Historical biogeography shapes functional ecology: 
Inter-continental contrasts in responses of savanna ant communities to stress and disturbance

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Abstract

Most comparative studies of biological communities in different biogeographical regions highlight ecological convergence under matched environments. Here we use savanna ant communities as a striking example where such convergence has not occurred. The savanna ant faunas of Australia, Brazil and Africa have very different functional composition due to their highly contrasting evolutionary origins.

We synthesise the literature relating to the diversity and composition of savanna ant communities in the three continents, along with ant community responses to fire and aridity.

Australian savannas evolved in association with a desert biome and its fauna is strongly arid adapted: it is exceptionally thermophilic, granivorous species are extremely diverse and abundant, high diversity is maintained with increasing aridity, and communities are highly resilient to simplification of vegetation structure induced by frequent fire. Brazilian savannas evolved surrounded by rainforest and have a forest-derived ant fauna; this fauna is not so highly thermophilic, granivory is almost absent, diversity declines with increasing aridity and communities are highly sensitive to fire-induced vegetation change. Africa has a very generalised ant fauna that has moderate representations of highly thermophilic and granivorous species, diversity appears to decline with increasing aridity, but communities are highly resilient to fire.

The different biogeographical histories of tropical savannas in Australia, Brazil and Africa have led to functionally distinct ant faunas that display contrasting responses to environmental stress and disturbance. Phylogenetic niche conservatism seems to be particularly strong for granivory and thermophilia. Such intercontinental differences have important implications for understanding biodiversity responses to land management and climate change.

Keywords
Africa, ants, Australia, biogeographical history, Brazil, community ecology, macroecology, tropical savannas
1 | INTRODUCTION

Biological communities from different parts of the world have different taxonomic composition because of their different biogeographical and therefore evolutionary histories. Different biogeographical histories often also lead to regional differences in taxonomic richness (Cadle & Greene, 1993; Latham & Ricklefs, 1993; McCoy & Heck Jr., 1976; Ricklefs, 2004). However, despite their different histories there is often striking functional convergence among communities throughout the world sharing common environmental conditions (Agrawal, 2017; Brown & Gibson, 1983). This is especially the case for vegetation, such as under a Mediterranean-type climate (Davis & Richardson, 1995) or in the seasonal tropics (Bourlière, 1983), but often also likewise for fauna (Ford, 1989; Melville et al., 2006; Moen et al., 2016; Trontelj et al., 2012; Winemiller & Pianka, 1990). When functional differences do occur, they are typically attributed to ecological factors that differ between the ‘matched’ environments (Morton, 1979; Morton & Davidson, 1988; Pianka, 1986).

Despite ecological convergence attracting so much attention, biogeographical and phylogenetic history is recognised as playing a potentially important role in species assemblages because of phylogenetic niche conservatism (Cavender-Bares et al., 2009)—the tendency of species to retain ancestral ecological characteristics over evolutionary time (Peterson et al., 1999). For example phylogenetic conservatism explains variation in the relative diversity of aquatic and semi-terrestrial turtles in eastern North America (Stephens & Wiens, 2009). However, there are few well-documented cases of inter-continental contrasts in community function due to a persistent legacy of biogeographical history. One familiar example involves eucalypts (species of Eucalyptus, Corymbia and Angophora), which evolved in Australia and dominate that continent’s vegetation to an extent unparalleled by any comparable taxon elsewhere in the world. The unique water-use efficiency, flammability and fire resilience of eucalypts make them highly distinctive functionally (Bond et al., 2012), imparting Australian ecosystems with a unique flavour (Keith, 2017). Here we document another example, involving a globally dominant faunal group and one of the world’s major biomes: ants of tropical savannas.

Although the C₄ grasses that dominate tropical grassy biomes emerged in the late Oligocene up to 30 Ma, their expansion throughout the tropics has occurred only in the last 10 Myr, facilitated by fire (Keeley & Rundel, 2005), low CO₂ (Cerling et al., 1997) and mammalian herbivory (Charles-Dominique et al., 2016). Savanna is now the most extensive biome in the tropics, is exceptionally biodiverse, supports a substantial proportion of the world’s population, and experiences high levels of both natural and anthropogenic disturbance, especially fire and grazing (Murphy et al., 2016). We show that the contrasting histories of the world’s three largest tropical savanna estates—in Australia, Brazil and Africa (Figure 1), have led not only to contrasting ant diversity, but to major differences in ant functional composition that result in markedly different responses to environmental stress and disturbance. Such differences are not only fundamental for understanding the nature of savanna ant communities, but they also have important implications for land management and for likely impacts of climate change.

FIGURE 1 (a) Equal area projection Map showing the distribution of tropical savannas and (b) photos of tropical savannas from Brazil (c) Africa and (d) Australia
The savanna biome of the northern third (monsoonal zone) of Australia is a product of the continent’s 20 million-year history of aridification (Bowman et al., 2010; Byrne et al., 2008). During this time its only land-based contact has been to the south, where it grades into the vast central arid zone (Bowman et al., 2010), and this is the historical source of much of Australia’s savanna ant fauna. Indeed, Australia’s savanna ants are part of a taxonomically and functionally coherent, arid-adapted fauna that occurs throughout the 90% of the continent that is either arid, semi-arid or seasonally arid (subsequently referred to simply as ‘arid’; Andersen, 2003). This fauna is characterised by exceptionally high diversity, abundance, behavioural dominance and thermophilia, and by a high incidence of granivory.

The ant fauna of arid Australia (including tropical savannas) has been estimated to contain up to a phenomenally high 7500 species (Andersen, 2016). The vast majority of these are undescribed and so the actual number is highly uncertain, but it seems clear that the size of the fauna rivals that of Amazonia, which is widely recognised as the global centre of ant diversity. This is especially remarkable given that faunas of arid regions outside Australia have relatively low ant diversity (Andersen, 2003). The extraordinary ant diversity in arid Australia is largely unrecognised because most of the land is extremely remote and unsampled, and taxonomic revisions have failed to appreciate the significance of morphological variation within widespread ‘species’. Recent assessments that integrate morphological, genetic and distributional information from increasingly extensive sampling are now demonstrating the remarkable extent of diversity (Andersen, 2016; Andersen et al., 2020, 2022; Oberprieler et al., 2018). The fauna includes the endemic arid-specialist genus Melophorus with at least 1000 species (Andersen et al., 2016, 2020), along with three cosmopolitan genera (Monomorium, Camponotus and Pheidole) with likely more than 500 arid Australian species, and several others with more than 100 (Andersen, 2003, 2016). Outside Australia, Cataglyphis (occurring throughout northern Africa, the Palearctic and much of Asia) is regarded as the most diverse arid-adapted genus with about 100 species (Agosti, 1990). Despite occurring across three continents, species richness in Cataglyphis is an order of magnitude lower than in Melophorus.

Ant diversity in Australian savannas is exceptionally high at all spatial scales. At least 15 species of a single genus (Monomorium), all nesting in the ground, were recorded in a 10 × 10 m plot near Darwin in the NT (Andersen et al., 2013). This includes up to seven species per plot from a taxon (the M. nigrus group) formally considered a single species; this taxon is now recognised as likely including more than 200 species in Australia’s savanna zone (Andersen et al., 2020). Observed hectare-scale richness on sand and loam soils ranged from about 70 to 100 along a 1000-km transect in the NT (Andersen et al., 2015) and actual site richness has been estimated to be as high as 130 (Del Toro et al., 2019). At a regional scale, the ant fauna of the 400,000-km² ‘Top End’ (northern third) of the NT includes well over 1000 species, with a remarkable >60% of these apparently endemic to the region (Andersen et al., 2018, 2020, 2022). Other major biogeographical regions in Australia’s savanna zone appear to have comparable levels of diversity and endemism (Andersen et al., 2018; Bowman et al., 2010), indicating that the total Australian savanna ant fauna numbers in the several thousands, by itself rivalling or exceeding that of Amazonia.

Casual observation indicates that ant abundance in arid Australia is also exceptionally high (Andersen, 2003). This has been documented in savannas by a comparative study using identical trapping techniques in sites with similar climate in Australia and Brazil, which found that ant catches per trap were three times as high in Australia, both on the ground and on trees (Campos et al., 2011). One of the most distinctive features of ant communities in arid Australia is the extreme abundance of behaviourally dominant (highly aggressive, fast-moving ants that occur in large colonies and have large foraging territories) species of the genus Iridomyrmex (subfamily Dolichoderinae), which are among the most common ants at most sites (Andersen, 2003). There are clear parallels between Iridomyrmex and eucalypts in terms of their unique dominance of continental biotas. Behaviourally dominant dolichoderines are often among the leading dominant ants at the most favourable sites for ants throughout the world, but nowhere else is such dominance anywhere near as pronounced as in arid Australia (Andersen, 2003). In the Campos et al. (2011) savanna study, the most abundant ant in Australia was a species of Iridomyrmex (I. pallidus) that was more than five times as abundant as the most common species (Pheidole oxyops; referred to in the paper as P. fallax) in Brazil. These two species have similar body size and so the different abundances also reflect differences in biomass.

Arid zones throughout the world feature exceptionally thermophilic taxa that can tolerate extremely high temperatures, enabling them to forage during the middle of hot days when most other ants are inactive. This is taken to the extreme by Melophorus (Christian & Morton, 1992), but many other ant taxa in arid Australia are also highly thermophilic, notably most ecologically dominant species of Iridomyrmex. All these highly thermophilic taxa are extremely diverse in Australian savannas (Andersen, 2000).

Finally, deserts throughout the world feature diverse assemblages of post-dispersal granivores because seeds are such valuable resources in arid ecosystems, and harvester ants are prominent components of most arid ant faunas (Brown et al., 1979). Harvester ants are especially diverse and abundant in arid Australia (Morton & Davidson, 1988). This extends into Australian savannas, which support highly diverse, specialist seed-harvesting assemblages from a wide range of genera, including Monomorium (rothsteini group), Pheidole (especially the mbjobergi group), Meranoplus (especially the diversus group), Cheianer (insolescens and bifidum groups) and even Melophorus (wheeleri group), the only example anywhere in the world of specialist harvester formicines (Andersen, 1991). These harvester
ants target the seeds not only of grasses, but also of the dominant eucalypts, where they can have a significant impact on seedling recruitment (Setterfield & Andersen, 2018).

3 | THE FOREST-DERIVED BRAZILIAN FAUNA

In striking contrast to Australian savannas, the evolutionary history of savannas (‘cerrado’) in Brazil is in association with rainforest—the Amazon to the north and west and Atlantic forest to the east and south. Cerrado is considered to have a relatively recent (<10 Ma) origin, with most plant lineages diversifying from only about 4 Ma (Simon et al., 2009). However, the origin and initial diversification of most Neotropical ant lineages took place much earlier, during the Eocene (30–50 Ma), coincident with the expansion of tropical forests (Moreau & Bell, 2013; Price et al., 2014). These forest lineages are the dominant source of the cerrado ant fauna. For example, phylogenetic analyses of two prominent groups of cerrado ants, the turtle ants of the genus Cephalotes (Price et al., 2014) and the fungus-growing ants (including the leaf-cutter genus Atta; Branstetter et al., 2017), indicate that both originated in rainforest and more recently diversified in dry habitats. Generic composition of the cerrado ant fauna is very similar to that of rainforest (Vieira et al., 2021), which is in striking contrast to the case in Australia where rainforest and savanna faunas are highly disjunct at the genus level (van Ingen et al. 2008). Moreover, many ants in cerrado are widespread forest species, and these extend not just into cerrado but also into semi-arid Caatinga (Leal et al., 2018). A compelling illustration of the forest-derived nature of the cerrado ant fauna is its exceptional diversity of specialist arboreal species (Table 1), a feature otherwise unknown in ant faunas of open habitats.

Its relatively recent forest derivation makes the cerrado ant fauna very different both structurally and functionally from that in Australian savannas (Table 2). Its local diversity is very high as reflects that of surrounding tropical forest, in part due to its unusually diverse arboreal fauna (Campos et al., 2011). The mean number of species collected in four 400-m transects was about 80 (Campos et al., 2011), and up to 121 species were recorded in three such transects within 1 km of each other (Vasconcelos et al., 2018). The Brazilian ant fauna is comparatively well-known taxonomically, as evidenced by an extensive CO1 analysis of the fauna of southern Atlantic forest, which revealed that its size was likely only 6%–10% larger than currently recognised (Hanisch et al., 2017). This allows for a reliable assessment of the total size of the cerrado ant fauna, which is estimated to comprise about 700 species (R. Feitosa, personal communication). The total size of the cerrado fauna is therefore only about half that of just the Top End of the Northern Territory, and only a fraction of the total Australian savanna fauna. It indicates remarkably low levels of species turnover given the vast size of the Cerrado biome and reflects the extremely widespread distribution of many species, not just within Cerrado but also in other biomes (Leal et al., 2018). In addition to the relatively young age of cerrado vegetation, it presumably also reflects the relatively weak biogeographical differentiation within the Cerrado biome, along with the absence of a diverse arid-adapted element in adjacent semi-arid Caatinga, whose ant fauna is essentially a depauperate subset of the Cerrado fauna (Leal et al., 2018).

Overall ant abundance in cerrado appears to be high by most standards, but as previously mentioned it is only a fraction of that in Australian savannas. Behaviourally dominant dolichoderines (species of Dorymyrmex, Linepithema and Azteca) can be abundant locally, but they are very patchily distributed and often in low abundance; in terms of prominence, they bear no comparison with that of Iridomyrmex in Australia. The cerrado ant fauna contains very few highly thermophilic elements (Camacho & Vasconcelos, 2015; Campos et al., 2011), including no specialist sun-loving formicines such as occur in open habitats of most hot regions elsewhere in the world (species of Melophorus in Australia, Myrmecocystus in Mexico, and southwestern USA, and Cataglyphis in Africa, Mediterranean southern Europe and the Middle East). The critical thermal maximum of the open cerrado specialist Ectatomma opaciventre is 45.6°C (L. Zuanon & H. Vasconcelos, unpublished data), compared with 56.7°C for Melophorus bagoti in Australia (Christian & Morton, 1992). Finally, specialist harvester ants are largely absent from cerrado, with the widespread Pagonomyrmex naegeli (Belchior et al., 2012) being a notable exception.

4 | THE HIGHLY GENERALISED AFRICAN FAUNA

Savanna underwent a major expansion in Africa 10–15 Ma and has been the dominant vegetation in tropical and subtropical regions

| TABLE 1 Number of arboreal (tree-nesting) ant species recorded in four savanna sites in each of Australia and Brazil using identical survey techniques (data from Campos et al., 2011) |
|-----------------------------------|-----------------|-----------------|
|                                   | Australia       | Brazil          |
|-----------------------------------|-----------------|-----------------|
| Azteca                            | 4               | 4               |
| Dolichoderus                      | 2               | 2               |
| Tapinoma                          | 1               | 1               |
| Camponotus                        | 10              | 10              |
| Oecophylla                        | 1               | 1               |
| Cephalotes                        | 8               | 8               |
| Crematogaster                     | 3               | 3               |
| Leptothorax                       | 2               | 2               |
| Wasmannia                         | 1               | 1               |
| Pachycondyla                      | 2               | 2               |
| Pseudomyrmex                      | 12              | 12              |
| Tetraponera                       | 1               | 1               |
| Total                             | 5               | 48              |
The ant fauna of African savannas is mixed in terms of biogeographical origin. Drier savannas (<700 mm mean annual rainfall) include specialist arid-adapted taxa such as the highly thermophilic, African-endemic genus Ocyomyrmex and specialist seed harvesters such as species of Messor and the Tetramorium solidum-group. Species from forest genera such as Polyrhachis, Cataulacus, Dorylus and Paltothyreus occur in wetter savannas. Wetter savannas also support a range of arboreal genera, including Crematogaster, Tetraponera, Melissotarsus, Terataner, Atopomyrmex and Cataulacus—aside from Crematogaster, these genera are represented by relatively few species and so although richness is somewhat higher than in Australia it is nowhere near that of Brazil. A notable feature of the African savanna ant fauna is the unusually high generic diversity of large ponerines, including charismatic specialist termite predators of the genera Megaponera and Ophthalomopone (Fisher & Bolton, 2016). However, most of the above taxa are relatively low in diversity and make comparatively small contributions to overall ant biomass. The most diverse and abundant taxa are highly generalised ecologically, comprising species of the cosmopolitan genera Pheidole, Monomorium, Crematogaster and Tetramorium (Fisher & Bolton, 2016).

Notably, behaviourally dominant dolichoderines are totally absent from African savannas, which is in striking contrast to regions with warm climates throughout the rest of the world. However, southern African savannas feature behaviourally dominant species of the Anopolepis custodiens group (subfamily Formicinae), which can be highly abundant locally (Slingsby, 2017). In the field they are reminiscent of meat ants (Iridomyrmex purpureus group) in Australia and red wood ants (Formica rufa group) in temperate forests of the northern hemisphere. It is the only behaviourally dominant, ground-nesting formicine taxon occurring in tropical savannas anywhere.

Local ant species richness in African savannas is only moderate, with 20–50 species typically recorded per hectare (Mauda et al., 2018; Munyai & Foord, 2012; Parr et al., 2004; Yeo et al., 2017), which represents about half the number of species recorded in Australia using similar methodology. For example the Parr et al. (2004) study deployed the same grids of pitfall traps as routinely used in Australia to survey ants at 24 sites covering the southern half of Kruger National Park; repeat sampling always yielded <50 species and typically <30 species. The total African savanna fauna has not been systematically documented, and even an approximate estimate is not possible given that a substantial proportion of species remain undescribed and that collected specimens are scattered among many institutions. Robust comparative data are unavailable, but the senior author’s experience is that overall ant abundance in African savannas appears to be only moderately high (Table 2).

## 5 | RESPONSES TO ARIDITY AND FIRE

The contrasting functional composition of different savanna ant faunas due to different biogeographical histories produces contrasting responses to key factors influencing the structure and dynamics of savanna ecosystems. A primary factor is aridity (Bourlière, 1983). Mean annual rainfall in tropical savannas ranges from less than 500 mm (as occurs in much of Africa) to more than 1500 mm (as occurs in Cerrado and subcoastal northern Australia). Australian savannas occur across an especially pronounced rainfall gradient, from up to 2000 mm on the northern coast to less than 500 mm on the fringes of the central arid zone, with a concomitant simplification of vegetation structure and reduction in plant diversity (Bowman, 1996; Hutley et al., 2011). However, similarly, high ant diversity is maintained along this gradient (Andersen et al., 2015), which reflects the arid-adapted nature of the savanna fauna and the exceptionally high ant diversity of arid Australia.

The rainfall gradient in Brazilian cerrado extends down to only about 800 mm, but there is still a marked decline in ant species richness with decreasing rainfall, especially for rainfall in the warmest quarter (Vasconcelos et al., 2018). This is consistent with the forest-derived nature of the fauna, lacking a high diversity of arid-adapted elements. Comparable data are very limited for African savannas, but ant diversity also appears to decline markedly with decreasing rainfall (Parr et al., 2004), again reflecting a fauna without a high diversity of arid-adapted elements.

Frequent fire is another key factor driving savanna structure and dynamics, maintaining its open structure and in mesic regions preventing transition to forest (Bourlière, 1983). The primary effect of fire on ant communities is indirect through its effects on habitat structure, and the sensitivity of ant communities to fire depends on their responses to such structural changes, especially relating to vegetation openness (Andersen, 2019). Frequent fire in Australian savanna
savannas strongly favours thermophilic species at the expense of those preferring shady habitats, as illustrated by the contrasting responses of arid-adapted Iridomyrmex and forest-associated Oecophylla (Andersen, 2019). One would therefore expect that the arid-adapted nature of savanna communities in Australia would make them highly tolerant of frequent fire, which is indeed the case (Andersen et al., 2012). For example in a long-term fire experiment near Darwin, ant species composition was not significantly different between sites burnt annually or biennially, and there was substantial overlap between these sites and those burnt less frequently (Figure 2a).

In contrast to an arid-adapted fauna, one would expect a forest-derived fauna to be particularly sensitive to frequent fire because it is not strongly adapted to the open habitat created by it. This appears to be the case in Brazilian cerrado according to ant responses to experimental burning every 2, 4 years and remaining unburnt near Brasilia (Maravalhas & Vasconcelos, 2014). Each experimental fire regime resulted in compositionally distinct ant communities with no overlap (Figure 2b). This contrasts with responses of savanna ant communities to fire in Africa as well as in Australia. Results from a long-term fire experiment in South Africa’s Kruger National Park show little effect of varying fire frequency and season, other than long-term fire exclusion, even after 50 years (Figure 2c). Such resilience can be attributed to the highly generalised nature of the African fauna along with the long evolutionary history of fire in African savannas.

6 | CASCADING EVOLUTIONARY EFFECTS

The contrasting histories of different savanna regions appear to have had cascading effects on regional ant faunas that go beyond the direct effect of differences in original source taxa. There is strong circumstantial evidence that intercontinental differences in the abundance of behaviourally dominant dolichoderines have influenced the evolution of other taxa. For example species of the Pheidole fallax group are ecologically dominant ants in open habitats throughout the Neotropics, occurring in large colonies with large foraging ranges, having gracile morphology and rapid locomotion, and exhibiting aggressive behaviour. These are all the features of behaviourally dominant ants and are highly atypical for the cosmopolitan genus. The dominant cerrado species, P. oxyops, is most abundant at sites of moderate to relatively high canopy cover, where dominant dolichoderines are usually uncommon. Species of the African Pheidole megacephala group are similarly atypical for the genus and the senior author’s experience is that such species play an ecologically dominant role in savannas of Africa (and regrettably throughout much of the rest of the world as an introduced pest), where behaviourally dominant dolichoderines are lacking entirely. Australia—where behaviourally dominant dolichoderines are exceptionally abundant, has an extremely diverse Pheidole fauna (likely well over 500 species; A. Andersen, unpublished data), but none exhibit a syndrome of behavioural dominance.

Another indication of the evolutionary consequences of high behaviour dominance involves the shield ants of the genus Meranoplus, most species of which have elaborate defensive morphology and specialised behaviour that protects them from attack by aggressive ants (Andersen, 2006). The dorsal surface of their body forms an expansive shield and their heads have deep grooves that receive their antennae; when threatened the ants tuck their legs under the shield, retract their antennae, lie on their sides and play dead. The defensive morphology is taken to the extreme in the aptly named turtle ants of the M. testudineus group (Figure 3a,b). Meranoplus is widespread in the Old-World tropics but the vast majority of the hundreds of species occur in arid Australia (Andersen, 2006). These are the only ground-nesting ants anywhere in the world with such morphology. However, comparable morphology has evolved independently in two separate lineages of arboreal ants from tropical rainforest, Cephalotes (also commonly known as turtle ants; Figure 3c) in the Neotropics and Cataulacus (Figure 3d) in the Old-World tropics. Outside arid Australia, behaviourally dominance is most pronounced in the canopies of tropical rainforest (Blüthgen et al., 2000), making a clear association between a high level of behavioural dominance and the evolution of such elaborate defensive morphology. Several
species of *Meranoplus* occur in African savannas (Slingsby, 2017), but these have box-shaped mesosomas without such elaborate dorsal shields.

Competition is typically highest in the most productive environments (Grime, 1977), and so the contrasts in abundance of behaviourally dominant dolichoderines (and ants overall) are suggestive of major intercontinental differences in ant productivity. This points to ecological factors as important contributors to biogeographical differences in ant communities. Liquid carbohydrate is a critical resource for behaviourally dominant ants, providing the metabolic energy required for their high rates of activity and aggression (Blüthgen et al., 2000; Davidson et al., 2004). Dolichoderines and formicines have specialised proventricular structure that allows them to harvest high loads of liquid carbohydrate (Davidson et al., 2004). We hypothesise that intercontinental differences in ant productivity are driven by differences in the availability of plant-based liquid carbohydrate. The exceptional abundance of *Iridomyrmex* in arid Australia has been hypothesised to be due to an exceptional supply of honeydew (Andersen, 2003). In cerrado, extra-floral nectaries are a far more prominent source of liquid carbohydrate than is honeydew (Ribeiro et al., 2018) and they are a much less attractive resource for behaviourally dominant ants (Blüthgen et al., 2000). We hypothesise that the patchy distribution of behaviourally dominant dolichoderines in Brazil reflects a patchy distribution of honeydew-producing hemipterans. The complete absence of behaviourally dominant dolichoderines in African savannas is suggestive of an unusually low availability of liquid carbohydrate, especially honeydew. We hypothesise that the behavioural dominance of *Anoplolepis* is driven by access to honeydew underground from root-feeding hemipterans, a resource that is unavailable to most ants, and that its highly patchy distribution reflects that of subterranean Hemiptera.

**7 | CONCLUSION**

Most comparative studies of species assemblages in different biogeographical regions highlight ecological convergence under matched environments. However, we have shown that the contrasting geographical histories of tropical savannas in Australia, Brazil and Africa have led to profound differences in ant functional composition that result in markedly divergent responses to environmental stress (aridity) and disturbance (fire). Our study of savanna ants provides a graphical illustration of the potential importance of historical factors in community ecology and regional macroecology. Such importance is a direct function of the strength of phylogenetic niche conservatism (Peterson et al., 1999)—the stronger that niches are conserved phylogenetically, the stronger will be the imprint of historical biogeography on the functional composition of communities. Our study has identified two ant niches that appear to be particularly constrained by phylogenetic niche conservatism: thermophilia and granivory. The almost complete absence of harvester ants in Brazilian cerrado is particularly striking given that grass seeds are such a prominent resource in savannas.

We have shown that an understanding of biogeographical history is fundamental for understanding the nature of savanna ant communities and their macroecological patterns in different continents. These differences have significant implications for conservation management. The major intercontinental differences in responses of savanna ant faunas to vegetation openness point to major differences in sensitivity to any ecological disturbance that significantly affects
The same disturbance that promotes local diversity in the arid-adapted Australian fauna may reduce diversity in the forest-derived Brazilian fauna. An important lesson for conservation management is that the same management action can have different consequences for the same taxa in the same biome in different biogeographical regions (Wiens, 1991). Similarly, major differences in responses to aridity mean that communities in different continents are likely to have different responses to climate change. Diversity in the arid-adapted savanna ant fauna in Australia is likely to be far more resilient to any future declines in rainfall compared with the forest-derived Brazilian and highly generalised African savanna faunas.

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CONFLICT OF INTEREST
The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT
This paper is based entirely on previously published data and no new data sets were generated.

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