Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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CONTENTS

Geography of the highlands and escarpments

Diversity and endemism

Ant endemicity in the highlands and escarpments of Angola and Namibia (Hymenoptera, Formicidae)

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ABSTRACT
We present the results of a spatial analysis of available ant distribution records for Angola and Namibia, identifying those species that occur within the highlands and escarpments in these countries. Within this region we document 36 described species and 78 morphospecies, including several potentially undescribed species. From the data available, *Monomorium borlei* Santschi, 1937 is recognised as the one described species endemic to these highlands. The geographic location and topographic complexity of the highlands and escarpments of Angola and Namibia form a highly interesting area, but one that has been vastly undersampled; our results therefore may not reflect the potential endemic fauna of the region. The implementation of both intensive and extensive sampling in the region could reveal a rich ant fauna with a high endemicity potential.

Keywords: Angola, ants, endemism, escarpments, Formicidae, highlands, Namibia

INTRODUCTION

The highlands and escarpments of Angola and Namibia (HEAN) fall within a narrow band running north–south through western and central Angola and Namibia, stretching some 2,700 km between the Congo River in the north and the Orange River in the south. We restrict the focus of our study on two formations within this highland band: inselbergs (isolated mountains) higher than 1,000 masl, and plateaus (flat extensions) that range from 1,600 masl to 2,500 masl (Figure 1). Although they are known to be home to large numbers of endemic plant and vertebrate species, very little is known about the endemicity of invertebrates in these highlands. Here we analyse available data on a key invertebrate group, the ants, to establish what is known and what still needs to be determined for an assessment of their endemicity in this region.

Ant diversity generally follows one of three patterns across elevational gradients: (i) most common is a mid-elevation peak in diversity, but (ii) a purely monotonic decline with increasing altitude, or (iii) constant diversity over about the first 300 m followed by a decline with further increases in altitude have also been reported (Dunn *et al*. 2010, Szewczyk & McCain 2016, Subedi & Budha 2020). In all cases, however, above about 1,500 masl there is a continuous decline with increasing altitude, often dropping to near-zero around 2,500–3,000 masl, depending on whether forest (Longino *et al*. 2019) or grassland (Bishop *et al*. 2014) sites are considered. Accompanying the decline in species richness at high altitude, there is usually also turnover in species composition, sometimes with series of congeneric cryptic species spread along altitude gradients (Delsinne *et al*. 2012). As a result, a relatively small number of species, comprising mainly high-altitude specialists, persist above about 2,000 masl. Such species do not occur at lower altitudes, so their populations are often fragmented and distributed among isolated peaks.

Isolated mountains and high plateaus therefore offer the best chance to find relict and/or endemic ant species in the Afrotropical region. In the intervening lower-lying lands, it is not uncommon for most ant species to have wide distributions, ranging across the West African forests, the Congo Basin, or the savannas of eastern and southern Africa.

Confirming the presence of endemic species in the highlands, though, is extremely difficult. The relatively poor state of taxonomy in the region, combined with the lack of intensive ant sampling over most of the Afrotropics, make it difficult to establish whether or not an apparently restricted species is truly endemic to a small area.

The first obstacle is that, despite huge advances during the past 50 years (due in large part to the extraordinary efforts of Barry Bolton), the taxonomy of many ant genera in the Afrotropical region remains in a very poor state. Of the nine most diverse genera, six (*Camponotus* Mayr, 1861, *Carebara* Westwood,

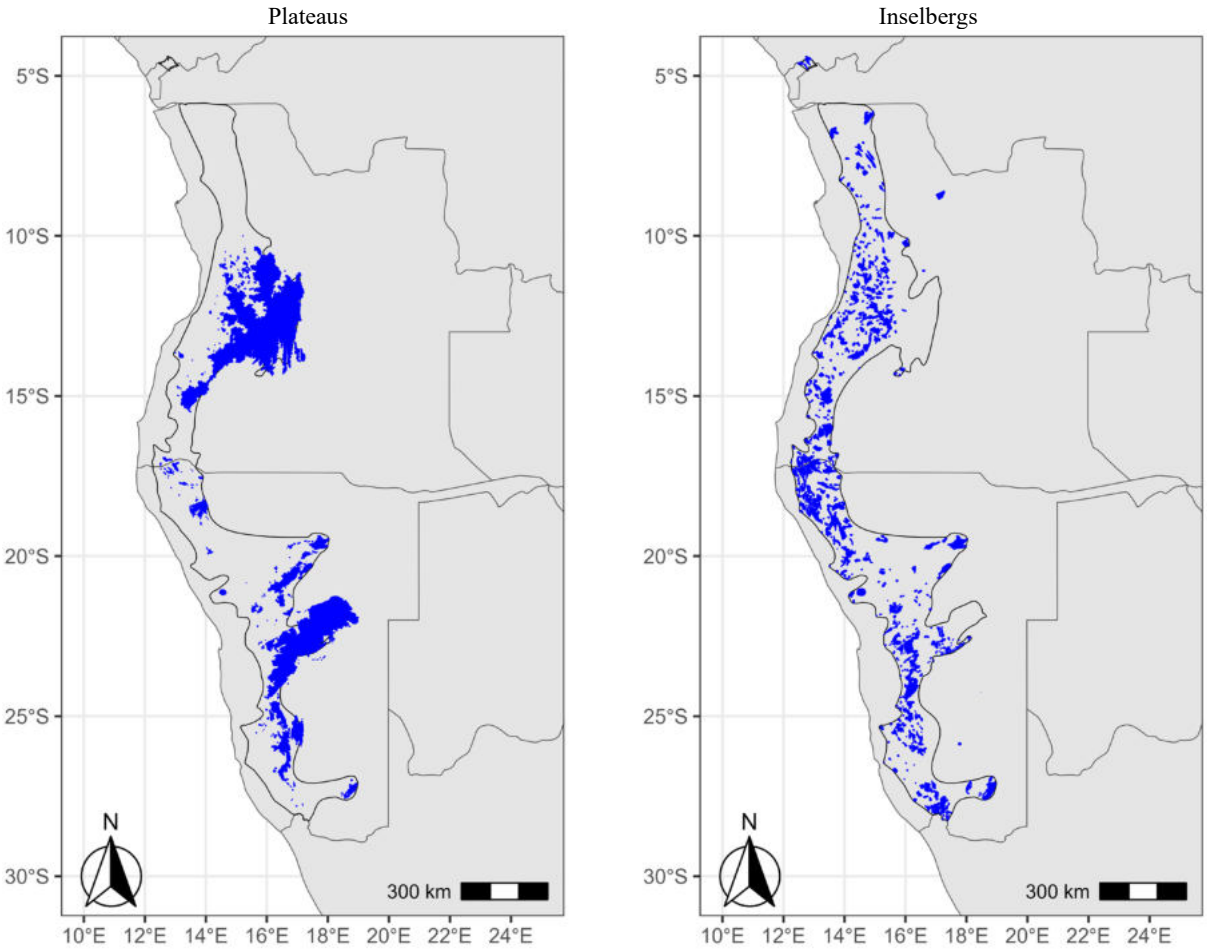

Figure 1: *Plateaus (left) and inselbergs (right), illustrated in blue, of the highlands and escarpments of Angola and Namibia (outlined in black).*

1840, *Crematogaster* Lund, 1831, *Dorylus* Fabricius, 1793, *Lepisiota* Santschi, 1926 and *Pheidole* Westwood, 1839) have never been revised except for small subgroups, and even the three that have undergone complete modern revisions (*Monomorium* Mayr, 1855, *Strumigenys* Smith, 1860 and *Tetramorium* Mayr, 1855) are each known to have several dozen newly discovered undescribed species.

This landscape has experienced some improvements, especially in the last 25 years. A major milestone was the publication by Fisher and Bolton (2016) offering a regional synopsis and keys to genus level for the Afrotropical and Malagasy ant faunas. Since 2000, other publications have provided revisions of entire genera or parts of genera and have added nine new genera: *Boloponera* (Fisher 2006), *Eburopone* (Borowiec 2016), *Erromyrma* (Fisher & Bolton 2016), *Feroponera* (Bolton & Fisher 2008), *Fisheropone* (Schmidt & Shattuck 2014), *Loboponera* (Bolton & Brown 2002), *Parvaponera* (Schmidt & Shattuck 2014), *Ravavy* (Fisher 2009) and *Vicinopone* (Bolton & Fisher 2012). From the start of 2000 to mid-2022, 250 new species have been added in 32 genera, the new species representing a 67% increase over the previously known total (373) in these genera (Bolton 2022).

Despite all these efforts, identifying Afrotropical ants to species level remains challenging, and sometimes impossible, for many genera. As a result, morphospecies are accumulating in collections, waiting to be described.

The second obstacle is a lack of information derived from both intensive and extensive sampling. A combination of both is required to properly assess levels of endemicity. A species known only from, or near its type locality might be: (i) truly restricted to a small region; (ii) widespread but not collected subsequent to its original discovery due to rarity, small size, cryptic lifestyle or a lack of (appropriate) sampling; or (iii) actually widespread and already collected elsewhere, but erroneously described several times under different names from different parts of its range (a common mistake in the late 1800s and early 1900s), and therefore might appear to represent a suite of range-restricted species. Also, the

opposite has already happened: species that were thought to be the same have been split, and what once were considered widespread species have each become a series of species with far smaller distributions, potentially including localised endemics. An example is the works on *Lasius* (Linneus, 1758) (e.g., Schär *et al*. 2022), including the endemic mountain ant *Lasius balearicus* Talavera, Espadaler & Vila (Talavera *et al*. 2015), previously identified as *L. niger* (Linneus, 1758). Similar patterns can result from misidentifications.

Which of these scenarios applies to a given species can be determined only with adequate distribution data, the development of well-resolved taxonomy and the cultivation of taxonomic expertise within the region.

Although study of the Afrotropical ant fauna has a long history, survey coverage of the region is extremely patchy. As a continent, Africa has possibly the most poorly known ant fauna on Earth. Most of the historical expeditions are well known, for example, Angola (Santschi), Mt Nimba in Guinea and Côte d'Ivoire (Bernard), Imatong Mountains in South Sudan and Uganda (Weber), Ghana (Bolton), Nigeria (Bolton & Taylor) and Democratic Republic of the Congo (previously Belgian Congo; Wheeler). However, these were conducted more than 50 years ago and were quite limited in extent, duration and collecting methodology. Modern expeditions have included other interesting locations, for example, Angola (Brian L Fisher (BLF) and Peter G Hawkes (PGH)), Central African Republic (BLF), Gabon (BLF), Gambia (Kiko Gómez (KG)), Ghana (BLF, Flávia Esteves (FAE), KG and PGH), Ivory Coast (Kolo Yeo and KG), Kenya (Francisco Hita Garcia and Georg Fischer), Mozambique (BLF, FAE and PGH), Namibia (PGH), Rwanda (KG, Wouter Dekoninck and Venuste Nsengimana), Senegal (KG), South Africa (PGH), Tanzania (PGH), Zambia (BLF, PGH and John LaPolla) and Zimbabwe (PGH), but were also mostly of limited extent and covered only a small proportion of African countries. These expeditions have, however, revealed an extremely rich biodiversity, partially due to the inclusion of modern collecting techniques (e.g., mini-Winkler leaf-litter extraction and canopy fogging) as well as more intense, quantified and replicated sampling.

Even with these modern expeditions, the Congo Basin remains undersampled, as do wide expanses of southwestern Africa, including Angola and much of Namibia. The intensive regional sampling that would be required to evaluate endemicity in the HEAN is entirely lacking. Even in more intensively surveyed countries such as South Africa, where the total number of species recorded is higher than any other non-tropical area of equivalent size, many new species continue to be discovered annually and the distributions of most described species are largely unknown (PG Hawkes, unpublished data).

The main consequence of these two factors is that the actual distribution of most Afrotropical ant species is unknown. For this reason, declaring a species 'endemic' is often difficult to justify, even when a name can be applied to a specimen, or it can be recognised as a new species. This is particularly true in the highlands and escarpments of Angola and Namibia.

MATERIALS AND METHODS

To assess ant species richness from the HEAN, we compiled specimen records from Namibia and Angola from the online resources AntWeb (AntWeb 2021) and AntMaps (Janicki *et al*. 2016, Guénard *et al*. 2017, AntMaps 2021), our own collections and available publications (Santschi 1930, Robertson 2000). From these resources, we compiled 7,529 specimen records for both countries and georeferenced localities when needed. We then performed spatial queries against topography with the sf package in R (Pebesma 2018) to select the species present in the HEAN (Table 1, Figure 2). This list was then checked against global species distributions available at AntMaps (Janicki *et al*. 2016, Guénard *et al*. 2017, AntMaps 2021) to find rare or endemic species.

RESULTS

Data in the studied localities are extremely scarce (Table 1, Figure 2) and, based on our spatial assessment, only 36 described species were recorded from the HEAN:

Acropyga arnoldi Santschi, 1926
Anochetus levaillanti Emery, 1895
Anoplolepis steingroeveri (Forel, 1894)
Bondroitia lujae (Forel, 1909)
Camponotus vestitus (Smith, 1858)
Cardiocondyla emeryi Forel, 1881
Crematogaster melanogaster Emery, 1895
Euponera brunoi (Forel, 1913)*
Lepisiota monardi (Santschi, 1930)
Megaponera analis termitivora (Santschi, 1930)
Melissotarsus emeryi Forel, 1907
Messor denticornis Forel, 1910
Monomorium australe Emery, 1886
Monomorium borlei Santschi, 1937
Monomorium esharre Bolton, 1987
Monomorium exiguum Forel, 1894
Monomorium fugelanum Bolton, 1987
Monomorium havilandi Forel, 1910
Monomorium schultzei Forel, 1910
Monomorium vatranum Bolton, 1987
Monomorium viator Santschi, 1923
Myrmicaria irregularis Santschi, 1925

Myrmicaria natalensis obscuriceps Santschi, 1937
Ocymyrmex velox Santschi, 1932
Paratrechina zanjensis LaPolla *et al.*, 2013
Pheidole megacephala duplex Santschi, 1937
Pheidole tenuinodis Mayr, 1901
Platythyrea cribrinodis (Gerstäcker, 1859)
Plectroctena subterranea Arnold, 1915
Promyopias silvestrii (Santschi, 1914)
Tapinoma danitschi Forel, 1915
Tetramorium clunum Forel, 1913
Tetramorium khyarum Bolton, 1980
Tetramorium rufescens Stitz, 1923
Tetramorium subcoecum Forel, 1907
Trichomyrmex robustior (Forel, 1892)

* Listed as *Euponera sharpi* Forel, 1901, which is an Indomalayan species, but almost certainly represents a misidentification of the very similar and widespread Afrotropical species, *Euponera brunoi* (Forel, 1913).

Table 1: *Total numbers of ant specimen records compiled from all resources (online, authors' collections and publications), and those restricted to plateaus and inselbergs within the highlands and escarpments of Angola and Namibia.*

	Namibia	Angola	Total
All records	5,524	2,005	7,529
Plateaus	985	523	1,508
Inselbergs	810	271	1,081

In addition, 78 morphospecies, some of which may turn out to be described species, but many of which are likely to be new to science, have been recorded within the HEAN, listed by genus in Table 2.

With the limited data available, one described species is currently known from within the HEAN and nowhere else: *Monomorium borlei* (Figure 3) from Sangueve, Angola (13.89S, 15.82E). There are three good candidates to be new species in the genera *Anochetus*, *Lioponera* and *Strumigenys*. However, considering that Robertson (2000) found nine *Leptanilla* species on the Brandberg in Namibia, and in 2023 there are still only three described *Leptanilla*

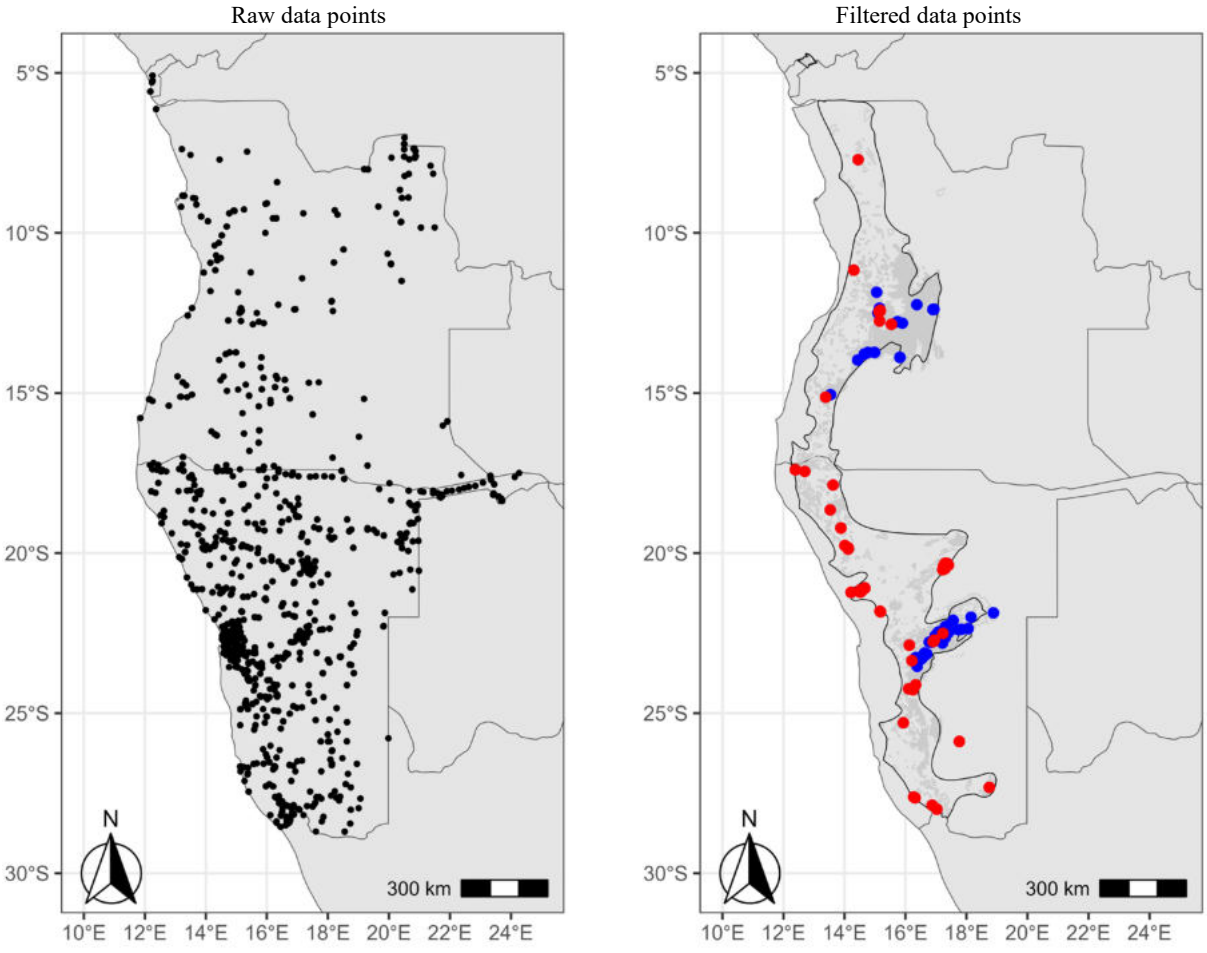

Figure 2: *Raw ant data for Angola and Namibia (left) and records filtered to the inselbergs (red dots) and plateaus (blue dots) of the highlands and escarpments of Angola and Namibia (right).*

Table 2: *Numbers of morphospecies of ants recorded in the highlands and escarpments of Angola and Namibia.*

Genus	Number of morphospecies
Aenictus	1
Anillomyrma	1
Anochetus	2
Baracidris	1
Bothroponera	2
Calyptomyrmex	1
Camponotus	8
Cardiocondyla	1
Carebara	2
Crematogaster	2
Dorylus	1
Euponera	1
Hypoponera	7
Leptanilla	10
Leptogenys	1
Lioponera	1
Megaponera	1
Mesoponera	1
Monomorium	11
Nylanderia	1
Paraparatrechina	1
Pheidole	4
Plagiolepis	2
Polyrhachis	1
Solenopsis	2
Stigmatomma	1
Strumigenys	1
Tetramorium	10

species in the Afrotropical region (*L. africana* Baroni Urbani, 1977, *L. australis* Baroni Urbani, 1977 and *L. boltoni* Baroni Urbani, 1977, none of which has been recorded from Angola or Namibia), clearly a minimum of six undescribed *Leptanilla* species inhabit the Brandberg alone. It is likely that there are many endemic ant species within the inselbergs and plateaus of the HEAN. At present, these are hidden within unidentified material collected to date, or have never been sampled and are awaiting discovery.

Monomorium borlei is known only from the type series collected at about 1,600 masl by Monard in 1933, and there is no information on its biology or habitat in the original description by Santschi (1937). For this, and any other species identified as being candidate endemics, studies of habitat requirements and biology would help to determine their likely sensitivity to influences such as habitat transformation and climate change.

DISCUSSION

Little is known about the ant fauna of Angola and Namibia. AntMaps (2021) listed 308 indigenous ant taxa for Angola and 194 for Namibia. Combining the lists gave a total of 440 species and subspecies for the two countries, with only 62 species common to both. In comparison, South Africa, with a land area of 1,221 million km^2, just over half the combined area

Figure 3: *Holotype of* Monomorium borlei *Santschi, to date known only from Sangueve, Angola. A) Full-face view, B) profile view, C) dorsal view and D) labels. Images of CASENT0913564 photographed by Z Lieberman, from AntWeb (2021).*

(2,071 million km^2) of Angola and Namibia, has a far higher total with 764 species and subspecies. To develop a clearer picture of both true diversity and endemicity of the ant fauna of Angola and Namibia, more intensive long-term sampling expeditions at both local and regional levels are needed. This needs to be combined with thorough taxonomic investigations of material that cannot be identified using currently available identification resources.

Southwestern Africa has been dramatically under-sampled, so our knowledge of both the overall diversity and the degree of endemicity of the ant fauna of the HEAN is extremely limited. Based on the available data we think that these highlands and escarpments have the potential to house a rich endemic fauna. Indeed, despite limited sampling, several species currently await formal description. Our findings agree with those of Robertson (2000) on the Brandberg (Namibia), as he found that even in ant genera with well-developed taxonomy, 30% of the species were potentially new to science. Interestingly though, Kass *et al*. (2022) predict that the northern, but not the southern, parts of the HEAN are expected to become a centre of ant species richness under increased sampling. Additionally, apart from a small area around Windhoek in central Namibia, no area of this region is predicted to become a centre of ant rarity or endemicity, and the current very small areas of empirical ant rarity within the HEAN are mostly predicted to fall away with further sampling. Extensive and intensive sampling of the region would provide interesting tests of these predictions.

Intensive ant-sampling expeditions, especially in the least explored areas, such as the high mountains and plateaus, would also massively increase the known biodiversity. However, this research should ideally be complemented by surveys at mid and low elevations in the surrounding areas to determine which of the species present at higher altitudes also occur lower down and are likely to be widespread.

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