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The curious case of the camelthorn: competition, coexistence and nest-site limitation in a multispecies mutualism

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Key words: ant-plant interactions, coexistence, domatia, myrmecophytes, mutualism, nest-site limitation

Elements for expanded online edition

Online appendix A – Expanded methods and results

(methods; randomisation results, tables A1-4; diagrammatic representation of multiple species co-occupancy on *V. erioloba* trees, figure A1; results for species pairs Spearman's rank correlation, table A5; review of myrmecophyte plant and domatia occupancy studies, table A6)

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Abstract

Myrmecophyte plants house ants in domatia in exchange for protection from herbivores. Ant-myrmecophyte mutualisms exhibit two general patterns due to competition between ants for plant occupancy: i) domatia nest-sites are a limiting resource and ii) each individual plant hosts one ant species at a time. However, individual camelthorn trees (*Vachellia erioloba*) typically host two to four ant species simultaneously, often coexisting in adjacent domatia on the same branch. Such fine-grain spatial coexistence brings into question the conventional wisdom on ant-myrmecophyte mutualisms. Camelthorn ants appear not to be nest-site limited, despite low abundance of suitable domatia, and have random distributions of nest-sites within and across trees. These patterns suggest a lack of competition between ants for domatia and contrast strongly with other ant-myrmecophyte systems. Comparison of this unusual case with others suggests that spatial scale is crucial to coexistence or competitive exclusion involving multiple ant species. Furthermore, coexistence may be facilitated when co-occurring ant species diverge strongly on at least one niche axis. Our conclusions provide recommendations for future ant-myrmecophyte research, particularly in utilising multispecies systems to further our understanding of mutualism biology.

Introduction

Ant-plant interactions are used as model systems to test hypotheses about ecological networks (Lange and Del-Claro 2014), mutualism dynamics (Heil and McKey 2003) and the effects of global change on interacting species (Mayer et al. 2014). Interactions vary from facultative to obligate, and range from mutualism to parasitism. Plants benefit from ants via services including seed dispersal (Gallegos et al. 2014), pollination (de Vega et al. 2009), nutrient enrichment (Wagner and Fleur Nicklen 2010) and protection against herbivory (Trager et al. 2010). In exchange myrmecophilic plants provide food to ants, a process that is taxonomically widespread (Weber and Keeler 2013). Food may take the form of extrafloral nectar, honeydew via sap-feeding insects and food bodies rich in lipids and proteins (Heil and McKey 2003). In addition, myrmecophytic plants also provide housing for ants within domatia. These are modified plant structures such as thorns, stems and leaves that form hollow chambers specifically for ant nest-sites (Davidson and McKey 1993). Myrmecophytes are restricted to the tropics (Heil and McKey 2003) with well-studied taxa including *Cecropia* (Dejean et al. 2012), *Macaranga* (Nomura et al. 2011), *Tococa* (Michelangeli 2003) and, perhaps most famously, *Vachellia* (formerly *Acacia*, Janzen 1974; Palmer et al. 2008).

Most studies support the common view that there is intense inter and intra-specific competition between ant colonies for sole occupancy of myrmecophytes (Davidson et al. 1989; Kautz et al. 2012; Palmer 2004; Webber et al. 2007), and that plant-ants are extremely aggressive and territorial (for example, Palmer et al. 2000). Ant colonies may compete for food resources provided by the plant, but also for domatia in which to nest (Fonseca 1999). We define three occupancy categories for ants on a given myrmecophyte plant at a given time: a) single colony occupancy (SCO); b) single species (multiple colony) occupancy (SSO) and multiple species co-occupancy (MSC). An individual plant usually shows SSO (which may be SCO, but is often not tested), although the plant species may associate with more than one ant species (Davidson et al. 1989; Gaume and McKey 1999; Palmer et al. 2003). An individual plant may show MSC as a sapling (Djiéto-Lordon et al. 2005; Longino 1989) or sequentially throughout its lifetime, because ant colonisation is moderated by species dominance hierarchies (Palmer et al. 2000). Outside of myrmecophyte systems, nest-site limitation influences ant species richness, and therefore possibly coexistence, for cavity-nesting ants, although the effect is variable across arboreal (Philpott and Foster 2005) and leaf-litter assemblages (Byrne 1994). In myrmecophytes, ant colony size is limited by the size and availability of domatia for nesting-sites (Campbell et al. 2013a; Fonseca 1993; Fonseca 1999), but the effect on species coexistence is unknown.

Competition is a key element in structuring ant communities (see review by Cerdá et al. 2013). Interspecific competition leads to non-random structure in communities, because species with similar niches co-occur less often than expected by chance (Diamond 1975), as demonstrated across multiple taxa (Gotelli and McCabe 2002). In arboreal ant assemblages dominant species defend “absolute territories” - discrete spatial units extending beyond the location of individual food or nest resources. This leads to a patchy distribution of ant species across the forest canopy, known as an ant mosaic (Dejean et al. 2007; Jackson 1984; Room 1971; Room 1975). However, outside forest ecosystems the arboreal patterns of ant species coexistence and competition are less well documented. In savannas, where trees are widely spaced, there is no continuous canopy layer in which ant mosaics can form (Dejean et al. 2007). The dominant trees of African savannas are acacias, many of which are myrmecophytes that possess swollen-thorn domatia inhabited by ants (Dharani 2006). Coexistence of ant species on neighbouring myrmecophyte acacias is thought to result from dominance hierarchies and competitive trade-offs (Palmer et al. 2010; Palmer et al. 2000;

Stanton et al. 2005). However, coexistence at a finer spatial scale, across or within branches of the same tree, has seldom been studied. This is largely because the few intensively studied systems (for example, Gaume and McKey 1999; Palmer et al. 2010) do not show long-term MSC. MSC on myrmecophytes or semi-myrmecophytes has been documented occasionally (Gaume et al. 2005b; Moog et al. 2002; Raine et al. 2004; Rico-Gray and Thien 1989a; Rico-Gray and Thien 1989b), but these unusual examples contrast with the many myrmecophytes that exhibit competitive exclusion and SSO.

In this study we investigated the camelthorn tree, *Vachellia erioloba* (fig. 1A), a southern African myrmecophyte with swollen-thorn domatia (fig. 1B and C) inhabited by four ant species; an unidentified *Crematogaster* species, *Cataulacus intrudens*, an unidentified *Tapinoma* species and *Tetraponera ambigua*. A previous study revealed 41% MSC of *V. erioloba* trees, with some evidence of species sorting through nest-site selection based on domatia characteristics (Campbell et al. 2013a). Given this surprising finding, we undertook comprehensive sampling specifically to quantify MSC in *V. erioloba* and to test for evidence of nest-site limitation and competition. We also test if nest-site selection differs between ant species based on microhabitat characteristics related to the location of domatia on the tree.

Our findings bring into question two widely held assumptions; i) myrmecophyte ants utilising domatia are nest-site limited; and ii) ant species compete for sole occupancy of individual plants. To establish if the unusual patterns in the camelthorn system are unique, we then review published patterns of plant and domatia occupancy to test for nest-site limitation and MSC in other myrmecophyte systems.

Methods

Study site and sampling

Field work was conducted in savanna at Kuzikus Wildlife Reserve (23°13'S, 18°24'E, elevation 1340m) in Namibia (for full site description see Campbell et al. 2013b). Surveys were completed in April, September and October 2011 for ant occupants within swollen-thorns on camelthorn trees, *Vachellia erioloba* (E. Mey) P.J.H. Hurter. Ants defend *V. erioloba* trees from insect herbivores (Campbell et al. 2013b) and low intensity sampling in an earlier study suggested MSC of individual trees (Campbell et al. 2013a). For each of 20 haphazardly selected trees we surveyed 8-13 branches, except for one tree with only four branches accessible. Using secateurs, branches were removed and all thorns opened to examine the contents. We also recorded microhabitat data on: branch height from ground (to nearest 0.1m); branch cardinal direction (bearing in °); thorn status (swollen or non-swollen); thorn age (new, young, old or dead); and thorn position on branch (surveying from the tip inwards towards the trunk, 1 being the most distal thorn sampled). For each thorn we recorded ant species identity and an estimate of the number of ants at different life stages (workers, brood, alates and queens).

Analysis

To test for associations between ant species at the branch level we performed Spearman’s rank correlations on the presence of species on the same branch. To assess the role of competition in structuring within-tree patterns of ant species co-occurrence we assembled a presence-absence matrix for each of the 20 trees and then performed Monte Carlo randomisation tests on each matrix. We used three co-occurrence indices (CHECKER, COMBO and C-score) under two null models (fixed-fixed and fixed equiprobable, for details see Appendix A). We calculated the Standardised Effect Size (SES) to allow comparison between matrices (Gotelli and McCabe 2002). To test the null hypothesis that the mean SES measured did not differ from zero we used a one-sample Wilcoxon test to compare across matrices. We performed six tests (three indices x two null models) and therefore applied a Bonferroni correction.

To assess whether the distribution of nest-sites across a tree was influenced by microhabitat we tested for correlations of ant species with thorn and branch variables. In tests of branch variables we analysed only species presence / absence on a branch. We tested ant species identity against branch height and cardinal direction using ANOVA and made multiple post hoc comparisons using Tukey Honest Significant Differences Tests (Crawley 2005). Thorn variables and ant species identity were only tested for occupied thorns (i.e. domatia that were currently in use as nest-sites). Although ants may be defend empty neighbouring thorns prior to colony expansion it was impossible to assign species identity to an unoccupied thorn so this is not accounted for in our analysis. Due to differential branch growth across trees, thorn position along a branch does not directly predict thorn age, so, for all occupied thorns, we tested separately if species identity was correlated with thorn position or thorn age using Fisher’s exact tests (Crawley 2005). Thorn position was converted to a categorical variable, assigned as: distal (thorns 1-8); medial (thorns 9-15); or proximal (thorns 16+).

We assessed species co-occurrence with respect to microhabitat characteristics of branch height and cardinal direction (following the procedure of Belinchón et al. 2012). We constructed 16 presence-absence matrices representing branch cardinal direction (North: 316-45°, East: 46-135°, South: 136-225° and West: 226-315°) combined with one of four branch height categories (Low: 0-1.50m; Medium Low: 1.51-2.0m; Medium High: 2.01-2.5m and

High: 2.51m+). These analyses followed the same procedure described for within-tree matrices (methods A1). To test the effects of branch height and direction on species interactions, we performed ANOVA on all co-occurrence indices generated from these matrices.

Co-occurrence randomisation analyses (further details in Appendix A) were conducted in EcoSim (Gotelli and Entsminger 2009). All other statistical analyses were performed in R (R Core Development Team 2012).

Literature review

To establish if the unusual patterns in the camelthorn system are unique, we reviewed published patterns of plant and domatia occupancy to test for nest-site limitation and MSC in other systems. We examined 34 primary studies relating to 49 plant species (table A6) for examples of MSC. We included studies featured in three meta-analyses of ant-plant mutualisms (Chamberlain and Holland 2009; Rosumek et al. 2009; Trager et al. 2010) as a representative subset of studies likely to have suitable data. We also added data from several studies published after these meta-analyses and for cases where inadequate data were provided in the original cited references.

Results

Multiple species co-occupancy (MSC) on camelthorn trees

We collected data on 3448 thorns from 197 branches across 20 *V. erioloba* trees (Campbell et al. 2015), confirming that *V. erioloba* domatia were occupied by four ant species; an unidentified *Crematogaster* species, *Cataulacus intrudens*, an unidentified *Tapinoma* species and *Tetraponera ambigua* (hereafter referred to by genus). The smallest, *Tapinoma*, was the most abundant, accounting for 77% of all individual ants surveyed (fig. 2), followed by *Crematogaster* (13%), *Cataulacus* (8%), and then *Tetraponera* (2%). *Tapinoma* was also the most prevalent, found on 19 of 20 trees. Despite the numerical dominance of *Tapinoma*, it occupied a similar proportion (41%) of nest-sites to *Crematogaster* (42%, see fig. 2), while the other two species occupied far fewer (*Cataulacus* 14%; *Tetraponera* 3%).

Most trees (16/20) were co-occupied by two or three ant species and 3/20 by all four. The only tree with a single ant species was occupied by *Crematogaster*. Although MSC was common within trees, at the branch level the figure fell to 27%, while 50% of branches were occupied by a single species (figure A1). On branches, *Cataulacus* and *Tapinoma* were positively associated (Spearman correlation test: $r_S = 0.17$, $S = 1051634$, $P < 0.05$), but there were no other significant associations between species pairs (table A5).

Nest-site limitation and interspecific competition

Only 31% ($n = 1052$) of thorns were suitable as nest-sites, because ants were not found inside soft, new growth thorns or non-swollen thorns. Hereafter the term domatia refers only to swollen and hardened thorns suitable as nest-sites. Only 37% of domatia were occupied by nesting ants. Nest-site density varied significantly between species, with *Crematogaster* occupying the most domatia per branch and *Cataulacus* the least (fig. 3).

Within-trees we found little evidence of positive or negative associations between ant species. Only one tree showed a non-random distribution of species with an observed C-score of 17.33 that was significantly larger ($P = 0.001$) than the mean simulated C-score of 7.95. The SES was 3.104, indicating segregation of ant species on that tree (table A1). Our meta-analysis across matrices for all trees showed that the mean SES did not differ significantly from zero for any of the indices under either null model (table A3).

Microhabitat preferences

We found no evidence that different ant species used domatia in different locations on trees, with regard to branch height (ANOVA, $F_{3,211} = 1.16$, $P = 0.33$), branch cardinal direction (ANOVA, $F_{3,211} = 2.048$, $P = 0.11$) or thorn position along a branch (Fisher's exact test, $P = 0.14$). Nor did we detect evidence of non-random patterns for nest-sites grouped by microhabitat characteristics (table A2). This was confirmed by meta-analyses of co-occurrence indices that showed species distributions are not influenced by branch height or direction (table A4). However, *Cataulacus* and *Tapinoma* were associated with old thorns and *Crematogaster* and *Tetraponera* with young thorns (Fisher's exact test, $P < 0.01$).

Discussion

Ant community ecology has focused heavily on the role of competition in structuring ant assemblages (Cerdá et al. 2013; Parr and Gibb 2010; Parr et al. 2005) but this has been less frequently applied to ants on myrmecophilic or myrmecophytic plants (however, see review by Palmer et al. 2003). Given the abundance of studies on ant-plant mutualisms the data is most likely already available for studies of competition within these systems and would significantly advance our understanding of the dynamics of ant-ant interactions as well as mutualism biology. Whilst it is thought that ants compete for host plants (Stanton et al. 2005) or that domatia nest-sites are limiting (Longino 1989), there has been little experimental proof to find evidence of competition in these systems, or to identify the mechanisms for this (Palmer et al. 2003).

There is no evidence that ants on *V. erioloba* are nest-site limited, because only 38% of domatia are occupied. This rate of domatia occupancy does not seem atypical of ant-plant systems in general (see table A6). In the studies we reviewed domatia occupancy ranged from 42-64 % (Maschwitz et al. 1994; Moog et al. 2002), although for one species variation was high (0-100%) between individual plants (Dyer and Letourneau 1999). *Zanthoxylum myriacanthum* was the only MSC myrmecophyte with rate of domatia occupancy reported (table 1; table A6), which at 42% is very similar to domatia occupancy on camelthorn trees. However, it is striking that domatia occupancy was not reported in 93% of primary studies even though this information was very likely collected. Overall, the few existing studies do not support the notion that individual domatia are a limiting resource, but this does not rule out availability of whole plants as limiting for ant colonies.

At the whole plant level, overall occupancy of myrmecophytes was between 41-100% in the reviewed studies (table A6) and 100% on *V. erioloba*. Focusing on MSC myrmecophytes, the rate of plant occupancy was slightly higher, ranging from 62-100%. The high rate of plant occupancy relative to domatia occupancy implies that availability of individual plants may often be the key to ant colony success. This also explains why competition between foundresses and young colonies for possession of a host plant is so intense (Stanton et al. 2005). Whereas once a colony has secured a plant then individual domatia availability may exceed colony requirements.

The apparently random distribution of species within trees provides further evidence that *V. erioloba* ants are not competing for domatia. This pattern is surprising and contrasts with spatial patterns on a Neotropical acacia exhibiting MSC (Raine et al. 2004). We propose that on *V. erioloba* fine scale within-tree coexistence and lack of strong spatial structure reflect an absence of competition for individual domatia. Moreover, each ant species tends to choose different subsets of nests (e.g. species sorting according to thorn age and size, see Campbell et al. 2013a), as well as exhibiting different patterns of nest-site distribution and density. Species coexistence on *V. erioloba* may also be facilitated by the differing life history strategies of each ant species (Campbell et al. 2013a), as has been demonstrated in acacia-*Pseudomyrmex* interactions (Kautz et al. 2012). Establishing colony boundaries between conspecific ants co-occupying a tree is the next step in understanding spatial patterns of domatia-inhabiting ants on *V. erioloba*. However, in a pilot study to test colony boundaries we did not observe any intra- or interspecific aggression between *V. erioloba* ants. Future work could compensate for the lack of behavioural assay data by utilising genetic microsatellite and cuticular hydrocarbons data instead (Kautz et al. 2012).

At the species level, most plants (30/49 species, table A6) associate with multiple ant species and this is very likely an underestimate. Most myrmecophytes associate with a guild of ants, via either a) an individual plant associating with multiple ant species over its lifetime, or b) different individual plants in a population associating with different ant species. Ant partners may also vary across geographic scales (Longino 1989) and some myrmecophytes lose their mutualist ants altogether (Moraes and Vasconcelos 2009). This highlights the important issues of scale and specificity in studying species interactions (Thompson 2005). A 1:1 level of partner species matching may often be recorded on individual plants, but additional ant partners may be added by looking across plants in a population, or across populations through the plants geographic range.

It was typically difficult to establish species occupancy states (unknown for 10/49 species, table A6) and particularly MSC from the literature as authors were not always explicit about this. Ultimately, we found only four examples (table 1) of MSC (Gaume et al. 2005a; Moog et al. 2002; Rico-Gray and Thien 1989a) and only one of these described the pattern of ant species coexistence within individual host plants (Raine et al. 2004). These four cases appear extremely divergent, and occur on different continents, in contrasting habitats and incorporate a diversity of plant types and domatia structures (table 1). In our study, 95% of individual camelthorn showed MSC. Ant species were the same as a previous study (Campbell et al. 2013a), suggesting temporal stability of species assemblages, at least over short periods of time. This level of simultaneous coexistence is highly unusual and, to our knowledge, has not previously been recorded for an African ant-acacia. It contrasts directly with other African acacias, notably, the intensely studied *V. drepanolobium* system where trees are occupied not only by a single species (SSO) but usually also by a single colony of ants (SCO) (Palmer et al. 2000; Stanton et al. 2005). This raises the questions, do mutualism dynamics differ when a plant has one or more ant partners? And what drives transitions between SCO, SSO and MSC states?

In systems where guilds of ants inhabit different individual host plants within a population it is frequently discovered that not all ants are mutualists (Edwards et al. 2010; Gaume and McKey 1999; Itioka et al. 2000) and that mutualists differ in their effectiveness (Frederickson 2005; Young et al. 1997). Although increased competition can actually encourage co-operation of multiple mutualist partners (Adam 2010). Nonetheless, it is critical to understand the nature of the relationship between ants and their host plant since parasites may be more likely to co-occupy host plants (Kautz et al. 2012). A great deal of literature is directed towards analysing the costs and benefits of interactions and how systems may allow for the existence of “cheaters” (for example, see Clement et al. 2008; Edwards et al. 2006; Kautz et al. 2012). The key difference in myrmecophytes exhibiting MSC is the scale at which coexistence occurs i.e. tree or branch level rather than population level. However, both empirical and theoretical frameworks designed to tackle population level questions of ant species coexistence (as reviewed by Palmer et al. 2003) are equally applicable to this finer spatial scale. The main difficulty in performing experimental work in MSC cases is logistical. Manipulations on mature plants would be complex and the best approach would be to perform exclusions and additions of different combinations of ant species using seedlings until plants reach maturity. This would be problematic on a large, slow-growing tree such as *V. erioloba*, but better suited to a pioneer species such as the MSC myrmecophyte, *Z. myriacanthum* (Moog et al. 2002). This would also allow for experimentation over a longer time scale, and facilitate cost-benefit analysis over the lifetime of a plant or ant colony that may potentially reveal differing insights to a short-term study (e.g. short term, Palmer et al. 2000; vs long term, Stanton and Palmer 2011).

Multispecies mutualisms may arise as evolutionary “by-products” (Fayle et al. 2011) when ants defend trees as part of their normal foraging activity. Multiple simultaneous ant partners may provide more (greater defence) or wider (defence against diverse foes) benefits to an individual host plant. In this context tree size or density may influence the costs and benefits of MSC for myrmecophytes. Large, isolated desert or savanna trees, might benefit from a suite of ant occupants in order to be effectively defended. Smaller plants or those found in dense forests with many potential opportunistic ant mutualists may fare well with one resident ant colony. MSC might alternatively arise from a lack of host sanctions resulting in the presence of multiple, opportunistic species. For example, an inability to limit access to domatia leads to the presence of parasites on the rattan ant-palm *Korthalsia furtadoana* (Edwards et al. 2010).

Environmental stress can determine levels of species diversity in ant assemblages. Habitat productivity may also play a role in diversity within mutualisms via species coexistence mechanisms, for example, competitively dominant ants occupy faster-growing host plants and more productive habitats (Palmer 2003). Subsequently, should we expect MSC systems to be found in more or less stressful environments? Multiple limiting resources can increase niche dimensionality, leading to higher levels of diversity. Conversely a decline in the number and heterogeneity of limiting resources causes fewer trade-off opportunities, decreased niche dimensionality and fewer co-existing species (Harpole and Tilman 2007). If niche dimensionality does influence myrmecophyte-inhabiting ants, we predict that that more stressful environments with multiple limiting resources will contain a greater number of MSC plants and a higher diversity of ant partners. Although data is limited the anecdotal evidence somewhat supports this prediction; *V. erioloba* is a savanna/desert species in a high temperature and aridity region and mangrove orchids with MSC are found in very high salinity environments (Rico-Gray and Thien 1989b). To test stress-diversity relationships in ant-myrmecophyte systems, MSC mutualisms could be compared across environmental (stress/productivity) gradients, or subjected to local resource availability manipulations. A factorial experiment of this kind could not only tease out the relative importance of different resources on species, but changes observed in number of ant occupants following restriction or addition of resources would indicate a role for niche dimensionality in ant-myrmecophyte interactions.

Two widely-held assumptions about ant-myrmecophyte mutualisms are challenged by our findings on *V. erioloba*: 1) ant-plants are inhabited by a single species at a time and, therefore, ant coexistence only occurs across a population of plants or a single plant’s lifetime; 2) plant-ants are nest-site limited on their host myrmecophyte (Fonseca 1993; Yu et al. 2004). We found other examples of MSC in the literature (Moog et al. 2002; Raine et al. 2004; Rico-Gray and Thien 1989b), but domatia occupancy rates are sorely missing from most published studies. Despite this, the few studies reporting patterns suggest no saturation of domatia (Dyer and Letourneau 1999; Maschwitz et al. 1994; Moog et al. 2002). Competition-colonization trade-offs (Stanton et al. 2002) and dispersal-fecundity trade-offs (Yu et al. 2004) have both been highlighted as likely mechanisms for species co-existence on myrmecophytes, but most research has focused on a few popular study species. The approaches taken with these species could easily be expanded to MSC myrmecophytes to aid our understanding of competition and coexistence in ant/plant systems. The study of multispecies systems has been highlighted as vital to progress our understanding of mutualisms (Fayle et al. 2011; Palmer et al. 2003). We hope that the opportunity presented to study ant communities on *V. erioloba,* as well as the other MSC systems highlighted here, provides a starting point for a better understanding of multispecies mutualism dynamics.

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Online appendix A - Expanded methods and results

Methods

Many studies of coexistence use ants as a model system and utilise null model analyses to examine species co-occurrence patterns (Albrecht and Gotelli 2001; Gotelli and Ellison 2002; Sanders et al. 2007). A study of myrmecophytes and their associated ant species used a Monte Carlo randomisation and cluster analysis to reveal a highly structured community (Fonseca and Ganade 1996). Here we employ randomisation procedures to a smaller spatial scale to assess within-tree patterns of species co-occurrence and evidence of competition between plant-ants sharing access to nest resources on a myrmecophyte. A study of lichen distributions used co-occurrence indices as community metrics in a modelling approach (Belinchón et al. 2012). We employ the same principles in our methodology to assess microhabitat variables (branch height and direction) in relation to ant species nest-site distributions on *V. erioloba* camelthorn trees.

Methods for testing within-tree species co-occurrence patterns

We constructed 20 presence-absence matrices to assess ant species co-occurrence within individual trees. Each matrix represented a single, isolated *V. erioloba* tree, with ant species as rows (n = 4 species) and branches on the trees as columns (n = 4 to 12 branches). A species was scored as present if it had one or more nests on the branch.

We used three different indices to quantify patterns of nest site co-occurrence of ant species occupying *V. erioloba* trees; CHECKER, COMBO and C-score. CHECKER is the number of species pairs that never co-occur and therefore form a checkerboard distribution within the matrix. If this rule exists in an assemblage, then more species pairs should form checkerboard distributions than expected by chance (Gotelli and McCabe 2002). COMBO is the number of species combinations within an assemblage and may reveal the presence of forbidden species combinations. The C-score is the most widely used index of species co-occurrence (Sanders et al. 2007) as it has greater statistical power than the other indices (Gotelli 2000; Gotelli and McCabe 2002). This index is also a measure of "checkerboardness", but is less restrictive than CHECKER, as it calculates the degree of coexistence between species pairs rather than only counting completely segregated pairs (Gotelli 2000; Gotelli and McCabe 2002; Stone and Roberts 1990). The indices CHECKER and COMBO are more sensitive than the C-score, which is not only less restrictive but also less prone to false positives (Gotelli 2000). Generally, if a community is structured by competition the observed assemblage should have more species forming a checkerboard distribution, less species combinations and a higher C-score than in a random community (Diamond 1975; Gotelli 2000), although other mechanisms can affect community structure and therefore the interpretation of indices (for a comprehensive review of null model testing in ecology see, Gotelli and Ulrich 2012; Ulrich and Gotelli 2013).

We used two null models to randomise the observed matrices and create simulated matrices. The fixed-fixed model preserves the row and column totals of the observed matrix. This means that the random community has the same number of species in each sample unit (column total), in this case branches, and each species occurs at the same frequency (row total). This model maintains the differences between the sites and species in the matrix, and for this reason has been suggested as appropriate for analysis of island species lists (Sanders et al. 2007). Isolated trees can be considered as islands of biodiversity and assemble in a similar way (Gove et al. 2009), so we consider this an appropriate model for analysing community patterns on individual trees *V. erioloba* trees in a savannah.

The second, fixed-equiprobable model allows random variation in the total number of species found on each branch but maintains the same frequency of species within the overall matrix. This model treats all the branches on an individual tree as being equally suitable as nest sites for each of the species that are recorded on that tree. It is considered suitable for testing co-occurrence patterns at a local spatial scale (Sanders et al. 2007). The fixed-equiprobable model has been recommended for comparison of standardised sampling procedures, such as baiting or pitfall trapping, in a homogenous habitat (Gotelli 2000). We utilise the fixed-equiprobable model in our analyses because the spatial scale is local (at the tree level). Additionally, it allows any number of species to co-occur on a single branch, which reflected our field observations of nest-site distributions.

To enable us to make comparisons across matrices, we calculated the standardised effect size (SES) for each matrix as follows; $(I_{obs} – I_{sim})/S_{sim}$ where I_{obs} is the observed value for the index, I_{sim} is the mean value of the index based on 5,000 null randomisation matrices and S_{sim} is the standard deviation of the index based on 5,000 null randomisation matrices (Gotelli and McCabe 2002). A one-sample Wilcoxon test was used to test the null hypothesis that the mean SES measured for the 20 presence-absence matrices did not differ from zero. We performed six tests (three indices using two null models) and applied a Bonferroni correction for multiple tests ($P < 0.05/6$). Co-occurrence analyses and Wilcoxon tests were conducted using EcoSim (Gotelli and Entsminger 2009) and R (R Core Development Team 2012), respectively.

Methods for testing ant species microhabitat preference

We constructed 16 presence-absence matrices to test if different ant species nest-sites are associated with different microhabitat characteristics. Each presence-absence matrix represented one of the four cardinal directions (North, East, South and West) combined with one of four height categories (Low: 0-1.50m; Medium Low: 1.51-2.0m; Medium High: 2.01-2.5m and High: 2.51m+). In a matrix, each row represented an ant species and each column represented a different branch that had been sampled. The branches (columns) within a matrix can be drawn from data for different individual trees and were included in a particular matrix based only on their shared microhabitat characteristics. The analyses performed on microhabitat matrices followed the same procedures as for the within-tree matrices. Three co-occurrence indices (CHECKER, C-score and COMBO) were generated under two null models (fixed-fixed and fixed equiprobable) and the standardised effect size (SES) was calculated for each microhabitat matrix. A one-sample Wilcoxon test was used to test the null hypothesis that the mean SES measured for the 16 microhabitat presence-absence matrices did not differ from zero. We performed six such tests (three indices using two null models) and applied a Bonferroni correction for multiple tests ($P < 0.05/6$).

The co-occurrence indices can be considered as community attributes and used in a modelling approach (Belinchón et al. 2012). To evaluate the effects of branch height and aspect on species interactions, we performed ANOVA on all co-occurrence indices. Beginning with the maximal model, we implemented stepwise model simplification to find the minimal adequate model for each index. Co-occurrence analyses were conducted in EcoSim (Gotelli and Entsminger 2009) and Wilcoxon tests and ANOVA were conducted in R (R Core Development Team 2012).

Table A1 Randomisation results for 20 matrices of within-tree species co-occurrence patterns

	C-score				CHECKER				COMBO			
Tree	I_{obs}	I_{sim}	*P*	SES	I_{obs}	I_{sim}	*P*	SES	I_{obs}	I_{sim}	*P*	SES
fe model												
73	0	4.3	1.0	-0.8	0	0	1.0	0.0	3	3.4	1.0	-0.8
76	~				~				~			
89	8	7.2	0.6	0.2	0	0.2	1.0	-0.4	4	3.8	0.8	0.5
90	6.7	6.8	0.6	-0.1	0	0.4	1.0	-0.7	7	6.1	0.3	1.2
96	0	2.9	1.0	-0.8	0	0.4	1.0	-0.8	3	3.0	1.0	0.0
215	4	8.2	0.9	-1.4	0	0.0	1.0	0.0	6	6.3	0.9	-0.5
216	12	7.5	0.1	1.7	1	0.4	0.3	1.1	5	6.1	1.0	-1.6
217	17.3	7.9	**0.0**	**3.1**	1	0.3	0.3	1.3	5	6.0	1.0	-1.5
218	7	7.3	0.6	-0.1	1	0.8	0.6	0.2	8	8.2	0.8	-0.2
219	5.8	5.7	0.5	0.1	2	1.8	0.6	0.2	8	7.2	0.3	1.1
220	2	2.7	0.8	-0.5	0	0.9	1.0	-1.3	5	4.7	0.8	0.6
227	5	3.6	0.2	0.8	1	0.3	0.3	1.3	5	5.3	0.9	-0.5
230	8	4.0	0.3	1.3	0	0.0	1.0	-0.1	4	3.8	0.8	0.5
231	~				~				~			
247	2	3.2	0.9	-0.6	0	0.4	1.0	-0.7	4	3.5	0.5	0.9
248	1	1.6	0.9	-1.4	3	4.4	1.0	-1.3	5	4.9	0.8	0.1
251	1	0.8	0.8	0.6	1	0.7	0.7	0.6	3	2.7	0.7	0.6
252	1	2.3	0.9	-0.9	0	0.8	1.0	-1.1	5	4.4	0.4	1.2
253	0.3	3.5	1.0	-1.9	0	0.2	1.0	-0.5	5	5.3	0.9	-0.4
254	6	4.3	0.5	0.6	0	0.0	1.0	0.0	4	3.9	0.9	0.4
ff model												
73	~				~				~			
76	~				~				~			
89	8	8.0	1.0	0.0	0	0.0	1.0	0.0	4	4.0	1.0	0.0
90	6.7	7.1	1.0	-1.0	0	0.4	1.0	-0.9	7	6.1	0.3	1.2
96	~				~				~			
215	4	4.2	1.0	-1.2	0	0.0	1.0	0.0	6	6.0	1.0	0.0
216	12	10.5	0.1	2.5	1	0.8	0.7	0.3	5	6.1	1.0	-1.6
217	17.3	16.4	0.2	1.2	1	1.3	1.0	-0.7	5	4.7	0.7	0.7
218	7	6.9	0.4	0.2	1	0.9	0.7	0.1	8	8.4	0.9	-0.4
219	5.8	6.1	0.9	-0.8	2	1.8	0.7	0.3	8	7.4	0.4	1.0
220	2	2.0	1.0	0.0	0	0.0	1.0	0.0	5	5.0	1.0	0.0
227	5	4.7	0.2	0.8	1	0.7	0.7	0.6	5	5.5	0.9	-0.7
230	8	8.0	1.0	0.0	0	0.0	1.0	0.0	4	4.0	1.0	0.0
231	~				~				~			
247	2	2.0	1.0	0.0	0	0.0	1.0	0.0	4	4.0	1.0	0.0
248	1	1.1	1.0	-0.8	3	3.0	1.0	0.0	5	4.6	0.6	0.8
251	1	1.0	1.0	0.0	1	1.0	1.0	0.0	3	3.0	1.0	0.0
252	1	1.0	1.0	0.0	0	0.0	1.0	0.0	5	5.0	1.0	0.0
253	0.3	0.3	1.0	0.0	0	0.0	1.0	0.0	5	5.0	1.0	0.0
254	6	6.0	1.0	0.0	0	0.0	1.0	0.0	4	4.0	1.0	0.0

Note: Local scale co-occurrence patterns on 20 individual *V. erioloba* trees at Kuzikus Wildlife Reserve, Namibia as measured by three co-occurrence indices for coexisting ant species. The presence-absence matrices analysed represent one of 20 different individual trees, with columns as sites (branches) and rows as species. Two null models were used for the analyses, fixed-equiprobable (fe model) maintains row sums but allows column totals to vary and fixed-fixed (ff model) maintains all row and column totals. C-score is the C-score calculated from the observed assemblages, CHECKER is the number of species forming a checkerboard distribution in the observed assemblages and COMBO is the number of species combinations in the observed assemblages. I_{obs} is the observed value for the index and I_{sim} is the mean value of the index based on 5,000 null randomisation matrices. The SES is calculated from $(I_{obs}-I_{sim})/S_{sim}$ where S_{sim} is the standard deviation of the index based on 5,000 null randomisation matrices. An SES value greater than 2 indicates segregation of species and an SES of less than -2 indicates significant species aggregation. Significant *P* and SES values are highlighted yellow in bold type.

Table A2 Randomisation results for 16 matrices representing different microhabitat characteristics

		C-score				CHECKER				COMBO			
Direction	Height	I_{obs}	I_{sim}	*P*	SES	I_{obs}	I_{sim}	*P*	SES	I_{obs}	I_{sim}	*P*	SES
fe model													
North	Low	6.2	5.0	0.2	0.9	4	3.7	0.6	0.3	6	6.1	0.8	-0.2
	MedLow	4.3	6.2	0.9	-0.9	1	1.2	0.8	-0.3	6	5.3	0.4	1.1
	MedHigh	1.7	2.8	0.7	-0.6	0	0.8	1.0	-1.3	5	4.4	0.4	1.2
	High	4.5	2.9	**0.05**	1.7	5	3.6	0.2	1.3	5	5.6	1.0	-1.0
East	Low	7	7.1	0.5	0.0	2	1.6	0.6	0.4	7	7.8	0.9	-1.0
	MedLow	17.7	14.9	0.2	0.8	2	0.8	0.2	1.6	10	9.1	0.3	1.2
	MedHigh	2	3.3	0.9	-0.8	0	1.0	1.0	-1.4	5	4.9	0.9	0.4
	High	13.3	7.3	0.1	1.9	2	0.9	0.2	1.5	5	5.0	1.0	0.1
South	Low	1.7	4.5	0.9	-1.3	0	1.3	1.0	-1.8	5	4.7	0.7	0.6
	MedLow	18.7	16.6	0.4	0.4	0	0.0	1.0	-0.1	8	7.1	0.3	1.3
	MedHigh	8	3.4	**0.01**	**2.6**	2	1.1	0.3	1.2	4	4.7	1.0	-1.6
	High	8	12.8	0.9	-1.3	0	0.3	1.0	-0.6	7	6.6	0.6	0.6
West	Low	0	1.2	1.0	-1.2	0	0.6	1.0	-1.2	3	3.0	1.0	0.0
	MedLow	5	3.9	0.4	0.6	1	0.5	0.5	0.9	6	5.3	0.4	1.1
	MedHigh	2	2.0	0.8	0.0	2	1.9	0.8	0.1	4	3.9	1.0	0.3
	High	2.7	3.2	0.6	-0.3	0	0.4	1.0	-0.8	5	4.9	0.8	0.1
ff model													
North	Low	6.2	5.7	0.2	1.2	4	4.2	1.0	-0.5	6	6.2	0.9	-0.4
	MedLow	4.3	4.7	1.0	-1.0	1	0.8	0.8	0.3	6	5.5	0.6	0.8
	MedHigh	1.7	1.7	1.0	0.0	0	0.0	1.0	0.0	5	5.0	1.0	0.0
	High	4.5	4.4	0.6	0.2	5	5.0	1.0	0.0	5	5.4	1.0	-0.8
East	Low	7	6.5	0.1	1.5	2	1.7	0.5	0.4	7	8.2	1.0	-1.6
	MedLow	17.7	18.7	1.0	-1.5	2	1.1	0.3	1.2	10	9.4	0.5	0.8
	MedHigh	2	2.0	1.0	0.0	0	0.0	1.0	0.0	5	5.0	1.0	0.0
	High	13.3	13.8	1.0	-0.9	2	1.5	0.5	1.1	5	5.0	1.0	0.0
South	Low	1.7	1.7	1.0	0.0	0	0.0	1.0	0.0	5	5.0	1.0	0.0
	MedLow	18.7	18.9	0.8	-0.4	0	0.0	1.0	0.0	8	7.1	0.2	1.5
	MedHigh	8	6.7	0.1	**2.4**	2	2.0	1.0	0.0	4	4.6	1.0	-1.3
	High	8	8.4	1.0	-0.7	0	0.0	1.0	0.0	7	7.0	0.8	-0.1
West	Low	~				~				~			
	MedLow	5	5.5	1.0	-0.9	1	0.9	0.8	0.3	6	5.5	0.6	0.8
	MedHigh	2	2.2	1.0	-0.4	2	2.0	1.0	0.0	4	3.9	0.9	0.4
	High	2.7	2.7	0.5	0.0	0	0.0	1.0	0.0	5	5.5	1.0	-1.1

Note: Local scale co-occurrence patterns based on shared microhabitat characteristics of four coexisting ant species on *V. erioloba* at Kuzikus Wildlife Reserve, Namibia. The presence-absence matrices analysed represented different microhabitat characteristics, with columns as sites (branches) and rows as species. Two null models were used for the analyses, fixed-equiprobable (fe) maintains row sums but allows column totals to vary and fixed-fixed (ff) maintains all row and column totals. C-score is the C-score calculated from the observed assemblages, CHECKER is the number of species forming a checkerboard distribution in the observed assemblages and COMBO is the number of species combinations in the observed assemblages. In the table the first two columns indicate the cardinal direction the branch was facing and the height of branch sampled for all sites in the matrix. I_{obs} is the observed value for the index and I_{sim} is the mean value of the index based on 5,000 null randomisation matrices. The SES is calculated from $(I_{obs}-I_{sim})/S_{sim}$ where S_{sim} is the standard deviation of the index based on 5,000 null randomisation matrices. An SES value greater than 2 indicates segregation of species and an SES of less than -2 indicates significant species aggregation. Significant *P* and SES values are highlighted yellow in bold type.

Table A3 Summary of the null model tests for deviations of ant species co-occurrence matrices from randomness using three co-occurrence indices under two null models

Index	Null Model	Average SES	*n*	*V*	*P*
Tree matrices					
C-Score	fe	0.33	17	73.5	0.91
C-Score	ff	0.05	16	17	0.94
CHECKER	fe	-0.12	18	55	0.52
CHECKER	ff	-0.02	16	10	1.00
COMBO	fe	0.10	18	92	0.48
COMBO	ff	0.07	16	18	0.55
Microhabitat matrices					
C-Score	fe	0.15	16	71	0.90
C-Score	ff	-0.04	15	34	0.72
CHECKER	fe	-0.01	16	70	0.94
CHECKER	ff	0.19	15	17	0.21
COMBO	fe	0.27	16	85	0.16
COMBO	ff	-0.06	15	30	0.82

Note: The indices were; CHECKER - the number of species pairs forming a checkerboard distribution, COMBO - the number of species combinations, and C-score - a measure of species co-occurrence. The null models were; Fixed-fixed (ff) = null model in which the matrix row and column sums are preserved; Fixed-equiprobable (fe) = null model in which the rows are fixed and the column total of the matrix are allowed to vary freely. To enable us to make comparisons across matrices, we calculated the standardised effect size (SES) for each matrix as $(I_{obs}-I_{sim})/S_{sim}$ where S_{sim} is the standard deviation of the index based on 5,000 null randomisation matrices (Gotelli and McCabe 2002). A one-sample Wilcoxon test was used to test the null hypothesis that the mean SES measured for the 20 within-tree presence-absence matrices and 16 microhabitat presence-absence matrices did not differ from zero. We performed six tests for each set of matrices (three indices x two null models) and applied a Bonferroni correction for multiple tests ($P < 0.05/6$).

Table A4 Results from ANOVA examining the influence of microhabitat variables on co-occurrence indices

	CHECKER		C-score		COMBO	
	ff	fe	ff	fe	ff	fe
SES						
Height of branch	3.05 (0.19)	0.27 (0.85)	3.59 (0.05)	0.24 (0.87)	3.76 (0.07)	1.15 (0.37)
Aspect of branch	1.71 (0.32)	0.56 (0.65)	0.18 (0.91)	0.15 (0.93)	0.03 (0.99)	0.12 (0.95)

Note: F ratio values of the variables are indicated with *P* values in brackets. CHECKER = number of species pairs forming a checkerboard distribution; COMBO = number of species combinations. Fixed-fixed (ff) = null model in which the matrix row and column sums are preserved; Fixed-equiprobable (fe) = null model in which the rows are fixed and the column total of the matrix are allowed to vary freely. SES is the standardised effect size.

Table A5 Spearman’s rank correlation of association of nest sites on branches of *V. erioloba* for occupant ant species

	Cataulacus	*Crematogaster*	*Tapinoma*	*Tetraponera*
Cataulacus	-	-0.01	0.17	-0.09
Crematogaster	0.934	-	-0.10	-0.08
Tapinoma	**0.014**	0.161	-	-0.05
Tetraponera	0.211	0.275	0.476	-

Note: Above the diagonal indicates the estimated measure of association, Spearman's *rho* statistic, below the diagonal indicates *P* values with significant values in bold.

Table A6 Summary of ant-myrmecophyte systems with particular reference to species occupancy state, and rate of plant and domatia occupancy

Plant species	Ant species	Number of ant species	Occupancy rate of plants (%)	Occupancy rate of domatia (%)	Author
SINGLE-SPECIES OCCUPANCY (SSO) STATE					
Barteria fistulosa	*Pachysima* spp.	2	60 (n=68)	˜	(Janzen 1972)
Cecropia concolor	*Azteca alfari*	1	52.8	˜	(Vasconcelos and Casimiro 1997)
Cecropia distachya	*Az. alfari*	1	85.5	˜	(Vasconcelos and Casimiro 1997)
Cecropia purpurascens	*Az. alfari*	1	80	˜	(Vasconcelos and Casimiro 1997)
Cecropia ulei	*Az. alfari*	1	46.8	˜	(Vasconcelos and Casimiro 1997)
Cordia nodosa	*Az. depilis* + 4 spp.	5	80	˜	(Frederickson 2005)
Duroia hirsute	*Az. depilis; Myrmelachista schumanni*	2	80	˜	(Frederickson 2005)
Hirtella myrmecophila	*Allomerus octoarticulatus*	1	97 (n=600)	˜	(Izzo and Vasconcelos 2002)
Korthalsia furtadoana	*Camponotus* spp. + others	2+	75	˜	(Edwards et al. 2010)
Leonardoxa africana	*Petalomyrmex phylax; Cataulacus mckeyi*	2	92	˜	(Gaume and McKey 1999; Gaume et al. 1997)
Macaranga bancana	*Crematogaster borneensis*	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga beccariana	*Cr. decamera*	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga havilandii	*Cr. decamera*	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga hosei	*Crematogaster* sp.	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga hosei	*Cr. borneensis*	1	41 (n=139)	˜	(Fiala et al. 1989)
Macaranga hullettii	*Cr. borneensis*	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga hullettii	*Cr. borneensis*	1	66 (n=109)	˜	(Fiala et al. 1989)
Macaranga hypoleuca	*Cr. borneensis*	1	64 (n=159)	˜	(Fiala et al. 1989)
Macaranga kingii	*Cr. borneensis*	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga lamellata	*Cr. decamera; Camponotus macarangae*	2	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga trachyphylla	*Cr. borneensis*	1	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Macaranga triloba	*Cr. borneensis*	1	68 (n=348)	˜	(Fiala et al. 1989)
Macaranga winkleri	*Crematogaster* spp.	2	100	˜	(Itino and Itioka 2001; Itino et al. 2001)
Maieta guianensis	Mixed assemblage	2-3	70 (n=23)	˜	(Joly et al. 2014; Valentini et al. 2009)
Piper cenocladum	*Pheidole bicornis*	1	100	56	(Dyer and Letourneau 1999)
Ryparosa fasciculata	*Cladomyrma* spp. + others	5+	91.5-100	˜	(Webber et al. 2007)
Tachigali myrmecophila	*Ps. concolor* + others	8	˜	˜	(Fonseca 1994)
Tococa bullifera	*Cr. laevis; Azteca* sp. + others	2-6	67	˜	(Joly et al. 2014)
Tococa guianensis	*Az. bequaerti; Cr. laevis* + 10 spp.	12	Approx. 96	˜	(Valentini et al. 2009)
Tococa guianensis	*Pheidole sp.; Crematogaster sp.*+ others	4	98	˜	(Alvarez et al. 2001)
Tococa spadaciflora	*Pheidole sp.; Crematogaster* sp.+ 2 spp.	4	98	˜	(Alvarez et al. 2001)

Vachellia allenii	*Ps. ferruginea*	1	~	~	(Janzen 1974)
Vachellia chiapensis	*Ps. ferruginea;* unidentified sp.	2	~	~	(Janzen 1974)
Vachellia collinsii	*Pseudomyrmex* spp.	5			(Janzen 1974)
Vachellia melanoceras	*Ps. satanica*	1	~	~	(Janzen 1974)
Vachellia drepanolobium	Mixed assemblage	1-7	87-100 (n=285)	~	(Stapley 1998; Young et al. 1997)
Vachellia hindsii	*Ps. ferruginea; Ps. veneficus*	2	~	~	(Janzen 1974; Raine et al. 2002)
Vachellia seyal var. *fistula*	*Crematogaster* spp.*; Lepisota canescens*	3	~	~	(Young et al. 1997)
UNKNOWN OCCUPANCY STATE					
Caularthron bilamellatum	Mixed assemblage	11	85 (n=573)	~	(Fisher 1992; Fisher and Zimmerman 1988)
Ficus obscura var. *borneensis*	Mixed assemblage	8	~	64 (n=56)	(Maschwitz et al. 1994)
Piper sagittifolium	*Pheidole bicornis*	1	~	~	(Letourneau 1998)
Tillandsia bulbosa	Mixed assemblage	26	58 (n=100)	~	(Dejean et al. 1995)
Tococa coronate	*Az.* spp.; *Ps.* spp.	Many	~	~	(Michelangeli 2003)
Tococa macrosperma	*Crematogaster* spp.*; Allomerus* spp.	Many	~	~	(Michelangeli 2003)
Vachellia cornigera	*Camponotus planatus*	1	~	~	(Janzen 1974)
Vachellia ruddiae	Mixed assemblage	7	~	20[§]	(Janzen 1974)
Vachellia sphaerocephala	*Crematogaster* spp. + others	3	~	~	(Janzen 1974)
Vachellia zanzibarica	*Crematogaster* spp.	Many	~	~	(Cochard et al. 2008)
MULTIPLE SPECIES CO-OCCUPANCY (MSC) STATE					
*Humboldtia brunonis**[1]	Mixed assemblage	7	100	~	(Gaume et al. 2005a; Gaume et al. 2005b)
*Myrmecophila christinae**[2]	Mixed assemblage	20	85 (n=55)		(Dejean et al. 1995)
*Myrmecophila christinae**[2]	Mixed assemblage	13	~	~	(Rico-Gray and Thien 1989a; Rico-Gray and Thien 1989b)
*Myrmecophila christinae**[2]	Mixed assemblage	18	77.2 (n=333)		(Dejean et al. 2003)
*Vachellia mayana**[3]	*Ps. ferrugineus; Camponotus planatus*	2	100	~	(Raine et al. 2004)
*Zanthoxylum myriacanthum**[4]	Mixed assemblage	28	62-100	42	(Moog et al. 2002)

Note: Studies were selected if they featured in either of three meta-analyses (Chamberlain and Holland 2009; Rosumek et al. 2009; Trager et al. 2010) that incorporated 76, 59 and 81 primary studies of ant-plant mutualisms. A large majority of these primary studies were on myrmecophilic plants (plants provide food resources but no housing) and we therefore excluded them from this summary, reducing the number of primary studies listed here to 34. The studies represent 49 myrmecophyte species, although some species are included in the table multiple times to allow presentation of separate datasets. Occupancy of plants and domatia are given as percentages; the number in parentheses is the total sample size of either plants or domatia; ~ indicates that the data were not reported in the study. On *Vachellia ruddiae*[§] 20% of insect occupied thorns were inhabited by one of seven ant species, however no figure for overall domatia occupancy rate by ants was available.

Although seven ant species are found in domatia on the semi-myrmecophyte *Humboldtia brunonis*^{*1} there is one particular species that exclusively occupies host plants, whereas the remaining six species can co-occur simultaneously on the same tree (Gaume et al. 2005a; Gaume et al. 2005b). In the orchid, *Myrmecophila christinae*^{*2} (formerly *Schomburgkia tibicinis*), hollow pseudobulbs house ants and several species occur on an individual plant, although never within the same pseudobulb. Despite coexisting on *M. christinae* ants remain strongly territorial and only a single species controls foraging access to extrafloral nectar on a plant spike (Rico-Gray and Thien 1989a; Rico-Gray and Thien 1989b). The Mexican swollen-thorn acacia, *Vachellia mayana*^{*3} is co-occupied by two ant species, *Pseudomyrmex ferrugineus* and *Camponotus planatus* on 30.7% of mature plants. The mutualist ant *P. ferrugineus* occupied swollen-thorns near branch tips whereas the parasitic ant *C. planatus* generally occupied old or damaged domatia (Raine et al. 2004). The SE Asian myrmecophyte *Zanthoxylum myriacanthum*^{*4} possesses hollow-stem domatia that have slit like openings for ant access, which close over if not used as nest sites (Moog et al. 2002). Data on the number of myrmecophytes with multiple species co-occupancy (MSC) by different ants were only available for *V. mayana* (31% of plants show MSC) and *Z. myriacanthum* (83% of plants show MSC).

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Table 1 Summary of myrmecophytic plants that exhibit multiple species co-occupancy (MSC) by their resident ant species.

	Plant and domatia type	Habitat	Country	Common domatia-inhabiting ant species	Number of ant species	Plant/ domatia occupancy (%)	MSC occupancy (%)
Humboldtia brunonis (Fabaceae, Caesalpinioideae)	Tree with hollow internodes	Wet evergreen forest	India	Unknown	7	100/-	-
Myrmecophila christinae (Orchidaceae, Epidendroideae)	Epiphyte with hollow pseudobulbs	Coastal sand dune mattoral	Mexico	*Crematogaster brevispinosa, Camponotus planatus*, *Ca. abdominalis*, *Ca. rectangularis* and *Ectatomma tuberculatum*	13	-/-	-
		Flooded mangrove forest		*Dolichoderus bispinosus* and *Pachycondyla villosa*	18	77.2/-	-
				Ca. planatus, *Cyphomyrmex minutus* and *Monomorium ebeninum*	20	85/-	-
Vachellia erioloba (Fabaceae, Mimosoideae)	Tree with swollen-thorns	Savanna	Namibia	*Crematogaster* sp., *Cataulacus intrudens*, *Tapinoma* sp. and *Tetraponera ambigua*	4	100/37.45	95
Vachellia mayana (Fabaceae, Mimosoideae)	Shrub/small tree with swollen-thorns	Lowland wet forest	Mexico	*Pseudomyrmex ferrugineus; Ca. planatus*	2	100/-	30.7
Zanthoxylum myriacanthum (Rutaceae, Toddalioideae)	Tree with hollow-stems	Lowland forest	Malaysia	Many species including, *Cataulacus*, *Crematogaster*, *Tapinoma*, *Technomyrmex*, *Camponotus* and *Tetraponera*	28	62*/42	83

Note: For the full list of species included in our review of myrmecophyte occupancy states see Table A6. Occupancy rates for plants and domatia are given as percentages and - indicates that the data were not reported in the study. MSC occupancy is the percentage of plants that are occupied by colonies of multiple different ant species nesting within domatia. *On *Zanthoxylum myriacanthum* 62% of all trees sampled (including those with only closed stem domatia) were occupied by ants, however 100% of all trees sampled with open hollow-stem domatia were occupied by ants.

Figure legends

Figure 1 A, *Vachellia erioloba*, camelthorn tree in acacia-dominated savanna at Kuzikus Wildlife Reserve, Namibia. B, Swollen-thorn domatia of *V. erioloba* with ant nest entrance hole visible on left thorn. C, Open swollen-thorn domatia containing a *Tapinoma* nest.

Figure 2 Occupation of nest-sites and numerical dominance of four ant species on *V. erioloba* at Kuzikus Wildlife Reserve. White bars represent each species as a proportion of the total number of ant nests found on trees. Black bars represent each species as a proportion of the total number of individuals (including workers, alates, queens, and brood) recorded during surveying. Sample size is indicated by numbers above each bar. Data underlying figure 2 are deposited in the Dryad Digital Repository, doi:10.5061/dryad.s9f7c (Campbell et al. 2015)

Figure 3 Mean (±SE) number of nest-sites per branch for the four ant species on *V. erioloba* at Kuzikus Wildlife Reserve. Analysis of variance showed that nest-site density varies significantly ($F_{3, 211}$=3.603, $P < 0.05$) between ant species (*Cataulacus* $n = 40$, *Crematogaster* $n = 75$, *Tapinoma* $n = 94$ and *Tetraponera* $n = 6$). Different letters indicate significant differences ($P < 0.001$) using Tukey HSD test for post hoc comparisons.

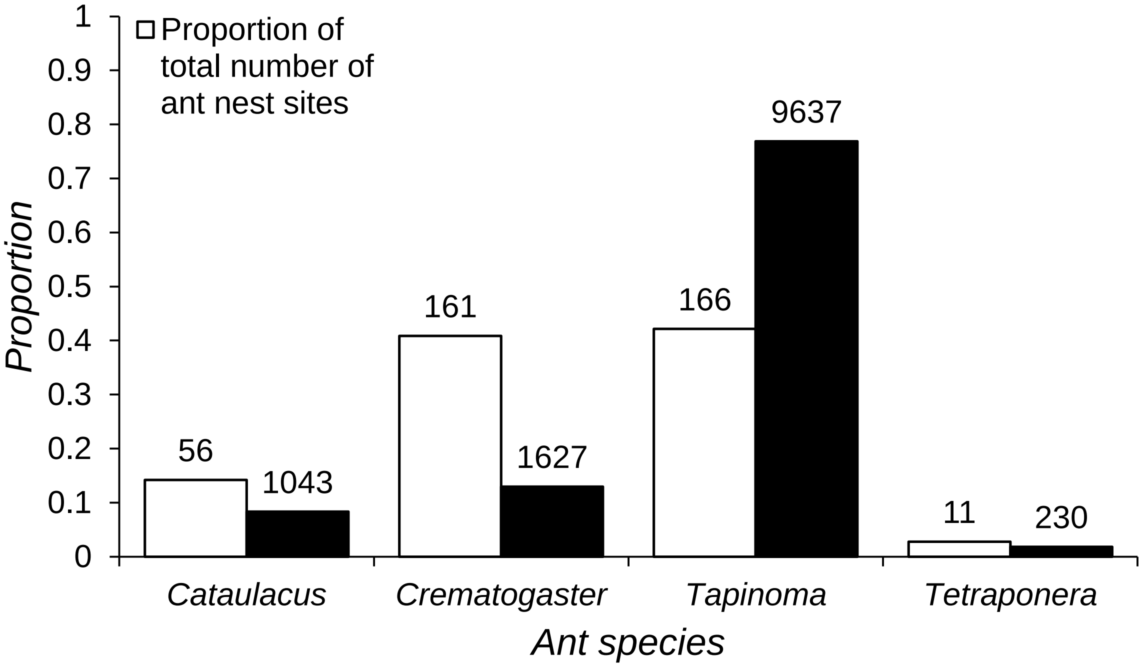
Figure A1 Diagrammatic representation of multiple species co-occupancy on *V. erioloba* trees at Kuzikus Wildlife Reserve, Namibia. Small circles indicate the presence of non-swollen thorns, large circles indicate swollen thorns, i.e domatia, that are suitable potential nest sites for ants. Occupants of domatia are indicated by the pattern within the large circle as follows; empty = no occupant, black = *Tapinoma*, dots = *Crematogaster*, vertical stripe = *Cataulacus*, horizontal stripe = *Tetraponera*

1A

1B

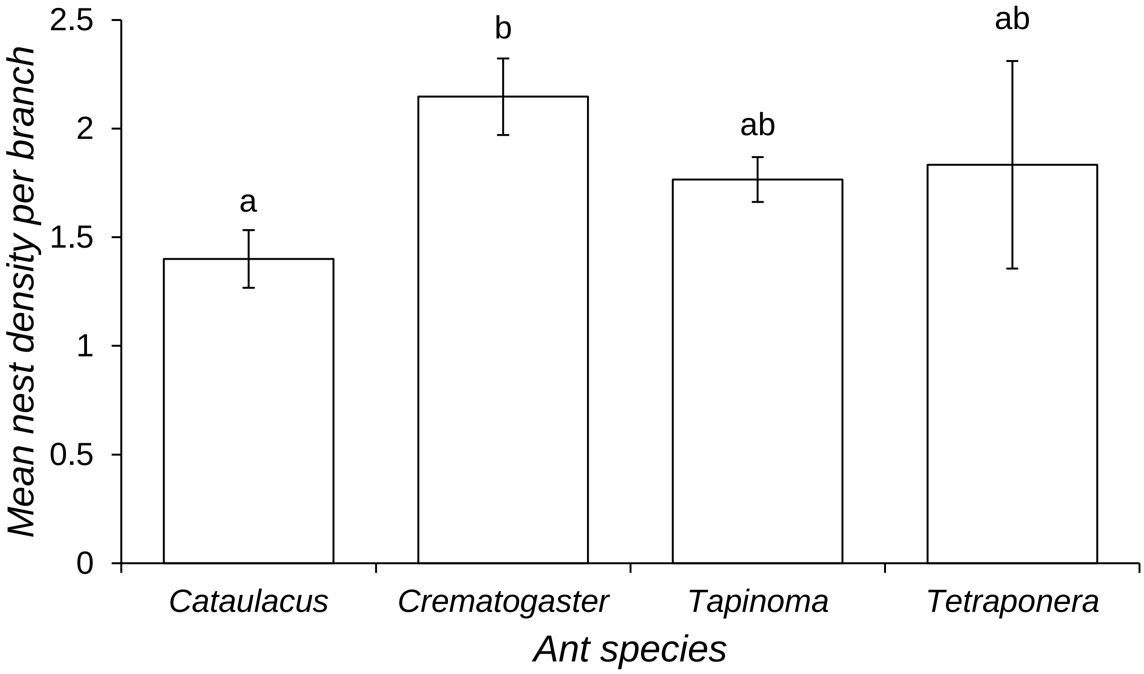
1C

Figure 2



1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion
☐ Proportion of total number of ant nest sites
56
1043
161
1627
166
9637
11
230
Cataulacus
Crematogaster
Tapinoma
Tetraponera
Ant species

Figure 3


2.5
2
1.5
1
0.5
0
Mean nest density per branch
a
b
ab
ab
Cataulacus
Crematogaster
Tapinoma
Tetraponera
Ant species