



# MULTI - SCALE ANT DIVERSITY IN SAVANNA WOODLANDS: AN INTER - CONTINENTAL COMPARISON

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## INTRODUCTION

The effect of spatial scale on ecological patterns is a key issue in community ecology and biogeography, and studies comparing community structure at different spatial scales have made important contributions to ecological theory (Spiesman & Cumming, 2008). The pervasiveness of scale - dependency is a key factor limiting the generality of ecological patterns and processes (Lawton, 1999).

There have been few studies purposely designed to investigate the importance of spatial scale on ant community structure (Spiesman & Cumming, 2008). Here we report on such a study, which incorporates an inter - continental comparison between Australia and Brazil.

Most studies of tropical ant diversity have focused on rainforest, however, the dominant tropical vegetation is savanna (Huntley & Walker, 1982). A comparison of Brazilian and Australian savannas is especially interesting because they are located at similar latitudes, are very similar in size (ca. 2,000,000 km<sup>2</sup>), and experience comparable rainfall and temperature regimes.

## OBJECTIVES

Here we used standardized sampling methodology to compare species richness in Australian and Brazilian savanna ant communities, and to examine how this comparison varies with spatial scale. The specific aims of this paper are to: i) compare the taxonomic composition of Australian and Brazilian savanna ants; ii) compare ant species richness and species turnover at multiple spatial scales; and iii) examine the extent to which intercontinental comparisons of ant diversity are scale - dependent.

## MATERIAL AND METHODS

### *Study area and ant sampling*

The study was conducted along eight 400 m line transects (four in Australia and four in Brazil). All transects were located in well preserved savanna areas around Darwin, NT in northern Australia and Uberlândia, MG and Caldas Novas, GO in central Brazil. Along each transect, the nearest tree taller than 2 m was located at each 20 m interval (n = 20 trees). Eight pitfall traps were established on and around each tree, four buried in the ground beneath the tree canopy and four fixed in the tree branches with masking tape, with traps spaced by at least 2 m. These eight traps will subsequently be referred to as a “tree”. Pitfall traps were 4 - cm diameter plastic containers partially filled with water and detergent. For each set of four ground and arboreal traps, two had their inner rims smeared with sardine oil, and two with honey, as ant attractants. Each trap was kept open for a 48 h period, and a total of 1,280 pitfalls were sampled on and around 160 trees. Ants were sampled during November and December (early rainy season) of 2005 in Brazil and during the same months and season of 2006 in Australia.

### *Data analysis*

A t - test was used to compare mean ant abundance at the pitfall trap scale, and mean species richness at the pitfall, ‘tree’ and transect scales, between Australia and Brazil. The data were LOG (x + 1) transformed prior to analysis to meet the assumption of normality. For each country, species turnover was calculated based on the proportion of unique species within sampling units at each scale. At the pitfall trap scale (n = 640 pitfalls), the number of unique species (those occurring in a single trap) for each “tree” (n = 8 traps) was divided by the total number of species collected for the respective “tree”. Likewise at the scale of “tree” (n = 80 “trees”), the number of unique species (those occurring in a single “tree”) within each transect (n = 20 “trees”) was divided by the total number of species collected for the respective transect. Finally at the scale of transect (n = 4 transects), species turnover was calculated as the number of unique species per transect, divided by the total number of species recorded in each country. T - tests

were used to compare mean species turnover at each scale between the Australian and Brazilian savannas. We based our species turnover calculations on unique species rather than using similarity indexes (e.g. Sørensen and Jaccard) because unique species directly affect species accumulation across sampling units.

## RESULTS AND DISCUSSION

### Results

In total, 185,334 individual ants representing 242 species, 48 genera and 7 subfamilies were collected in traps. Despite only eight (16%) genera co-occurring in Australia and Brazil, the composition of the two faunas was extremely similar at the sub-family level when considering species richness (Chi-square = 7.84; df = 6;  $p = 0.22$ ). In both cases, by far the richest sub-families were Myrmicinae and Formicinae, representing about one-half and one-quarter of total species respectively. However, there were very considerable differences when considering proportional abundance (Chi-square = 86.27; df = 6;  $p < 0.003$ ). Behaviorally dominant dolichoderines were proportionally far more abundant (around 65% of all individuals) in Australia, with myrmicines being likewise in Brazil. These differences were accounted by four genera: *Iridomyrmex* and *Papyrius* (Dolichoderinae, with 38 and 27% of all individuals respectively) in Australia, and *Pheidole* and *Solenopsis* (Myrmicinae, with 41 and 25% of all individuals, respectively) in Brazil.

Overall ant abundance was almost three times higher in Australia than in Brazil, both on the ground and on vegetation. For example, only four *Iridomyrmex* species were responsible for 36% of the total individual ant numbers. This becomes clear when we directly compare the total number of individuals of the most abundant species from both savannas (Australia: *Iridomyrmex pallidus* = 34258; Brazil: *Pheidole fallax* = 6646).

Despite markedly lower ant abundance, overall species richness was far higher in Brazil (150 species) than in Australia (93). Comparative species richness between Australia and Brazil varied markedly with spatial scale with similar results for ground, arboreal and combined data. Despite the marked overall difference, there was no significant difference in the mean number of species per pitfall trap (combined data:  $t = 1.48$ ; df = 1278;  $p = 0.14$ ). On the other hand, the mean number of species was significantly higher in Brazil at the tree scale (combined data:  $t = 5.53$ ; df = 158;  $p < 0.001$ ), and also significantly higher at the transect scale (combined data:  $t = 2.62$ ; df = 6;  $p = 0.04$ ).

Comparative species turnover between Australia and Brazil also varied markedly with spatial scale, and again we found similar results for ground, arboreal and combined data. Species turnover was significantly higher in Brazil than in Australia at the pitfall trap scale, and was more than twice as high at the transect scale (combined data: pitfall:  $t = 3.3$ ; df = 1278;  $p = 0.001$  and transect:  $t = 2.46$ ; df = 6;  $p = 0.049$ ). However, there was no significant difference for turnover at the tree scale (combined data:  $t = 0.061$ ; df = 158;  $p = 0.95$ ).

### Discussion

The Australian and Brazilian savanna faunas showed remarkable compositional similarity at the subfamily level in terms of relative contribution to species richness, despite the very low proportion of shared genera. Subfamily composition varies widely between habitats within any particular biogeographic region, so such similarity must be seen as adaptive convergence in response to similar climatic and other environmental conditions (Kelt *et al.*, 1996). However, there were very marked intercontinental differences in subfamily composition in terms of contribution to relative abundance, with dolichoderines (*Iridomyrmex* and *Papyrius*) being far more common in Australia, and myrmicines (*Pheidole* and *Solenopsis*) likewise in Brazil. This difference reflects the broader ecological domination of Australian ant communities by dolichoderines, which is unparalleled elsewhere in the world and arguably represents the most significant intercontinental 'anomaly' in ant community ecology (Andersen, 1995). Although the Brazilian species of *Pheidole* and *Solenopsis* can be considered as ecologically dominant ants, it is not a simple case of ecological equivalence to behaviorally dominant dolichoderines, as the myrmicines are functionally quite different in terms of their (lower) rates of activity and abundance (see below). Ground-nesting behaviorally dominant dolichoderines (species of *Dorymyrmex*) occur in Brazilian savannas, but they tend to be minor components of ant communities, especially in terms of abundance and behavioral dominance.

Overall ant abundance was almost three times higher in Australia than in Brazil, both on the ground and on trees. This difference indicates a major intercontinental difference in ant productivity. Arid, semi-arid and seasonally arid Australia is renowned for its remarkably high ant productivity (Andersen 2003), but this is the first time that standardized quantitative data have been obtained to document this difference. More specifically, much of the intercontinental difference is due to an extraordinarily high abundance of dolichoderines in Australia. Species of *Iridomyrmex* alone contributed to nearly 40% of total ant abundance in Australia, and the most common species in Australia (*Iridomyrmex pallidus*) was five times more abundant than the most common Brazilian species (*Pheidole fallax*).

Despite having far lower overall ant abundance, total species richness was markedly higher in Brazil (150) than Australia (93). Richness was similar at the pitfall trap scale, but the difference became more pronounced with increasing spatial scale. In particular, it was strongly influenced by species turnover at the transect scale, which was twice as high in Brazil as in Australia. This parallels with results from a comparative study of harvester ants in Australian and North American deserts, where richness was similar at small scales, but considerably higher in Australia at larger scales due to higher species turnover (Morton and Davidson, 1988).

Such scale-dependent patterns in comparative species richness indicate that comparative diversity is influenced more by regional than by local factors. The most obvious regional factor in our study is the very large regional pool of rain forest taxa, including very many arboreal species, in Brazil, a species pool that is virtually absent from savanna landscapes in Australia. Indeed, if species from rain forest

taxa are excluded, the total number of species recorded in Brazil (89) is almost identical to that in Australia (90). It is important to note that Brazilian savannas are surrounded by vast expanses of tropical rain forests, the Amazon to the north and the Atlantic to the south, and that the evolutionary history of the savanna biota is embedded in expansions and retractions of rain forest (Redford & Fonseca, 1986). In addition, within Brazilian savanna habitats there are many intrusions of gallery and other mesophytic forests that are extremely rich in forest ant species (Lopes & Vasconcelos, 2008), whereas Australian savanna landscapes contain very small and isolated forest patches, and these support a depauperated ant fauna (Andersen *et al.*, 2007).

There are two ecological factors that potentially contribute to higher ant diversity in Brazilian compared with Australian savannas. The first is a difference in structural complexity of savanna vegetation. Vegetation structure in Australian savanna woodlands is often strongly bimodal, with a poorly developed mid - storey. Moreover, Australian savannas are often dominated by just one or two tree species, such as *Eucalyptus tetradonta* and *E. miniata* (Mott *et al.*, 1985). In contrast, Brazilian savanna woodlands are multi - layered (Campos *et al.*, 2008), which might promote ant richness through greater habitat heterogeneity (Ribas *et al.*, 2003). Similarly, Brazilian savannas have greater tree species richness - we recorded a total of 41 tree species in Brazil, compared with only 19 in Australia. This might also contribute to greater ant richness species in Brazil, especially because there is a positive relationship between the number of tree species and ant richness in Brazilian savanna (Ribas *et al.*, 2003). However, there is no evidence that ant richness varies substantially with tree richness or vegetation structural complexity in Australian savannas. Indeed, transect 1 had lowest ant richness (45, compared with 62 - 68 at others) despite its high vegetation complexity, and the relatively high tree richness at sites 1 and 4 (Table 1) was not associated with higher ant richness. This suggests that the relationship between tree and ant species richness in Brazil (Ribas *et al.*, 2003) is contingent upon the regional availability of forest species, and especially tree - nesting specialists.

The second ecological factor potentially contributing to the observed intercontinental differences in ant richness is the higher abundance of behaviorally dominant ants, and therefore higher rates of competitive exclusion, in Australia. However, this seems unlikely for two reasons. First, differences in competitive exclusion would affect comparative species richness at small spatial scales, whereas the differences we have revealed operate at larger spatial scales. Second, although competition from dominant ants can strongly affect foraging success of subordinate species, there is little evidence that it prevents such species from occurring (Andersen, 2008). Indeed, within Australia there is a positive relationship between the abundance of behaviorally dominant dolichoderines and species richness (Andersen, 1995).

## CONCLUSION

### Conclusion

Our study has revealed scale - dependent differences in species richness between savanna ants in Australia and Brazil. Species richness was similar at very small (pitfall trap) scales, but was increasingly higher in Brazil with increasing spatial scale. We have attributed these intercontinental differences to biogeographical and historical factors in Brazil that have led to a large regional pool of species of rain forest origin. This further underlines the importance of biogeographical context when analyzing ant communities, following recent work showing that the responses of ant communities to disturbance are contingent upon their biogeographical history. It also further highlights the importance of processes acting at regional scales in determining species richness in ant communities.

Our study has compared savanna faunas at the highest end of the savanna rainfall gradient, and concluded that the large regional pool of rain forest taxa in Brazil has been a key factor contributing to higher species richness at larger spatial scales in Brazil compared with Australia. We would therefore predict that the intercontinental differences in species richness would diminish, and even be reversed, for savannas in lower rainfall zones. This is because the prevalence of rain forest taxa would be expected to decline with decreasing rainfall, with a concomitant favoring of arid - adapted taxa. Such a climatic shift would strongly change relative richness in Australia's favor. This would suggest that not only are cross - continental comparisons of species richness scale - dependent, but they are also likely to vary with the climate zone under investigation.

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