analysis gradually drills down from overall co-occurrence patterns across an entire

4 community to the analysis of co-occurrence in specific species pairs. Unlike previous studies,

5 we can detect segregation (or the opposite, species aggregation) not only at the level of the

6 entire community, but we can also identify specific species that co-occur with others less (or

7 more) often than expected – for example, species that competitively exclude each other.

8 Finally, we analyse co-occurrence between specific pairs of species, thus identifying pairs that

9 often co-occur (e.g. if they are mutualists, or host and parasite), or ones that do not co-occur

10 (e.g. through competitive exclusion).

11

12 The ant communities inhabiting litter-trapping epiphytic bird's nest ferns (*Asplenium nidus*)

13 are an ideal study system to analyse interspecific competition and community assembly: ants

14 are diverse, and often aggressively displace other species through direct behavioural

15 interactions. Thus, competition is often thought to be a major factor in structuring ant

16 communities, strongly affecting patterns of co-occurrence (Blüthgen and Stork, 2007; Cerdá

17 et al., 2013). Ants compete for food or for nest sites (Blüthgen and Feldhaar, 2010), and

18 should display direct competition for nest space within the fern's root mass. Thus the limiting

19 resource—space—is both clearly defined and quantifiable, depending on the size of the fern

20 (Ellwood and Foster, 2004; Ellwood et al., 2002; Fayle et al., 2012). In this view, the

21 inhabitants of epiphytic ferns are analogous to communities on oceanic islands (Collins et al.,

22 2011; Gotelli et al., 2010).

23

24 Explanations for large-scale patterns of ant co-occurrence sometimes refer to 'ant mosaics'.

25 The rationale behind ant mosaics is that a small number of species exclude or selectively

26 tolerate each other, while the remaining species are unaffected (Blüthgen et al., 2004).

4

1 Previous attempts to establish the existence of ant mosaics in tropical rainforest may have

2 been thwarted by insufficient spatial resolution and poor statistical power (Blüthgen and

3 Stork, 2007; Floren and Linsenmair, 2000; Ribas and Schoereder, 2002). Similarly, while it is

4 known that nest sites in tropical rainforests are limited (Blüthgen and Feldhaar, 2010),

5 previous studies (Fayle et al., 2013) of ant co-occurrence in bird's nest ferns have not

6 examined pairwise species interactions, so the absolute strength of interspecific competition

7 remains unclear. While our study of ant communities in epiphytic ferns is one of co-

8 occurrence patterns in well-defined patches rather than ant mosaics (i.e. territories) in a

9 contiguous habitat, we believe that studying the occupancy of patches that are competed for

10 will help to shed light on questions surrounding the existence of ant mosaics. Performing

11 analyses at small spatial scales may reveal patterns of aggregation or segregation that would

12 otherwise be overlooked.

13

14 In the present study, we searched for evidence of competition for nest sites among fern-

15 dwelling ants. Although our focus was on competition rather than environmental filtering, we

16 wanted to include species interactions throughout the entire rainforest, rather than from an

17 artificially delineated subset of the habitat. However, physical conditions differ between strata

18 – e.g. the canopy experiences harsher abiotic conditions with stronger climatic fluctuations

19 than the understorey (Nadkarni, 1994; Parker, 1995). Such environmental gradients affect

20 levels of competition in the fern's decomposer communities (Ellwood et al. 2009), and in the

21 structure of intertidal seagrass communities (Barnes and Ellwood, 2011a, b, 2012a). With this

22 in mind, we studied ant metacommunities in ferns from the canopy and the understorey. By

23 removing the entire fauna from within the ferns and then allowing them to be recolonised, we

24 were able to observe communities at different successional stages, where competition might

25 differ e.g. due to dispersal limitation. We firstly analysed negative and positive interactions

26 for the entire set of experimental ferns. Subsequently, we analysed whether competitive

1 exclusion was detectable in specific subsets of ferns. Compared to the understorey, we

2 expected that the harsher conditions of the canopy act as an environmental filter, thus

3 reducing competition and leading to a less structured community. Furthermore, community

4 structure should be lowest during early recolonisation, when dispersal-limited competitors

5 may have yet to reach the ferns. Finally, we searched for patterns of competition depending

6 on the ant's body size, and on their subfamily membership.

7

Materials and methods

Experimental design

10 We compared the structure of ant communities in 180 bird's nest ferns (*Asplenium nidus*)

11 sampled from five emergent *Parashorea tomentella* (Dipterocarpaceae) trees in undisturbed

12 lowland dipterocarp forest in Danum Valley, Sabah, Borneo (4°58´N, 117°48´E). We chose *P.*

13 *tomentella* which, being of similar height and appearance provided standard microhabitats for

14 epiphytic ferns. Along with other ferns, *A. nidus* is one of the most common epiphytes large

15 enough to provide nesting space for ants in Southeast Asian rainforests (Tanaka et al., 2010).

16 We distinguished 90 ferns from each of two heights: understorey (3–4m) and canopy (45–

17 50m). Within each height, mature ant communities were sampled from pristine sets of 30

18 ferns that we ensured were as homogeneous as possible, by controlling for fern size, for

19 season and for microhabitat. The entire fauna was removed from the ferns, which were then

20 standardised to the same size and reintroduced onto the five *P. tomentella* trees (n = 12 ferns

21 per tree each for canopy and understorey). Half of the defaunated ferns were sampled after

22 one month (early successional communities) and after eight months (more established

23 communities), respectively. All ferns were of a similar size (range 2.2–3.4 kg fresh weight).

24 See Appendix A1 for more details.

25

Statistical design

6

1   Our statistical approach measures whether the co-occurrence pattern for each species deviates

2   significantly from what would be expected if species co-occurred at random. For each

3   possible pair of species it calculates how many times those species co-occurred in the same

4   fern ('number of associations'). The dataset is then shuffled, and species occurrences are

5   randomly assigned to ferns. Like the C-score (Gotelli, 2000; Stone and Roberts, 1990), our

6   algorithm is based on a site (i.e. fern) by species matrix, and uses presence/absence data. We

7   present results from the C-score for comparison, using the fixed-equiprobable algorithm, in

8   which each species is assigned the same number of occurrences as in the actual dataset (i.e.

9   species abundances are maintained), but each fern is equally likely to be assigned an

10   occurrence (Appendix A2.3). This was the correct algorithm to use, since the numbers of

11   species per fern fitted a Poisson distribution significantly better than a negative binomial

12   distribution (AIC: 711.4 vs. 713.4). For each of 1000 random simulations, we calculated the

13   numbers of associations for each species pair. This distribution of numbers of associations

14   was then compared to the observed value. Deviations were considered significant if the

15   observed value fell into the lower or the upper 2.5% of random simulations, and additionally

16   at the species and species pair level (see below) if the difference between the observed and

17   expected values of the respective metric was at least 1. The latter criterion was applied to

18   avoid erratic results in rare species, whose numbers of occurrences were too low for reliable

19   conclusions. The P value (as shown in Table 1) is the proportion of simulated values that

20   were more extreme than the observed value in the direction of the relevant tail. Each

21   simulation thus yielded an upper and a lower P value (each one-tailed, with $\alpha = 0.025$). Since

22   these P values reflect either segregation or aggregation, we termed them P_{seg} and P_{agg},

23   respectively.

24

25   First, we analysed co-occurrences at the 'community' level (yielding two P values: P_{nw-agg} for

26   a test of aggregation and P_{nw-seg} for a test of segregation). This metric is analogous to the C-

7

1 score. However, unlike the *C*-score, our method can simultaneously detect aggregation and

2 segregation. Secondly, we analysed the 'species level', where we calculated whether every

3 *single* species *i* co-occurred with *any* of the other species more ($P_{\text{sp(tot)}(i)\text{-agg}}$) or less ($P_{\text{sp(tot)}(i)\text{-}}$

$_{\text{seg}}$) frequently than expected, and whether it was the solitary inhabitant of a fern more or less

5 often than expected ($P_{\text{sp(lone)}(i)\text{-agg}}$ and $P_{\text{sp(lone)}(i)\text{-seg}}$). Finally, we analysed the 'species pair

6 level' to see whether specific *pairs* of species occurred together more or less often than

7 expected ($P_{\text{spp-agg}}$ and $P_{\text{spp-seg}}$).

8 The proportion of species and the proportion of species pairs deviating from random were

9 used here as community-level measures of compartmentalisation. At the species and species

10 pair level, multiple *P* values were generated simultaneously. While we were able to analyse

11 the proportions of non-random species, potential inflation of type I errors due to multiple

12 testing could invalidate conclusions regarding the identity of the non-random species. In the

13 results, we therefore report uncorrected *P* values, but also give results corrected for false

14 discovery rate (FDR, see Appendix A2.1).

15

Comparison to a competitively structured community

17 To calibrate our results with data from a community known to be structured by competition,

18 we applied the same analyses to an existing dataset of ants attending baits in a Northern

19 Australian rainforest. In contrast to our fern dataset, which was based on nest sites, the

20 Australian ants were surveyed at artificial baits made up of sugar and amino acid solutions,

21 and thus competed for food instead of nest space. This dataset consisted of ant occurrence

22 data from 53 trees at Cape Tribulation, Queensland, Australia. In this study, multiple baits

23 were placed at each tree, and ant occupancy was recorded four to five times after placing

24 them. Data from different baits were pooled for each tree. The ant community at these baits

25 reflects a genuine ant mosaic, and aggressive displacement was confirmed by behavioural

1 observations. Different analyses based on this dataset have been published elsewhere

2 (Blüthgen and Fiedler, 2004; Blüthgen et al., 2004).

3

4 **Testing for non-random co-occurrence in species subsets**

5 Species that are more ecologically similar are expected to compete more strongly. We tested

6 this hypothesis in two ways. First, the theory of limiting similarity (Hutchinson, 1959;

7 MacArthur and Levins, 1967) predicts that species of similar body size should compete more

8 intensely. While many different traits should influence interspecific competition, we

9 hypothesized that similar body size should lead to similar nest site requirements, such that

10 species with different body sizes are more likely to co-occur than species of similar size. We

11 partitioned our dataset into species greater than or less than 5 mm and tested for competitive

12 exclusion within these subsets of similar size. Second, by pooling species according to

13 subfamily (see below), we were able to test for competitive exclusion between closely related

14 species (see Appendix A2.1). Closely related species should inhabit similar niches and

15 therefore compete more strongly. Having subsumed species into subfamilies, we were able to

16 use the same algorithm to analyse co-occurrences at the 'subfamily' or 'subfamily pair' level.

17 Subfamily co-occurrence was analysed using (1) a binary approach, i.e. presence or absence

18 of a subfamily in a fern (P values with index 'bin'), and (2) a quantitative approach, which

19 accounted for the number of species per subfamily present in a fern (P values with index

20 'quant'; see Appendix A2.1)

21

Results

23 *Ant community composition in epiphytic ferns*

24 Our experiment yielded 162,019 ants from six subfamilies, 47 genera and 118 species, and a

25 total of 379 occurrences (Table 1). Only 29 species occurred in more than five ferns. Species

1 richness was highest in the mature ant communities of pristine ferns (74 species, 3.8 ± 0.2 SE

2 spp. per fern), followed by recolonized ferns after eight months (59 species, 3.4 ± 0.3 spp. per

3 fern) and one month (46 species, 2.2 ± 0.3 spp. per fern) (Fig. 1). Species numbers per fern

4 differed between the three recolonisation stages but not between height levels (GLM: stage:

5 $\chi^2_2=25.3$, $p < 0.0001$, height: $\chi^2_1=0.6$, $p = 0.45$; interaction: $\chi^2_2=2.8$, $p = 0.25$). All categories

6 of ferns in the study had species in common. The number, and proportion, of shared species

7 between the understorey and the canopy increased markedly from one month (4 spp. / 9%) to

8 eight months (12 spp. / 20%) to mature communities in pristine ferns (23 spp. / 31%; Fig. 1).

9 The composition of the ant communities differed between successional stages and heights

10 (PERMANOVA: both pseudo-F > 1.3, $p < 0.0001$), but were not affected by the tree

11 individuals bearing the ferns (PERMANOVA: pseudo-F = 1.1, $p = 0.17$).

12

Species co-occurrence at the community level

14 In communities structured by competition the Stone and Roberts (1990) observed *C*-score

15 should be significantly higher than a *C*-score simulated at random (Gotelli, 2000). However,

16 the simulated and observed *C*-scores for the fern ant communities were not significantly

17 different (Table 1). To corroborate this seemingly anomalous result, we repeated our analysis

18 on co-occurrence data from a genuine ant mosaic published in Blüthgen and Fiedler (2004).

19 In this paper, ant communities from Australia were shown to be structured by competition,

20 with behavioural observations confirming overt aggression between participating ant species

21 (Blüthgen and Fiedler, 2004; Blüthgen et al., 2004). The simulated and observed *C*-scores for

22 the Australian ants were significantly different, but not in the direction we expected. Among

23 the Australian ants, the observed *C*-score was significantly *lower* than the simulated *C*-score,

24 suggesting aggregation rather than segregation. Similarly, our pairwise analysis at the

25 community level found significantly *more* positive associations than expected, rather than

26 fewer (Table 1). Our analysis also revealed significantly more positive associations (i.e.

10

aggregation) among the fern ants, even though this was not detected by the C-score (Table 1; Fig. 2).

Species co-occurrence at the species level

We found more positive than negative associations in our fern dataset, making it qualitatively similar to the Australian dataset, but the quantitative results from the two studies contrast sharply. In the Australian ant mosaic 18 out of 34 species (53%) were positively (16 spp.) or negatively (2 spp.) associated (Blüthgen and Fiedler, 2004) (Table 1; Fig. 3b). In contrast, of the 118 species found in the ferns, surprisingly few (5.9%) showed non-random associations with any other species: four showed more associations than expected (each $P_{sp(tot)agg} < 0.025$) (Table 1; Fig. 3a), and three showed fewer associations than expected (each $P_{sp(tot)seg}$ or $P_{sp(lone)seg} < 0.025$). After FDR correction, *Anonychomyrma gilberti* retained its negative association, and 15 species pairs retained their positive associations. In the fern dataset, no species remained significant after FDR correction.

Species co-occurrence at the species pair level

Among the fern ants, 33 unique pairs of species were positively associated with each other, and one pair was negatively associated. As in the previous species-level analysis, these are very few (0.5%) compared with the 6903 pairs possible (Table 1; Fig. 4a). Again, we see a sharp contrast with the strongly structured ant mosaic in Australia (Blüthgen and Fiedler, 2004; Blüthgen et al., 2004), which had 31 out of 561 non-random species pairs (5.5%) (Table 1; Fig. 4b). Remarkably, three of the 33 species pairs which showed positive associations in the fern dataset involved the same *Diacamma* species (each $P_{spp-agg} \leq 0.025$): three ant species (a *Polyrhachis* and two *Pheidole* species) were only found together with this *Diacamma* species but not without it. In particular, the *Polyrhachis* species occurred 11 times with, but never without it ($P_{spp-agg} < 0.00001$ in an analysis with 100,000 randomisations).

11

1   After FDR correction, only this pair remained significant in the fern dataset. In the Australian

2   dataset, three negatively (each involving *Anonychomyrma gilbertii*) and three positively

3   associated species pairs remained significant after FDR correction.

4

5   *Evidence for limiting similarity: body size*

6   A specific prediction from the principle of limiting similarity is that similar body size

7   increases competition between species, and therefore decreases the probability of co-

8   occurrence between those species. Overall, occurrence of smaller ants (< 5 mm) was

9   unaffected by the presence of larger ones (≥ 5mm) (Appendix A3). However, the size ratios

10   between the 33 positively associated species pairs was 0.53 ± 0.045 SE, i.e. one species was

11   roughly half the size of the other. In contrast, the single pair of negatively associated

12   (mutually exclusive) species was of similar size (size ratio 0.92). This difference is significant

13   (*t* test: $t = 8.7$, df = 32, $P < 0.0001$).

14   Large species rarely co-occurred with other large species: significant segregation was detected

15   in a dataset containing only large species ($N = 39$ species, including 24 formicine and 9

16   ponerine species, 173 occurrences on 114 ferns; $P_{nw\text{-seg}} < 0.001$). The *C*-score was

17   significantly higher than random, similarly suggesting structuring by interspecific competition

18   ($P < 0.001$, Table 1). In contrast, the communities of smaller species ($N = 79$ species, 411

19   occurrences on 157 ferns), did not deviate from random models using either index, despite

20   larger sample sizes (all $P_{nw\text{-seg}} \geq 0.16$).

21

22   *Evidence for limiting similarity: subfamily membership*

23   Another assembly rule based on the competitive exclusion principle is that competition

24   between closely related species should be stronger than between distant relatives. We

25   therefore analysed co-occurrence between and within subfamilies, assuming that mutual

26   exclusion should be greater in ecologically more homogeneous subfamilies. Members of the

1 Ponerinae, many of which are large and predatory, were more likely than expected by chance

2 to be the only ant species in a fern ($P_{sp(lone)\text{-}bin\text{-}seg}$ = 0.014, $P_{sp(lone)\text{-}quant\text{-}seg}$ = 0.005; N = 13

3 species; average size 7.8 ± 1.1 SE mm). This was not found for any other subfamily (all other

4 $P_{sp(lone)\text{-}bin\text{-}seg}$, $P_{sp(lone)\text{-}quant\text{-}seg}$ > 0.15). In contrast, levels of co-occurrence were greater than

5 expected among the Myrmicinae (2.5 ± 0.1 SE mm, N = 50), which are mostly small, and

6 among the Formicinae, which include small and large species (5.8 ± 0.5 SE mm, N = 37)

7 (Myrmicinae: $P_{sp(tot)\text{-}bin\text{-}agg}$ = 0.014, $P_{sp(ltot)\text{-}quant\text{-}agg}$ = 0.001; Formicinae: $P_{sp(tot)\text{-}bin\text{-}agg}$ = 0.005,

8 $P_{sp(ltot)\text{-}quant\text{-}agg}$ = 0.018).

9

10 By accounting for the *number* of co-occurrences between species within each subfamily,

11 instead of just noting whether a subfamily was present in a fern, we tested whether members

12 of the same subfamily excluded each other. However, despite a trend of competitive exclusion

13 among the Ponerinae ($P_{spp\text{-}quant\text{-}seg}$ = 0.062; N = 13 species), none of the subfamilies

14 significantly excluded each other (all other $P_{spp\text{-}quant\text{-}seg}$ > 0.13).

15

16 *Competition under harsh vs. more equable conditions: canopy versus understorey ferns*

17 We expected competition to be weaker in the canopy, where daily fluctuations in temperature

18 and humidity are greater than in the understorey. Indeed, neither the *C*-score, nor the overall

19 number of associations in our index, differed significantly from random expectations. Only

20 one out of 68 species (1.5%), and 18 out of 2278 species pairs (0.8%), differed positively or

21 negatively from random (Table 1). In the understorey, where physical conditions were more

22 moderate (e.g. reduced fluctuations in temperature and humidity) we found stronger evidence

23 for competition, but again this evidence took the form of aggregation rather than segregation.

24 The *C*-score was significantly lower in the understorey than expected, and our index found

25 significantly more positive associations (Table 1).

26

1 *Evidence for dispersal limitation: early, middle and late succession ferns*

2 In new communities, dispersal/competition trade-offs favour dispersers. Dispersal limitation

3 under these circumstances will engender randomness in community structure (Bell, 2001;

4 Hubbell, 2001). Indeed, after one month, neither the *C*-score nor the total number of

5 associations in our index differed from random expectations (Table 1). However, after eight

6 months, the *C*-score was significantly smaller than expected, again suggesting aggregation,

7 and our index revealed significantly more positive associations (Table 1). The proportion of

8 significantly associated species (i.e. $P_{sp(tot)seg}$, $P_{sp(tot)agg}$, $P_{sp(lone)seg}$ or $P_{sp(lone)agg} < 0.025$) was

9 also highest after eight months (Table 1). As with the communities after one month, co-

10 occurrence was random in the pristine, mature communities, suggesting that the strength of

11 interspecific competition between early and late successional species peaked at intermediate

12 stages of recolonisation.

13

14 Given the significant differences in competition between the canopy and the understorey, we

15 wanted to be sure that patterns of recolonization in the different habitats were not affected by

16 canopy-understorey differences. We therefore repeated separate analyses for each time period

17 in the two strata. Our results were unchanged. Pristine communities, and those after one

18 month in both the canopy and in the understorey, remained random ($P_{nw-agg} \geq 0.46$). Ant

19 communities in canopy ferns after eight months were weakly aggregated ($P_{nw-agg} = 0.029$),

20 although this effect was not strong enough to affect the overall canopy result. However,

21 understorey ferns after eight months remained strongly aggregated ($P_{nw-agg} = 0.005$).

22

23 **Discussion**

24 We used a novel statistical approach to test for effects of competition during patch occupancy

25 as ants colonized epiphytic bird's nest ferns in Borneo. Our statistical approach, in

26 combination with the experimental setup of standardised ferns at different heights and

1 different stages of recolonization, was designed to dissect the ant community at multiple

2 levels of environmental stress and ecological succession. We analysed the whole community,

3 as well as single species, species pairs, and subfamilies.

4

Effects of asymmetric competition

6 Remarkably, the observed C-scores from our eight month ferns and the Australian ant mosaic

7 were lower than C-scores simulated at random, although competition is thought to yield the

8 opposite effect (Gotelli, 2000). The C-score essentially measures how often two species fail to

9 occur together in a community; the underlying reasoning being that interspecific competition

10 creates species segregation, which in turn leads to a 'checkerboard' distribution of species

11 (Gotelli, 2000). But what if species aggregate rather than segregate? Competition between ant

12 species is often asymmetric, with species differing in their competitiveness (Menzel et al.,

13 2010a; Menzel et al., 2010b; Savolainen and Vepsäläinen, 1988). For example, a typical ant

14 mosaic is formed by dominant ant species, some of which (like *Oecophylla*) tolerate many

15 subordinate species, while others (like *Anonychomyrma*) do not. In such a case, the overall

16 species distribution will be clumped rather than uniform: some sites are occupied by

17 *Anonychomyrma*, while *Oecophylla* and most subordinate ant species crowd into the

18 remaining sites. For example, in the Australian ant metacommunity we analysed for

19 comparison, *Anonychomyrma* was significantly intolerant ($P_{sp(tot)\text{-}seg} < 0.001$; 1.5 ± 0.6 co-

20 occurring species), whereas *Oecophylla* was significantly tolerant ($P_{sp(tot)\text{-}agg} < 0.001$; $5.7 \pm$

21 0.5 co-occurring species) (Fig. 3b). Thus, all subordinate species and *Oecophylla* each co-

22 occurred with more species than they would if all species were randomly distributed across

23 the sites. Under such a scenario, the C-score will be lower than random, and our index will

24 give a higher number of associations (Fig. 2b). This result, while surprising, is plausible given

25 previous studies of ant mosaics in which the number of positive associations reached or even

26 exceeded the number of negative associations between abundant species (Blüthgen and Stork,

1   2007; Leston, 1975; Room, 1971). Such asymmetries may lead to species aggregation rather

2   than species segregation.

3

Evidence for competition from analysing co-occurrence patterns

5   Deciphering the signature of interspecific competition from co-occurrence patterns is difficult

6   and controversial. For example, the presence of highly dominant species alone may result in

7   deterministic patterns (Barnes and Ellwood, 2012b). The current study is no exception in that

8   we challenge current knowledge of species coexistence among ants. Our results suggest a

9   shift in the relative importance of equalizing and stabilizing mechanisms, which essentially

10   govern how rare species increase, and common species decrease in abundance (Chesson,

11   2000).

12   Based on our results, we suggest that a re-analysis of species co-occurrence for a wide range

13   of taxa might be worthwhile. There may be structure in a community even if, at the

14   community level, there is no difference from random expectations. To use ant mosaics as an

15   example, let two mutually exclusive dominant ant species each tolerate a non-overlapping set

16   of subordinate species. Overall, this community may show neither a clumped nor a uniform

17   distribution, but one which—at the community level—does not differ from random. This will

18   be the case if neutral interactions between dominants and their subordinates are balanced by

19   the competitive interactions between pairs of dominants (Blüthgen and Stork, 2007; Menzel et

20   al., 2010a). Such a community is clearly structured: dominant species exclude each other, and

21   subordinate ones never co-occur if they are associated with different dominant species.

22   Although both the *C*-score and our community-level association index may fail to detect such

23   a pattern, it is detectable using the proportion of non-random species or species pairs. These

24   two measures will be higher in a structured community compared with a random one, and are

25   therefore useful as measures of compartmentalisation or modularity, analogous to those used

26   in bipartite communities (Dicks et al., 2002; Olesen et al., 2007).

16

Unexpectedly high stochasticity in community structure

It is striking that we found little evidence of species segregation and relatively little community structure in the ant communities of bird's nest ferns. This suggests that competition for nest sites is not as strong as assumed (Blüthgen and Feldhaar, 2010; Cerdá et al., 2013). One reason for the apparent lack of the 'traditional' hallmark of species segregation may be that some dominant canopy ants weave or excavate their own nests and therefore do not compete for nest sites. These species were outside the scope of the present study. However, our dataset included other dominants such as *Crematogaster difformis*, which nests in ferns (Tanaka et al., 2012), and several *Dolichoderus* and *Pheidole* species; competitive exclusion between these dominants at nest sites would have been detected. It is important to stress that the omission of some dominants from our dataset is not a sampling artefact; it is simply due to the fact that these species do not participate in competition for ferns as nest sites. Since species differ in their respective intensities of competition for different resources, it is probable that, depending on the resource under investigation, studies on interspecific competition may yield different results, even within the same community.

Is there limiting similarity?

Despite an overall lack of species segregation, large species showed strong competitive exclusion. We suggest that body size affects the degree of competition for nest sites between species, such that competition is highest for species with similar body sizes. The smaller species might have nesting habits diverse enough to co-exist in the same fern. Interestingly, the positively associated species pairs all were of different sizes, whereas the one pair of mutually exclusive species was of similar size. This corroborates the suggestion that co-existence in the same nest site is more likely among species of different body sizes

1   (Kaufmann et al., 2003). However, body size is but one trait that affects interspecific

2   interactions; and limiting similarity may apply for a wide variety of further ecological traits.

3   Among subfamilies, ponerine species excluded other ants, whereas members of other

4   subfamilies did not. Competitive exclusion has repeatedly been shown to be highest among

5   members of the same guild (Both et al., 2011; Collins et al., 2011), and should be more

6   pronounced among related species since they are likely to be ecologically more similar (but

7   see Beaudrot et al. (2013). It is possible that ponerines are ecologically more homogenuous –

8   most species are predatory – while members of other subfamilies have more diverse foraging

9   niches, diminishing interspecific competition and consequently species segregation.

10   Unfortunately, the feeding niches of most ants are not sufficiently studied to allow further

11   division into feeding guilds (Collins et al., 2011). Additional knowledge, such as guild

12   membership of species, has revealed structure in communities that had seemed random before

13   (Sanderson, 2004). However, even among ants, niche differentiation is not always sufficient

14   to explain the coexistence of similar species (Andersen et al., 2013; Houadria et al., 2015).

15

Do levels of competition differ at different stages of recolonisation and at different

heights?

18   Species diversity should be maximised at intermediate levels of succession, because under

19   these conditions both competitive (K-selected) and opportunistic (r-selected) species can

20   coexist (Connell, 1978). Our results are consistent with this hypothesis. At early stages of

21   succession, interspecific competition is thought to be relatively unimportant. Accordingly, our

22   community-level index, the ratio of significant species, and the C-score, all found competition

23   to be lowest in ferns after just one month of recolonisation. After eight months, which

24   represents an intermediate successional stage, we observed the greatest levels of community

25   structure, in terms of significant aggregation and the highest number of non-random species

26   interactions. However, pristine communities were randomly structured. In our tentative

1 interpretation, competition (which leads to non-random structures) is highest at intermediate

2 successional stages, where colonising species compete for nest space, while pristine ferns are

3 mainly inhabited by species that show little competitive exclusion.

4 In a parallel manner, the understorey communities showed non-random structure, while those

5 in the canopy were stochastic. This may be due to habitat filtering, where higher solar

6 radiation, stronger winds, and stronger fluctuations in humidity (Nadkarni, 1994; Parker,

7 1995) should result in a stronger desiccation stress in the canopy. Here, physical conditions

8 winnow certain species, thus reducing overall levels of interspecific competition and the

9 impact of biotic interactions (Lepori and Malmqvist, 2009; Luiselli, 2006). Note that despite

10 the lower community structure in the canopy, species numbers per fern did not differ between

11 canopy and understorey ferns.

12

13 Implications for the analysis of co-occurrence patterns in community ecology

14 We have outlined a statistical approach for the analysis of ecological communities which

15 allows a detailed analysis of species co-occurrence patterns. By analysing the associations

16 between each and every species, we can detect positive associations and mutual exclusion,

17 and obtain a more detailed picture than metrics such as the *C*-score (Stone and Roberts, 1990,

18 1992) or checkerboard units (Diamond, 1975; Gotelli and McCabe, 2002), although there are

19 other powerful approaches (Gotelli and Ulrich, 2010). Our approach may be particularly

20 useful to search for specialised, pair-wise associations that warrant further study. Such pair-

21 wise associations can indicate mutual tolerance, with a dominant and a submissive species

22 (Dejean and Corbara, 2003; Majer, 1976, 1993; Majer et al., 1994), or parasitic or mutualistic

23 association (Menzel and Blüthgen, 2010; Menzel et al., 2010a; Menzel et al., 2010b; Orivel et

24 al., 1997). In our dataset, one *Polyrhachis* and two *Pheidole* species always co-occurred with

25 the same *Diacamma* species, suggesting a close relationship between them and *Diacamma*.

26 Such intriguing associations have been shown before for other members of these genera

19

1 (*Polyrhachis:* social parasitism; *Pheidole*: cleptobiosis; (Kaufmann et al., 2003; Maschwitz et

2 al., 2000), which underpins the biological relevance of our results.

3

4 Generating large numbers of *P* values with regard to species or species pair levels inevitably

5 increases type I error. This does not affect our statements about proportions of deviant

6 species, but it may affect statements regarding the significance of specific associations. In our

7 study, the *Diacamma-Polyrhachis* association remained significant after correction for

8 multiple testing, but the others did not. Correction over such a high number of *P* values may

9 inflate type II errors, making it more difficult to identify interesting associations: when strictly

10 applying these corrections, few ecological datasets would be large enough to provide the

11 statistical power to detect associations between less common species. For example, the

12 positive association of the *Diacamma* and a *Pheidole* species ($P_{spp-seg} = 0.00029$) did not

13 withstand correction, and even higher statistical power is required to detect negative

14 associations e.g. between competing species. Such problems of statistical power are typical

15 for multispecies ant mosaics and increase with the number, and rarity, of species considered

16 (Blüthgen and Stork, 2007) (Appendix A2.1). We therefore recommend that uncorrected

17 results on the species and on the species-pair levels should be viewed as a filter to detect

18 potentially interesting associations, rather than as strict hypothesis testing.

19 In conclusion, our analysis revealed patterns that would remain undetected by standard co-

20 occurrence metrics, which usually average levels of co-occurrence across pairs of species.

21 This approach may illuminate interesting and unexpected patterns when applied to other

22 ecological datasets. The strength of our method is that it allows to test for non-randomness in

23 co-occurrence for each species pair, and for the co-occurrence of each species with any other

24 one. Moreover, one can analyse data subsets to detect compartments where biotic interactions

25 are particularly intense – be they certain microhabitats, or subsets of species. For example,

26 species segregation was found for larger species, although this pattern was concealed in the

1 analysis of the total dataset. In our opinion, two more features of our method are useful and

2 go beyond previous, valuable approaches to measure species-co-occurrence (Collins et al.,

3 2011; Gotelli and Ulrich, 2010). First, the 'dilution' and, thus, masking, of patterns caused by

4 strongly interacting species in a community with few interacting species is not a problem for

5 our index since more weakly interacting species can still be detected via the proportion of

6 non-random species or species pairs. Second, the species level analysis of our approach

7 enables the assessment of rarer species that interact sparsely, but with many different species,

8 and thus would not reach sufficient statistical power at species pair level.

9 Recently, the importance of functional traits for community assembly and species co-

10 occurrence has been increasingly acknowledged (McGill et al., 2006). Although our method

11 cannot specifically detect the importance of such traits, or habitat filtering according to traits,

12 it can be used to analyse the role of trait *similarity* for species interactions. Firstly, trait

13 differences can be calculated separately and then related to pair-wise co-occurrence measures

14 (Kraft and Ackerly, 2010; Kraft et al., 2008), testing predictions about specific species pairs.

15 Secondly, species can be grouped according to functional traits, and quantitative co-

16 occurrence (i.e. co-occurrence of species with similar traits) can be analysed. This approach is

17 analogous to our quantitative analysis of co-occurrence within subfamilies. It enables

18 detection of whether species with certain traits are overdispersed or clumped. This way, niche

19 overlap can be related directly to co-occurrence (Fowler et al., 2014); and trait clumping can

20 be interpreted as evidence of habitat filtering (Kraft et al., 2015). Ultimately, our new

21 statistical method could help to explain the way in which interspecific, pairwise interactions

22 structure ecological communities.

23

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Table 1. Evidence for segregation (P_{seg}, P_{nw-seg}) or aggregation (P_{agg}, P_{nw-agg}) at the community level, and proportions of species or species pairs deviating significantly from random expectations. For the *C*-score and the community level indices, the table shows one-sided *P*-values for a test of the 'fixed-equiprobable' hypothesis. Proportions in bold are significant ($P < 0.025$). For the percentages of deviant species or species pairs (those that significantly deviate from random expectation), values in bold indicate that they differ among the communities of the same block, i.e. with the same footnote number. All data, except for 'Australian community', refer to the dataset from Borneo. Large ants: $\geq$ 5mm; small ants: < 5mm.

| | no. of species | no. of sites | no. of occur-rences | *C*-score | | Association index | | | |
| | | | | | | community level | | species level | species pair level |
				P_{seg}	P_{agg}	P_{nw-seg}	P_{nw-agg}	proportion of deviant species	proportion of deviant spp. pairs
Whole community	118	177	379	0.941	0.059	0.994	**0.006**	**5.9%**[1]	**0.49%**[2]
Australian community	34	53	286	1.000	**<0.001**	1.000	**<0.001**	**53.0%**[1]	**5.53%**[2]
Canopy ferns	68	81	272	0.557	0.443	0.909	0.098	1.5%[3]	0.79%[4]
Understory ferns	86	96	312	0.973	0.027	0.995	**0.009**	4.7%[3]	0.41%[4]
1-month ferns	46	32	86	0.15	0.859	0.916	0.100	**4.35%**[5]	0.39%[6]
8-month ferns	59	61	206	0.982	**0.018**	0.998	**0.003**	**16.95%**[5]	0.70%[6]
Pristine ferns	74	76	292	0.047	0.953	0.315	0.697	**0.00%**[5]	0.37%[6]
Large ants	39	114	173	**<0.001**	1.000	**<0.001**	1.000	7.7%	0.7%
Small ants	79	157	411	0.160	0.840	0.450	0.560	5.1%	0.5%

(1)χ^2=39.1,df=1,*P*<0.0001; (2)χ^2=146.5,df=1,*P*<0.0001; (3)χ^2=0.4,df=1, *P*=0.52; (4)χ^2=3.0,df=1,*P*=0.08; (5)χ^2=15.6,df=2,*P*=0.0004; (6)χ^2=2.6,df=2,*P*=0.28;
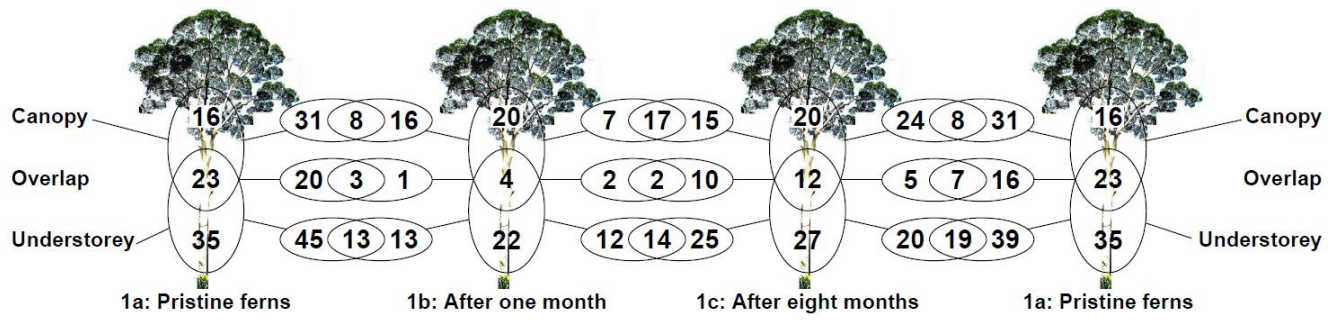
25

1　**Figure legends**

2　**Fig. 1** Venn diagrams showing numbers of species unique to a particular time and height, and

3　numbers of species shared between times and heights. For example, pristine ferns (1a) in the

4　canopy had a total of 16 + 23 = 39 species. Of these 39 species, 23 also occurred in pristine

5　understory ferns (and 16 did not), whereas eight species also occurred in canopy ferns one

6　month after defaunation (and 31 did not).

7　**Fig. 2** Total number of pairwise associations on the community level in (A) the epiphytic

8　ferns (Borneo) and (B) at food baits (Australia). The histograms show the values expected

9　from null model simulations (grey bars) and the observed value in the dataset (red line). For

10　both datasets, the number of associations is significantly higher than expected from the null

11　models ($P_{\text{nw-agg}}$; Table 1), indicating overall species aggregation.

12　**Fig. 3** Total number of pairwise associations at the ant species level in communities (A) in

13　epiphytic ferns and (B) at food baits, shown only for the 15 most common species. For each

14　species, boxplots indicate the simulated numbers of co-occurrences, while the red dots denote

15　observed numbers of co-occurrences (with any other species) relative to the boxplot for that

16　particular species. If the observed number of co-occurrences (red dot) is higher than the null

17　expectation, then the species shows aggregatory behaviour ('tolerant'), while if the observed

18　number of co-occurrences is lower than the null expectation, then the species shows

19　segregatory behaviour ('intolerant'). Significant deviation from the null model is indicated

20　with asterisks. The numbers give the number of occurrences for each species. The extent and

21　vertical position of each boxplot was standardised to fit the graph.

22　**Fig. 4** Numbers of associations between pairs of the most common species in (A)

23　communities in which ants compete for nesting space in epiphytic ferns and (B) communities

24　in which ants compete for food resources. Numbers refer to the number of co-occurrences

25　between each pair of species. Species pairs with significantly more co-occurrences than

26　expected (positive interactions) are denoted in green, those with significantly fewer ones

27　(negative interactions) in red.

28

26

Canopy — 16 | 31 8 16 | 20 | 7 17 15 | 20 | 24 8 31 | 16 — Canopy

Overlap — 23 | 20 3 1 | 4 | 2 2 10 | 12 | 5 7 16 | 23 — Overlap

Understorey — 35 | 45 13 13 | 22 | 12 14 25 | 27 | 20 19 39 | 35 — Understorey

1a: Pristine ferns   1b: After one month   1c: After eight months   1a: Pristine ferns

A

B

number of pairwise associations   number of pairwise associations

2

3

Fig. 3

A

| 48 | 43 | 38 | 35 | 28 | 21 | *18 | *16 | *16 | 15 | 14 | 13 | 12 | *11 | 11 |

number of associations

Monomorium sp. 26
Hypoponera sp.52
Diacamma sp.122
Crematogaster sp.131
Pheidole sp.25
Crematogaster sp.75
Diacamma sp.46
Pachycondyla sp.51
Carebara sp.76
Camponotus sp.82
Paratrechina sp.124
Paratrechina sp.90
Vollenhovia sp.170
Polyrhachis sp.70
Carebara sp.128

B

| *36 | *30 | *25 | *22 | *21 | *20 | *18 | *15 | *14 | *11 | *10 | *10 | *8 | *6 | *6 |

number of associations

Camponotus novae-hollandiae gp.
Oecophylla smaragdina
Paratrechina vaga gp.
Camponotus vitreus
Crematogaster aff. *fusca*
Pheidole aff. *platypus*
Dolichoderus sp. 1
Tapinoma melanocephalum
Crematogaster aff. *pythia*
Technomyrmex aff. *albipes*
Anonychomyrma gilberti
Tetramorium insolens
Tetramorium validiusculum
Echinopla australis
Pheidole cf. *athertonensis*

29

A
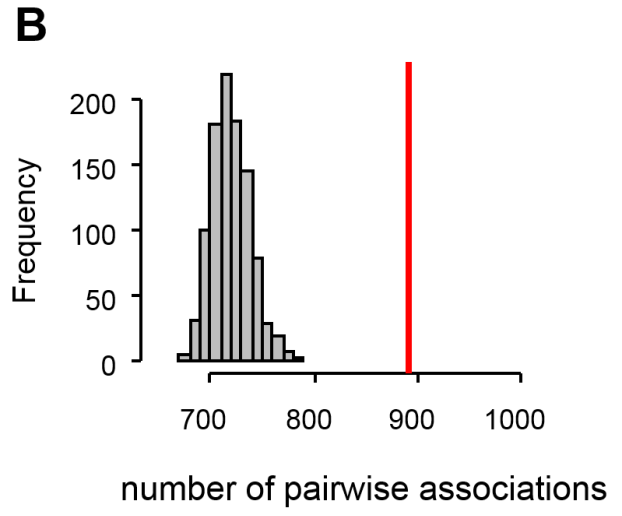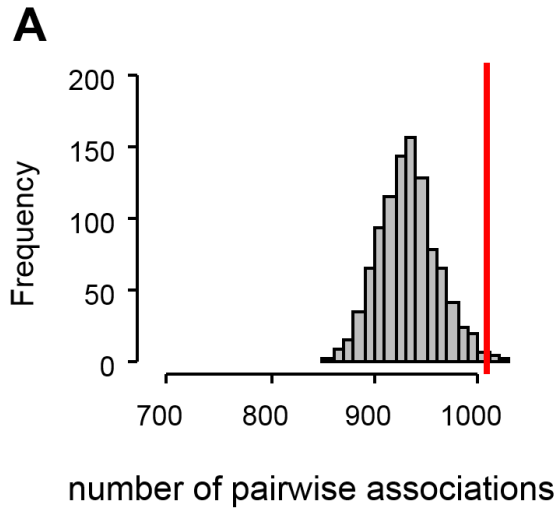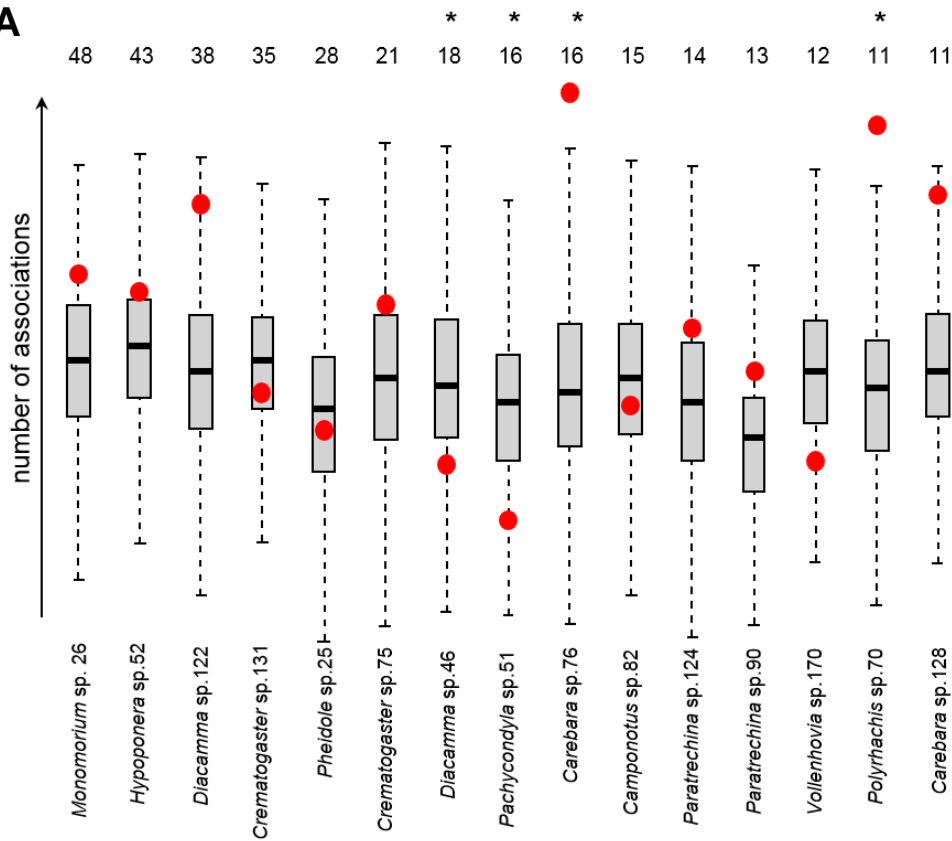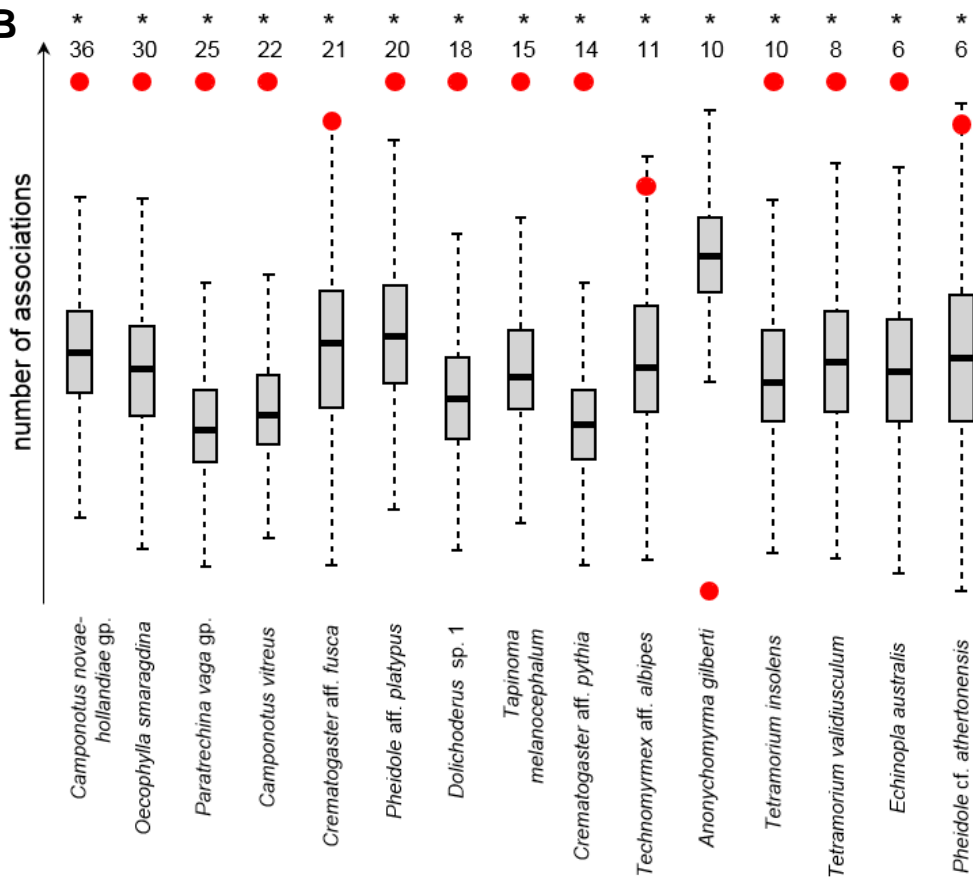
Panel A — column headers (left to right): *Hypoponera* sp.52, *Diacamma* sp.122, *Crematogaster* sp.131, *Pheidole* sp.25, *Crematogaster* sp.75, *Diacamma* sp.46, *Carebara* sp.76, *Pachycondyla* sp.51, *Camponotus* sp.82, *Paratrechina* sp.124, *Paratrechina* sp.90, *Vollenhovia* sp.170, *Carebara* sp.128, *Polyrhachis* sp.70, *Ponera* sp.136

	H.52	D.122	Cr.131	Ph.25	Cr.75	D.46	Ca.76	Pa.51	Cam.82	Par.124	Par.90	V.170	Ca.128	Pol.70	Po.136	Row
	12	14	12	12	7	4	7	1	5	2	2	3	3	3	4	*Monomorium* sp.26
		9	10	6	6	4	4	5	3	7	3	4	2	5	2	*Hypoponera* sp.52
			4	8	8	1	7	3	1	2	2	0	4	**11**	2	*Diacamma* sp.122
				3	**0**	6	6	2	5	4	4	**7**	1	2	1	*Crematogaster* sp.131
					6	0	6	2	2	1	0	0	3	2	4	*Pheidole* sp.25
						0	1	2	1	1	0	0	2	3	1	*Crematogaster* sp.75
							5	1	1	2	**5**	1	2	1	1	*Diacamma* sp.46
								1	1	3	2	1	2	2	2	*Carebara* sp.76
									1	0	1	0	1	2	2	*Pachycondyla* sp.51
										0	0	1	2	0	0	*Camponotus* sp.82
											0	**4**	1	0	0	*Paratrechina* sp.124
												1	1	1	1	*Paratrechina* sp.90
													0	0	0	*Vollenhovia* sp.170
														1	2	*Carebara* sp.128
															1	*Polyrhachis* sp.70

B

Panel B — column headers (left to right): *Oecophylla smaragdina*, *Paratrechina vaga* gp., *Camponotus vitreus*, *Crematogaster* aff. *fusca*, *Pheidole platypus*, *Dolichoderus* sp., *Tapinoma melanocephalum*, *Crematogaster* aff. *pythia*, *Technomyrmex* aff. *albipes*, *Tetramorium insolens*, *Anonychomyrma gilberti*, *Tetramorium validiusculum*, *Pheidole* cf. *athertonensis*, *Echinopla australis*, *Camponotus* sp.6 (*gasseri* gp.)

	O.sm	P.vaga	C.vit	Cr.fusca	Ph.pl	Dol	Tap.mel	Cr.pyth	Tech.alb	Tet.ins	An.gil	Tet.val	Ph.ath	Ech.aus	Cam.6	Row
	24	19	**19**	17	15	14	11	**14**	9	8	4	7	2	6	5	*Camponotus novae-hollandiae* gp.
		19	**18**	**17**	14	14	12	**13**	4	5	**0**	6	5	6	3	*Oecophylla smaragdina*
			16	10	12	**15**	**12**	**12**	8	9	**0**	5	**6**	5	**5**	*Paratrechina vaga* gp.
				11	9	11	**11**	**11**	6	6	**1**	5	4	5	3	*Camponotus vitreus*
					10	8	6	7	4	5	**0**	**7**	3	4	4	*Crematogaster* aff. *fusca*
						10	7	8	4	5	2	3	3	3	**5**	*Pheidole platypus*
							10	8	4	5	**0**	4	**6**	4	3	*Dolichoderus* sp.
								7	2	5	0	3	**6**	4	0	*Tapinoma melanocephalum*
									5	4	0	**5**	2	4	3	*Crematogaster* aff. *pythia*
										7	0	3	0	0	3	*Technomyrmex* aff. *albipes*
											0	2	2	1	3	*Tetramorium insolens*
												0	0	0	0	*Anonychomyrma gilberti*
													1	2	2	*Tetramorium validiusculum*
														2	0	*Pheidole* cf. *athertonensis*
															0	*Echinopla australis*

1 # Analysis of pairwise interactions reveals unexpected

2 # patterns in tropical ant communities

3 M. D. Farnon Ellwood, Nico Blüthgen, Tom M. Fayle, William A. Foster & Florian Menzel

4 ## Appendix

5 ## A1 Experimental Methods

6 **Processing of ferns and ants**

7 Ferns were placed in plastic bags to prevent the loss of animals or leaf-litter during collection.

8 Before being removed from the bags, they were fogged with Pybuthrin[®] 33 insecticide

9 (Ellwood et al. 2002) and left for two hours, then shaken to remove superficial animals, loose

10 soil and leaf-litter. Each fern was placed in a detergent water bath, which had no detectable

11 effect on the plant, but was effective at flushing the remaining animals from the soil and from

12 the roots of the plant. After rinsing the ferns, we microscopically examined roots and soil to

13 ensure that all ants had been collected. Before being transplanted, each fern core was

14 standardized at a uniform size with sterilized organic material taken from other bird's nest

15 ferns. Transplanted ferns were attached to branches with fishing nets and string. Tree crowns

16 were accessed using climbing ropes (Ellwood et al. 2001). Ants were identified to

17 morphospecies within genus (Bolton 1994). Sampling took place in January, 2001.

18 ## A2 Statistical Methods

19 **A2.1 Outline of the algorithm used**

20 Here, we describe in detail how our algorithm functions, and how we calculated expected

21 values. We used presence/absence data in order to avoid the misrepresentation in the model of

22 highly abundant species, i.e. those species with very large numbers of individuals. Our

23 algorithm calculates co-occurrence on three levels: co-occurrence in the whole network, co-

1 occurrence for each species i, and co-occurrence for each species pair i_1,i_2. By pooling species

2 to subfamilies, we analysed a 'subfamily' level and a 'subfamily pair' level in analogy to

3 'species' and 'species pair' level. Here, beside the presence/absence (binary) approach, we

4 also performed a second, quantitative analysis, where the numbers of species per subfamily

5 were taken into account. Finally, we used the proportion of species that deviated from random

6 expectation, and the proportion of species pairs that deviated from random expectation, as a

7 network-level measure of compartmentalisation. All calculations were performed in R 2.13.1.

8 For all binary metrics, we calculated theoretically expected values. The mean values obtained

9 from the null models were close to the expected values. Percentage deviations of randomized

10 values from the expected ones were calculated for the network level, for each species, and for

11 each species pair, as abs(mean(randomized)-expected)/expected). These deviations were

12 mostly below 1%, but increased with increasing rarity of the species or species pairs

13 (deviation on the network level: 0.05% (E_{nw}); mean deviation ± SE on the species level: (0.3 ±

14 0.02)% ($E_{sp(tot)}$); (0.96 ± 0.07)% ($E_{sp(lone)}$); on the species pair level: (6.7 ± 0.39)% (E_{spp} when

15 excluding species pairs that never co-occurred); (21 ± 0.25)% (E_{spp} when including them)).

16 For the quantitative metrics (on subfamily level only), theoretically expected values could not

17 be derived. Here, we compared observed values to the mean of the randomized values.

18

19 **Analysis of the network level**

20 In the following, a_i is the number of occurrences of ant species i, S is the total number of ant

21 species, J is the total number of ferns, and N is the total number of ant species occurrences in

22 all ferns. This metric is based on the total number of associations, where an association is

23 defined as a co-occurrence between any two ant species. It yields one expected value (E_{nw}),

24 and two P values (P_{nw-agg} and P_{nw-seg}) for the overall number of associations in the network. A

25 significant P_{nw-seg} indicates significantly *fewer* associations than expected, suggesting

26 *segregation* from other species; a significant P_{nw-agg} indicates significantly *more* associations

1 than expected, suggesting *aggregation* with other species. Its informativeness is comparable

2 to other metrics such as the *C*-score. Equation (1) outlines the formulation for (E_{nw}), while

3 equation (2) provides the definition of $E_{sp(tot)(i)}$.

$$E_{nw} = \frac{1}{2} \sum_{i=1}^{S} E_{sp(tot)(i)} \qquad (1)$$

5

6 **Analysis of the species or subfamily level**

7 On the species (or subfamily) level, we calculated two association metrics: firstly, as above,

8 we calculate the total number of pairwise associations for a given species or subfamily. In a

9 fern with, for example, three ant species, each one would have two associations, i.e. one to

10 each of the other two species. Thus, a competitive species that excludes other species will

11 have fewer associations than a tolerant one, which allows other species in the fern. The

12 expected value for ant species *i* was calculated as:

$$E_{sp(tot)(i)} = \frac{a_i \cdot (N - a_i)}{J} \qquad (2)$$

14 Secondly, we calculated the number of ferns where the given species or subfamily occurred

15 with one or more ant species, as opposed to being alone. Thus, in one fern with three species,

16 the association value for each species will be 1, due to not being the sole species, but zero if

17 one species is the only one in a fern. The expected value for ant species *i* was calculated as:

$$E_{sp(lone)(i)} = 1 - \left(1 - \frac{a_i}{J}\right)^{-1} \cdot a_i \cdot \prod_{n=1}^{S}\left(1 - \frac{a_n}{J}\right) \qquad (3)$$

19 The *P* values of the two metrics are reported as $P_{sp(tot)}$ and $P_{sp(lone)}$, respectively. As above, we

20 report two one-sided *P* values each. A significant $P_{sp(tot)(i)\text{-seg}}$ indicates that species *i* has

21 significantly *fewer* associations than expected, whereas a significant $P_{sp(tot)(i)\text{-agg}}$ indicates that

22 species *i* has significantly *more* associations than expected. Similarly, a significant $P_{sp(lone)(i)\text{-}}$

23 $_{seg}$ indicates that species *i* is the sole species in a fern significantly *more* often than expected,

1 whereas a significant $P_{\text{sp(lone)}(i)\text{-agg}}$ indicates that species i is the sole species in a fern

2 significantly *less* often than expected.

Analysis of the species pair or subfamily pair level

4 Finally, we tested whether certain pair-wise species (or subfamily) pairs co-occurred more or

5 less often than expected from a null model. Here, the number of pair-wise co-occurrences was

6 used as a metric. The expected value of co-occurrences of species i_1 and i_2 was calculated as:

$$E_{\text{spc}(i_1,i_2)} = \frac{a_{i_1} \cdot a_{i_2}}{J} \tag{4}$$

8

9 The corresponding P values are reported as $P_{\text{spp-seg}}$ and $P_{\text{spp-agg}}$ for each species pair.

10 Significant $P_{\text{spp-seg}}$ or $P_{\text{spp-agg}}$ indicate that the referring species i,i_2 co-occur on significantly

11 fewer or more sites (respectively) than expected.

Analyses of subfamily co-occurrence

13 We pooled the ant species according to subfamily, such that we obtained a matrix with the

14 number of ant species per subfamily per fern. We used a binary and a quantitative approach.

15 The binary approach only considered whether or not a subfamily was present on a fern, and

16 this matrix was analyzed as described above, only with subfamilies instead of species. In

17 contrast, the quantitative approach also accounted for the number of species per subfamily.

18 Thus, we were able to estimate the probability that two species of the same subfamily co-

19 occurred ($P_{\text{spp-quant}}$), which is not possible with the binary approach. On the species level, we

20 report $P_{\text{sp(lone)-bin}}$; $P_{\text{sp(lone)-quant}}$, which give information on whether or not a subfamily displaces

21 other subfamilies and hence is the only one in a fern.

Correcting for multiple testing

23 At the species and species pair level, multiple P values were generated simultaneously. This

24 does not influence the validity of analysing the proportions of deviant species, but may inflate

25 type I error if the identity of the deviant species is discussed. We therefore performed a

1   correction for false discovery rate (Benjamini et al. 1995). At the species level, we performed

2   corrections over all species in the network. At the species pair level, many pairs would never

3   be significant since they were too rare (e.g. two species that were positively associated but

4   occurred only once each would not be detected as 'associated' by our analysis). We therefore

5   determined the minimum abundance of a species to be, in theory, detected as positively or

6   negatively associated, and performed correction over only those species pairs that fulfilled

7   this criterion. This was done separately for positive and negative associations. The minimum

8   abundance for two species to be detected as significantly positively associated was 2 (both in

9   the Bornean and the Australian dataset), while for a negative association it was 12 (Australian

10   dataset) and 25 (Bornean dataset).

11

12   **A2.2 Comparison of our index to the *C*-score**

13   To evaluate our network-level index, we compared it to the *C*-score, which is among the most

14   frequently used metrics to analyze species co-occurrence at the network level (Stone et al.

15   1990; Stone et al. 1992; Gotelli 2000). We calculated the *C*-score using both our code and the

16   software EcoSim (Gotelli et al. 2012). The *C*-score is EcoSim's default co-occurrence index,

17   measuring the average number of checkerboard units between all possible pairs of species in a

18   co-occurrence matrix. A co-occurrence matrix is a matrix of 0's and 1's, in which the rows

19   correspond to the different species, and the columns correspond to the different sites. The

20   entry in (row i, column p) is 1 if species i is present on site p, and 0 otherwise. A

21   checkerboard unit for a pair of species (A, B) is a pair of sites such that species A occurs in

22   one of the two sites and not in the other, and species B in the other, but not in the first

23   (Diamond 1975). The total number of checkerboard units for each species pair (species i,

24   species j), given their row totals and their number of shared sites, is calculated as $C_{ij} = (r_i - S_{ij})$

25   $(r_j - S_{ij})$, where S_{ij} is the number of shared sites (sites containing both species), and r_i and r_j are

26   the row totals for species i and species j (i.e. the numbers of sites on which species i and j,

1   respectively, occur). Thus, C_{ij} represents the number of ways to choose a site containing

2   species i but not species j and a site containing species j but not species i. The C-score is the

3   average, over all species pairs (species i, species j; where each species occurs at least once), of

4   the number of checkerboard units C_{ij} for (species i, species j). For M species, there are $P =$

5    $M(M\text{-}1)/2$ species pairs, and hence the C-score is:

6    $$C = \sum_{i<j} \sum C_{ij}/P \qquad\qquad (5)$$

7

8   If a community is structured by competition, the C-score should be greater than expected by

9   chance (Gotelli 2000). We compared the patterns of species co-occurrence among the

10   observed ant communities with statistical randomizations of the original species occurrence

11   data. Using both EcoSim (Gotelli and Entsminger 2012) and our own implementation in R,

12   we simulated 5000 random matrices for each analysis and tested the differences between these

13   and the observed communities. Means and SD's of simulated C-score values from the two

14   programs were very similar, showing that our algorithm corresponded closely with that of

15   EcoSim.

16

17   **A2.3 Which randomization algorithm did we use, and why?**

18   Randomization algorithms produce large numbers of randomized matrices, each of which has

19   the same number of species, and the same number of sites, as the original data matrix (Connor

20   et al. 1979). Gotelli (2000) recommends two different algorithms: *fixed-fixed*, and *fixed-*

21   *equiprobable*. The fixed-fixed algorithm keeps both the abundance of each species and the

22   number of species per site (i.e. fern) constant. The column sum constraint ensures that each

23   site maintains the same number of species that it actually has (so that such patterns as the

24   species-area relationship continue to hold), while the row sum constraint ensures that each

25   species continues to occupy the same number of sites as it does in nature (so that widespread

26   species are still widespread, and narrowly distributed ones are still narrowly distributed).

1   Where sites vary in size, for example on islands, it makes sense to control for the species

2   richness of the islands and the number of occurrences of each species. However, in our

3   experimental 'island' system, all ferns were standardized at the same size, and at two specific

4   heights in the canopy. We detected no systematic effect of individual fern identity. We

5   therefore believe that the ferns represented qualitatively and quantitatively similar habitats.

6   For our network-level analyses we therefore used an algorithm which apportions species to

7   ferns with equal probability (*fixed-equiprobable*). This algorithm keeps fixed the number of

8   sites on which any species occurs, but randomly distributes its occurrences over sites with

9   equal probabilities. Thus, a species occurring on seven sites in the original dataset will also

10 occur on seven sites in each randomized network. The species occurrences are randomly

11 assigned to the sites (ferns) such that the numbers of species occurrences remain as in the

12 original dataset. If species colonize the ferns randomly, species numbers per fern should

13 follow a poisson distribution. In contrast, if unknown underlying variables additionally

14 determine the number of species per fern, the numbers should be inverse-binomially

15 distributed. We constructed GLMs for the species numbers per fern with recolonization stage

16 and altitude (canopy vs. understory) as fixed factors. The data matched a Poisson distribution

17 (AIC: 711.4) significantly better than an inverse binomial distribution (AIC: 713.4), which

18 supports that using the fixed-equiprobable algorithm is appropriate. We further argue that

19 fixing both the row and column sums would control for the very patterns that we wished to

20 detect. For comparison, we computed the *C*-score for the Bornean and the Australian network

21 using the *fixed-fixed* algorithm (using the software EcoSim). Even in the strongly structured

22 Australian ant network, we the *C*-score based on the *fixed-fixed* algorithm did not detect any

23 significant pattern ($P_{obs \leq exp} = 0.94$; $P_{obs \geq exp} = 0.067$). Likewise, it did not differ from random

24 in the Bornean ant network ($P_{obs \leq exp} = 0.88$; $P_{obs \geq exp} = 0.12$).

25

A3 Co-occurrence of large and small ants

Similar to the subfamily analysis, we pooled species according to whether they were large or small ($\geq$ 5 mm vs. < 5mm). We conducted binary and quantitative analyses on the species pair level, to look for aggregation or segregation between small and large species. However, we did not find any evidence for non-random co-occurrence of small and large species (all $P_{\text{spp-agg-bin}}$; $P_{\text{spp-seg-bin}}$; $P_{\text{spp-agg-quant}}$; $P_{\text{spp-seg-quant}}$ > 0.4).

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