# Tenebrionid Beetle Diversity Increases with Aridity Across the Namib Desert

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Keywords: biodiversity, abundance, detritivores, rainfall variability, darkling beetles, time niches.

## Abstract

Darkling beetles (Tenebrionidae: Coleoptera) are commonly associated with hot arid lands worldwide. In southern Africa, the number of species is reported to increase along the east-to-west gradient in aridity. The highest diversity is found in the Namib Desert, which occupies a 100 km by 2,000 km hyperarid strip along the west coast, from South Africa to the south into southern Angola. We sought to confirm this regional diversity pattern by collecting tenebrionids with pitfall traps at five SASSCAL observatories along a transect stretching from the hyperarid desert interior (MAP 25 mm, CV 130%) to semiarid conditions 260 km inland (MAP 343 mm, CV 36%). We collected tenebrionids during 11–20 month-long trapping sessions and identified species from seven tenebrionid tribes and subtribes which were previously recorded in half-degree squares across the arid western half of the southern Africa region. Even though there was a six-fold decrease in tenebrionid abundance, all diversity indices increased with increasing aridity (e.g. α-diversity inland: 1.40, desert interior 3.71). Community structure was very different in the interior highland plateau compared to the desert (ß-diversity 0.52–0.69), while adjacent sites in the desert differed less (ß-diversity 0.26–0.29). In the desert, tenebrionids were recorded most frequently at sheltered sites where windblown detritus is trapped, while in the interior, more were recorded away from sheltered locations where they might encounter sit-and-wait predators. Geomorphological processes and heterogeneous moisture conditions over space and time could explain how so many Namib Desert endemic tenebrionids evolved and coexist.

## Introduction

Darkling beetles (Coleoptera: Tenebrionidae) played a key role in the motivation for establishing a field station at Gobabeb in 1962. It was Charles Koch's extensive expeditions to the Namib, between 1948–1959 in pursuit of these beetles, that led him and his team to Gobabeb (Koch 1962). Their importance for research at Gobabeb is reflected in the fact that tenebrionids have been the subject of one in eight publications of the Gobabeb Namib Research Institute since its inception (Henschel & Lancaster 2013).

Research on Namib tenebrionids has since expanded far beyond taxonomy, biogeography and diversity studies to include life history, behaviour, physiology, ecology and ecophysiology in pursuit of answers to questions concerning these beetles' abilities to thrive in hyperarid conditions (Holm 1970; Seely 1973; Hamilton & Seely 1976; Seely & Hamilton 1976; Wharton & Seely 1982; McClain et al. 1985; Hanrahan & Seely 1990; Nicolson 1990; Rasmussen et al. 1991; Roberts 1991; Nicolson 1992; Ward & Seely 1996; Rössl 2000; Cloudsley-Thompson 2001; Parenzee 2001; Mitchell et al. 2020; Duncan 2021; Henschel 2021).

Namib tenebrionids are conspicuous, large, apterous omnivores—essentially detritivores—that integrate factors such as the availability of detritus and various soil characteristics such as moisture, hardness, and grain size composition (Koch 1961; Penrith 1979; Prendini 2001). They have unusual capabilities to obtain moisture and food from sources not conventionally accessible to many other surface-active animals. They can withstand long periods without these resources, even at high-temperature extremes, and actively search for scarce resources. They are generally long-lived with lifespans of several years, mainly as adults that can repeatedly reproduce with small clutches whenever resources permit.

There are over 300 tenebrionid species in the Namib, 200 of them endemic (Koch 1962; Schulze 1974; Penrith 1977, 1979; Endrödy-Younga 1982). Within walking distance of the Gobabeb Namib Research Institute field station, which is located in the most arid part of the desert, there are at least 82 species of tenebrionids (Henschel et al. 2003), and 54 at one site on the gravel plains (Henschel 2021). This diversity is especially remarkable because of the Namib's extremely low productivity (Seely & Louw 1980), more so considering how different it is for other desert taxa studied across this climatic gradient. For example, the highest levels of endemism in ants (Marsh 1986), moths (Mey 2010), plants (Yeaton 1988; Jürgens et al. 2013), birds and reptiles are associated with the Great Escarpment beyond the eastern border of the Namib (Simmons et al. 1998).

A frequently-posed question concerns why the diversity of tenebrionids increases with aridity across southern Africa (Koch 1962; Holm & Scholtz 1980; Crawford & Seely 1987). This question has yet to be answered satisfactorily. To better understand the relationship of the Namib tenebrionid community with aridity, we examined the general pattern of tenebrionid diversity across the arid western half of the southern African region (AWSAR, Table 1). We also examined tenebrionid diversity in more detail across the central Namib Desert (CND). Based on the pulse-reserve dynamics associated with the Namib (Henschel 2021), we predicted that 1) tenebrionid diversity correlates with rainfall variability, which correlates with aridity; and 2) tenebrionid abundance decreases with aridity due to declining productivity.

# Methods

## General diversity pattern

The distribution of tenebrionid species across the AWSAR between latitude 13–34.5°S and longitude 11.5–25.5°E was compiled from literature where overviews of their distribution were readily accessible from museum records (Koch 1955; De Moor 1970; Penrith 1975, 1977, 1979, 1980, 1981a, b, c, 1982a, b, c, 1983a, b, 1984, 1986a, b, c, 1987; Penrith & Endrödy-Younga 1994; Endrödy-Younga 1996, 2000). The tribes/subtribes for which this was possible, referred to as focal taxa, were Adesmiini, Caenocrypticini, Cryptochilini, Sepidiini: Molurina (in part), Sepidiini: Trachynotina (in part), Pedinini: Platynotina, and Zophosini. The number of focal species recorded in each half-degree latitude and longitude square (HDS) was correlated with the mean annual precipitation (MAP) obtained from WorldClim for each HDS (Fick & Hijmans 2017).

To compensate for the uneven sampling of tenebrionids, the distribution of each focal species across HDS cells was interpolated by broadening the footprint of a record and

*Table 1: List of acronyms*

| Acronym | Meaning |
|---|---|
| AWSAR | arid western half of the southern African region |
| CND | central Namib Desert |
| CV | coefficient of variation |
| HDS | half degree square of latitude and longitude |
| MAP | mean annual precipitation |
| SASSCAL | Southern African Science Service Centre for Climate Change and Adaptive Land Management |

bridging small locality gaps within the AWSAR boundaries. The linear interpolation process used a rule-based cellular automaton in Microsoft-Excel with two steps. The first extended occupancy to blank HDS cells adjacent to occupied cells. The second used the outcome of the first step to test whether a blank cell was located between two occupied cells. If so, the intervening blank cell was listed as occupied. The outcome yielded a putative distribution map for each species. Overlaying the 579 putative distribution maps of focal species provided a map of potential diversity at a spatial resolution of HDS cells.

## Detailed diversity pattern compared to ecological parameters

We examined the diversity trends and community patterns of focal taxa in greater detail across a 260 km long climatic gradient from near the coast of the CND eastwards across the Great Escarpment to the highland plateau, Khomashochland, in Namibia. We focused on the differences in hydrological regimes in terms of quantity and frequency of free moisture and primary productivity across this transect. Using pitfall traps, we examined beetle populations at five study sites (observatories) located at about 23°S latitude and half a degree longitude apart along a west to east transect. The transect represents a strong precipitation gradient, with extreme aridity at the western end on the coast (although tempered by frequent fogs for up to ~80 km inland, i.e. the two most western observatories) and a semiarid climate at the eastern end. At each site, we compared records from traps placed in the open versus in the proximity of shelter in different vegetation communities at each site (Jürgens et al. 2010).

The diversity pattern and underlying ecological factors were examined more closely by investigating tenebrionid communities along a transect across the CND. This study was conducted between 2004–2009 at five SASSCAL observatories (Kleinberg, Gobabeb, Ganab, Rooisand, Claratal) (Jürgens et al. 2010), distributed half a degree longitude apart at about 23°S latitude along a climatic gradient reaching from the foggy Atlantic coast (altitude 188 m a.s.l.) to the west across the CND plains, over the Great Escarpment, to the Khomashochland of the Namibian Highland Plateau (altitude 1865 m a.s.l.) to the east (Figure 1, Table 2).

These five sites straddle different climatic zones, which were chosen using data from a minimum of 23 years of data (maximum 58 years) obtained from: the Namibian Meteorological Services; Gobabeb Namib Research Institute; (Lancaster et al. (1984); SASSCAL weathernet (http://www.sasscalweathernet.org/index.php?MIsoCode=NA). The precipitation gradient across the study area (Table 2) stretches from Walvis Bay on the coast (Mean Annual Precipitation MAP=10.4 mm, CV=157%) to Windhoek on the highlands 260 km inland (371.4 mm, 35%).

At each observatory, we placed three roof-covered pitfall traps within each of six grid hectares chosen as focal study sites (Table 2). One covered trap was placed into or adjacent to shelter on the south side of shrubs or rocks or a south-facing slope (hereafter referred to as "sheltered traps"; Figure 2). A second trap was unsheltered on open ground

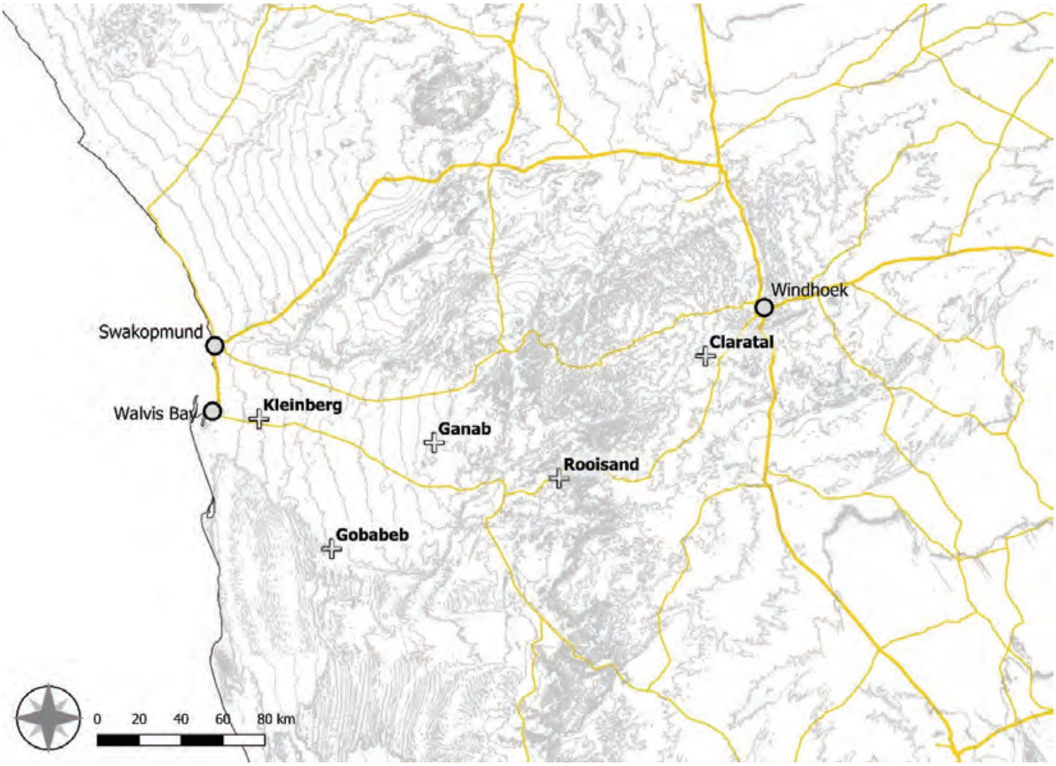

*Figure 1: The central Namib part of the study area, showing the locations of the five SASSCAL observatories where we collected data across the Namib Desert (Kleinberg, Gobabeb, Ganab), at the base of the escarpment (Rooisand), and on the highland plateau (Claratal)*

with north-facing slope. A third trap was placed in the open with south-facing slope, a short distance from shelter. The pitfall traps of 20 cm depth and 10 cm diameter contained mono-ethylene glycol as a preservative (Henschel et al. 2010). Standard trapping sessions were about a month long and were operated at irregular intervals as practically and logistically possible (Figure SM2). When not collecting, traps were closed with lids pegged into the ground. Collected specimens were sorted to order level in the laboratory and preserved in alcohol. Tenebrionid beetles were later separated from other beetles and were identified, ideally by comparing them to expert-verified voucher specimens or museum collections where available.

A list of focal species expected to occur at the observatories was compiled from the museum dataset mentioned above. Since previous records were not collected at exactly the current locations, the potential occurrence of a focal taxon in the adjacent half-degree latitude and longitude and small locality gaps between records was also considered. However, ultra-psammophilous species known to be confined to the Namib Sand Sea were excluded. For this reason, distribution data for Gobabeb were from the half-degree square north

*Table 2: Characterisation of the study sites in terms of location, rainfall (MAP), variability of rainfall (CV), fog nights per annum, and habitat characteristics in the six focal grid hectares in terms of the ground substrate (Gravel, Rocks, Sand), drainage lines (None, Lines), and shrubs (Bare, Few, Dense)*

| Characteristic | Kleinberg | Gobabeb | Ganab | Rooisand | Claratal |
|---|---|---|---|---|---|
| latitude | 22.989838 | 23.532409 | 23.12182 | 23.294542 | 22.779382 |
| longitude | 14.725183 | 15.04689 | 15.53844 | 16.104978 | 16.774852 |
| distance from coast (km) | 21 | 54 | 108 | 167 | 230 |
| altitude (masl) | 188 | 419 | 995 | 1160 | 1865 |
| aridity index[1] | 0.011 | 0.016 | 0.074 | 0.11 | 0.21 |
| MAP (mm) | 15.5 | 25.3 | 57.2 | 111.3 | 343.2 |
| CV of MAP (%) | 117% | 130% | 111% | 54% | 36% |
| n for MAP (y) | 38 | 58 | 39 | 26 | 55 |
| fog nights | 76 | 37 | 3 | 0 | 0 |
| plant richness[2] | 4 | 33 | 53 | 95 | 205 |
| lichen richness[3] | 12 | 5 | 1 | 20 | 14 |
| Lepidoptera richness[4] | - | 45 | 149 | 131 | 227 |
| grid hectare 1 | G-N-D | R-N-D | G-N-D | R-N-D | G-N-D |
| grid hectare 2 | G-N-D | R-N-D | G-N-D | R-N-D | S-L-D |
| grid hectare 3 | G-N-B | G-N-B | G-N-D | S-L-D | G-N-D |
| grid hectare 4 | G-L-D | G-N-B | S-L-F | G-N-D | R-N-D |
| grid hectare 5 | G-L-D | R-N-F | S-L-F | R-N-D | S-L-D |
| grid hectare 6 | G-N-B | R-N-F | G-N-D | G-N-D | G-N-D |
| ground cover[1] | 50% lichen | 0.2% grass | 2.2% grass | 7.6% grass | 18% grass |

[1] Trabucco & Zomer (2018).
[2] Schmiedel et al. (2010), Strohbach and Luther-Mosebach in (Jürgens et al., 2010).
[3] Wirth et al. (2010), Zedda and Rambold in Jürgens et al. (2010).
[4] Mey (2010).

(gravel plains), not south (dunes) of the Gobabeb observatory. Since we only used pitfall traps to record tenebrionids, we did not expect to collect all species that occur at a site as many more species are typically recorded where multiple methods are applied, especially when these include visual searching (Henschel et al. 2010).

We analysed only trapped tenebrionids listed as potential species from focal taxa (Table SM1). In other words, when referring to tenebrionids from the current study area, this should be understood as a subset of focal species from the 100 tenebrionid species that potentially occurred there, based on previous records from the tribes/subtribes Adesmiini, Caenocrypticini, Cryptochilini, Sepidiini: Molurina (in part), Sepidiini: Trachynotina (in

*Figure 2: Pitfall traps were placed either in sheltered locations near shrubs or rocks (left) or unsheltered in the open (right) with a third trap at a short distance from shelter. The examples shown are from the Gobabeb Observatory.*

part), Pedinini: Platynotina, and Zophosini (Table SM1). Other tenebrionids that could not be reliably identified to species level were grouped with other beetles and not analysed in detail.

Observatories were compared in terms of various diversity indices (Table 3) using only (a) species observed in the current study; (b) previously documented species; and (c) species with potential occurrence, as explained above. Abundance data, standardised relative to effort, were tracked in terms of season (early summer Oct-Dec, late summer Jan-Mar, early winter Apr-Jun, late winter Jul-Sep), shelter (sheltered, near shelter, fully exposed), and microhabitat conditions such as substrate characteristics, topographical features of water runoff (drainage lines), and the relative density of perennial plants. Species accumulation curves were used to indicate how the number of recorded species related to the trapping effort (Thompson et al. 2003) so the current data could be viewed in the context of the regional diversity. The asymptote of this curve, i.e. the number of species at each site, was calculated using the first-order jackknife estimator of species richness (Smith & Pontius 2006) (Table 3).

*Table 3: Diversity indices as applied in this study*

| Property | Abbreviation, Equation, Definition |
|---|---|
| Species richness | S = number of species at a defined location |
| $S_{\text{documented}}$ | Species previously recorded in the half-degree square (HDS) of Observatory[+] |
| $S_{\text{potential}}$ | Species recorded in adjacent HDS or small gaps between records (excluding ultra-psammophilous species)[+] |
| $S_{\text{observed}}$ | Tenebrionids of focal taxa identified at observatories in the current study |
| $S_{\text{jackknife}}$ | $S_{\text{jackknife}}=S_{\text{observed}}+((n-1)/n)(\Sigma r_i)$, where n=number of samples, $r_i$=species unique to only one sample[#] |
| Simpson diversity | $\lambda=\Sigma(n_i(n_i-1)/N(N-1)))$, and $n_i$ = abundance of species i, N = total abundance |
| Shannon evenness | $J'=H'/\ln(S)$ where $H' = -\text{sum}(P_i \times \ln P_i)$, and $P_i$ = proportion of species i |
| Fisher's α | $\alpha=N(1-x)/x$, where x varies with S/N* |
| ß-diversity | $ß_T=(g(H)+l(H))/2a$, where g(H)=species gained, l(H)=species lost, a=average S (ß-diversity is an index of change in species composition between sites) |

[+] (Koch, 1955; Penrith, 1977, 1979, 1980, 1981a, b, c, 1982b, c, 1983a, b, 1984, 1986a, b, c, 1987; Penrith & Endrödy-Younga, 1994; Endrödy-Younga, 2000).

[#] (Smith & Pontius, 2006).

[*] (Magurran, 1991; Hayek & Buzas, 1997).

# Results

## General Diversity Pattern

There were 579 focal species of tenebrionids across the AWSAR. The patchiness of diversity records (Figure 3a) reflects sampling bias that was not quantified, but its effects could be reduced by interpolation (Figure 3b). HDS cells with zero species records were probably not sampled. The collective distribution of tenebrionids in HDS cells across the AWSAR was negatively correlated ($r = -0.49$, $p<0.05$) with MAP (Figures 3 & 4). Most (62%) of cells with the highest quartile of diversity were located in the lowest quartile of MAP ($\chi^2 = 126$, $p<0.001$). Half of the top 10-percentiles of diversity (19-38 species) occurred where MAP was <122 mm.

Diversity was significantly higher in the Namib Desert, which covers 11% of the AWSAR, than in the remaining 89% of the area ($\chi^2 = 684$, $p<0.001$). The Namib contained 334 (52%) of the focal species, at least 177 (59%) of which were endemic.

## Abundance and Diversity across the Central Namib

Beetle abundance was lowest at Gobabeb, increasing eastwards and westwards (Table 4). Records of museum collections (Table SM1) indicated that the number of species previously recorded in the vicinity of observatories in the CND (Kleinberg, Gobabeb, Ganab)

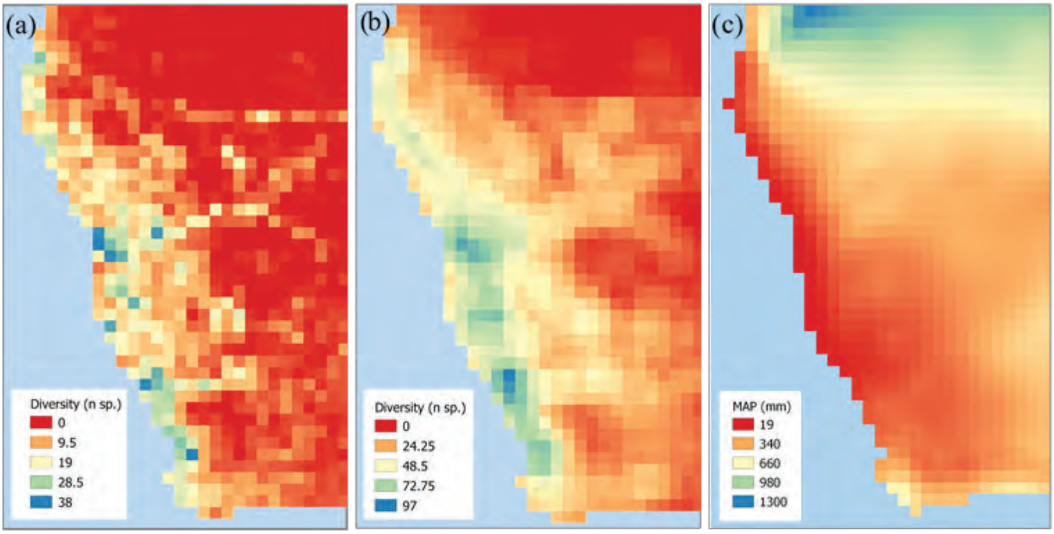

*Figure 3: Map of half degree latitude/longitude cells across the AWSAR showing (a) the actual diversity of tenebrionids, (b) the potential diversity of tenebrionids, and (c) mean annual precipitation (MAP)*

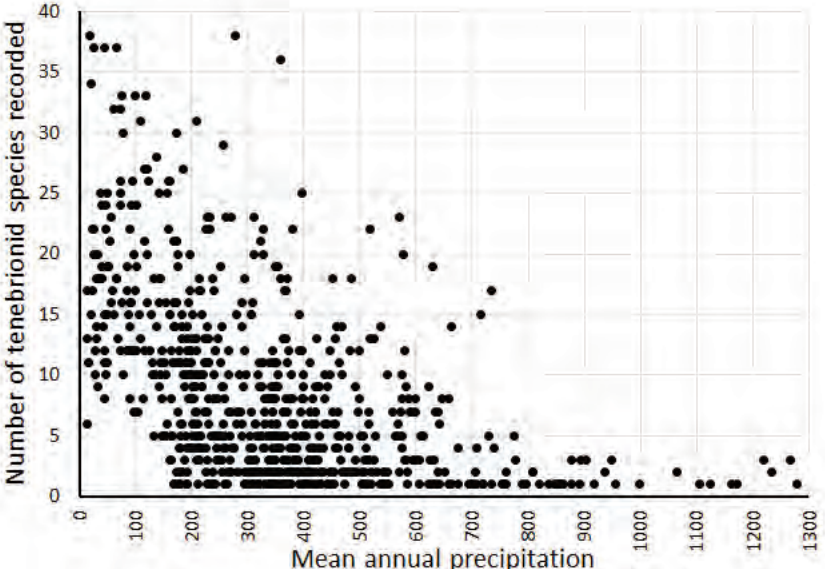

*Figure 4: Number of focal species recorded vs MAP in HDS across the AWSAR*

*Table 4: Abundance, species richness and diversity of tenebrionid beetles of focal species currently observed or collected at the five study sites or previously recorded in the vicinity. Indices are explained in Table 2.*

| Measure | Total | Kleinberg | Gobabeb | Ganab | Rooisand | Claratal |
|---|---|---|---|---|---|---|
| Distance from coast (km) | | 21 | 54 | 108 | 167 | 230 |
| Trapping Sessions (Samples) | | 18 | 20 | 16 | 14 | 11 |
| Total Abundance | | | | | | |
| Other beetles | 16512 | 270 | 122 | 2504 | 12227 | 1389 |
| Tenebrionids | 11119 | 2872 | 1062 | 1729 | 1802 | 3654 |
| Mean±SE per session | | 160±45 | 53±11 | 108±27 | 129±47 | 332±137 |
| Species Richness | | | | | | |
| $S_{potential}$ | 101 | 58 | 66 | 60 | 65 | 65 |
| $S_{documented}$ | 64 | 30 | 35 | 26 | 18 | 21 |
| $S_{observed}$ | 30 | 13 | 21 | 22 | 17 | 11 |
| $S_{jackknife}$ | | 18 | 27 | 26 | 22 | 14 |
| Diversity | | | | | | |
| Simpson λ | 0.12 | 0.50 | 0.19 | 0.26 | 0.32 | 0.40 |
| evenness J’ | 0.75 | 0.33 | 0.69 | 0.61 | 0.60 | 0.52 |
| Fisher’s α | 3.75 | 1.76 | 3.71 | 3.55 | 2.60 | 1.40 |
| ß-diversity | | | | | | |
| Kleinberg | | - | | | | |
| Gobabeb | | 0.29 | - | | | |
| Ganab | | 0.37 | 0.26 | - | | |
| Rooisand | | 0.53 | 0.37 | 0.28 | - | |
| Claratal | | 0.58 | 0.69 | 0.52 | 0.57 | - |

was higher (26–35) than further inland (18–21). The trend in diversity roughly formed a mirror image of the trend in abundance, with the highest species richness (observed and jackknifed) in the two middle sites and a decline both westwards and eastwards (Table 4). However, at Kleinberg, near the coast, the species accumulation curve did not level out (Figure 5). This site may thus have more rare species, as was also indicated by museum records of the focal taxonomic groups (Table SM1). The first order Jackknife estimates of species richness indicated that with the current methods, 3–6 more species should have been recorded at each site (Table 4).

All diversity indices were highest at Gobabeb, the next highest at Ganab, and declining stepwise eastwards (Table 4). At Kleinberg, where 96% of the samples comprised *Zophosis amabilis* and *Cauricara eburnea*, both diversity and evenness were generally low despite the high richness (Table 5). By contrast, 95% of the total abundance was

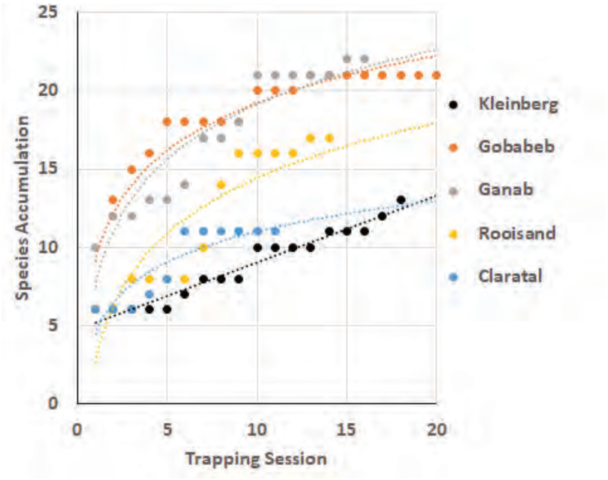

*Figure 5: Species accumulation curves for the five study sites, showing logarithmic trendlines except for Kleinberg, where the trendline was linear, reflecting that species accumulation was not beginning to show saturation over 18 trapping sessions*

reached with 11 species at Gobabeb and Ganab, nine at Rooisand, and five at Claratal (Table 5).

While abundance was positively correlated with MAP (r=0.80), α-diversity correlated negatively with MAP (r=-0.62) and positively with the CV of MAP (r=0.62) (Figure 6). The previously recorded number of species ($S_{documented}$ in Table 4) correlated even more strongly with MAP-CV (r=0.90) and was also negatively correlated with MAP (r=-0.63).

## Trapping Location, Shelter and Season

The trapping records were unevenly spread across grids ($\chi^2$: 168-969, df=5, p<0.001), degree of shelter ($\chi^2$: 106-665, df=2, p<0.001), and season ($\chi^2$: 105-696, df=3, p<0.001) (Figure 7). Of the three traps in each grid, the highest capture rates were in the sheltered traps at all sites except Claratal, where most captures were in unsheltered traps out in the open without a roof (Figure 7). At Kleinberg, the highest capture rates were in grids devoid of perennial vegetation or drainage lines, i.e. open gravel plains where the lichen cover was highest (Table 2, Figure 7). In contrast, at Gobabeb, the capture rate was lowest on the open plains without shrubs or rocks, intermediate on granite rocks where there were shrubs and highest on a quartz hill, where shelter and potential food in terms of accumulated detritus and hypolithic cryptophytes were highest. At Ganab, tenebrionid abundance was highest in a grid with a shrub-lined wash. At Rooisand, the highest captures were in a grid with a *Commiphora glandulosa-Adenolobus gariepensis* shrub community on a gentle slope with calcrete stones. At Claratal, a high abundance of tenebrionids was associated with *Acacia karroo – Cynodon dactylon* plant communities.

*Table 5: Number of individuals of different tenebrionid species recorded at the five study sites*

| | | | ←West | | | | East→ |
|---|---|---|---|---|---|---|---|
| | Species | Total | Kleinberg | Gobabeb | Ganab | Rooisand | Claratal |
| Widespread | *Physosterna cribripes* | 823 | 8 | 17 | 796 | 1 | 1 |
| | Zophosis kochi | 331 | 1 | 2 | 6 | 19 | 303 |
| | Epiphysa arenicola | 145 | 53 | 13 | 78 | * | 1 |
| | Zophosis infanda | 205 | 2 | 1 | 2 | - | 200 |
| | Gonopus tibialis | 21 | 9 | * | 10 | * | 2 |
| Widespread in Namib Desert, not on plateau | *Zophosis damarina* | 199 | 13 | 16 | 65 | 105 | - |
| | Metriopus depressus | 132 | 2 | 99 | 16 | 15 | - |
| | Stenocara gracilipes | 242 | 12 | 10 | 7 | 213 | - |
| | Onymacris rugatipennis | 187 | 2 | 168 | 15 | 2 | - |
| | Zophosis amabilis | 2,201 | 1,768 | 401 | * | 32 | - |
| | Physadesmia globosa | 377 | 4 | 28 | 345 | - | - |
| | Zophosis moralesi | 72 | 3 | 52 | 17 | - | - |
| Fog zone | *Cauricara eburnea* | 1,048 | 995 | 53 | - | - | - |
| | Zophosis dorsata | 2 | - | 2 | - | - | - |
| | Gonopus puncticollis | 1 | - | 1 | - | - | - |
| | Brinckia debilis | 1 | * | 1 | - | - | - |
| Namib interior and escarpment | *Zophosis mniszechi* | 152 | - | 11 | 80 | 61 | - |
| | Eustolopus octoseriatus | 119 | - | 73 | 38 | 8 | - |
| | Zophosis devexa | 119 | - | 28 | 90 | 1 | - |
| | Cauricara velox | 131 | - | 82 | 2 | 47 | - |
| | Zophosis lamentabilis | 13 | - | 3 | 9 | 1 | - |
| Eastern Namib and escarpment | *Cryptochile consita* | 1,007 | - | - | 35 | 972 | - |
| | Zophosis orbicularis | 7 | - | * | 7 | - | - |
| | Zophosis cerea | 1 | - | * | 1 | - | - |
| Eastern Namib and plateau | *Zophosis testudinaria* | 28 | - | 1 | 6 | - | 21 |
| | Renatiella fettingi | 2,290 | - | - | 12 | 143 | 2,135 |
| | Somaticus aeneus | 161 | - | - | 92 | 25 | 44 |
| | Metriopus hoffmannseggi | 910 | - | - | - | 95 | 815 |
| | Stenocara aenescens | 123 | - | - | - | 62 | 61 |
| Plateau | *Somaticus bisbicostatus* | 71 | - | - | - | - | 71 |
| | Total | 11,119 | 2,872 | 1,062 | 1,729 | 1,802 | 3,654 |

* known to occur at the site, but not recorded in the current study

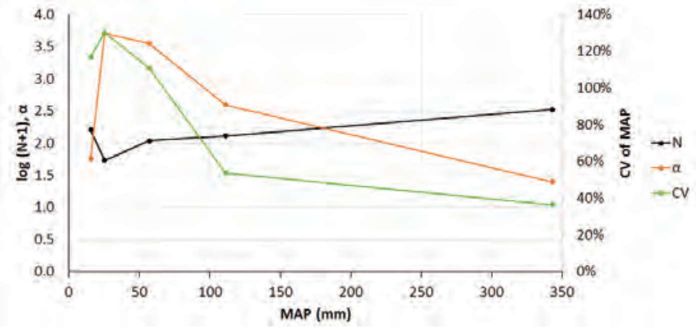

*Figure 6: Tenebrionid abundance (log N+1), α diversity, and the coefficient of variation (CV) of MAP plotted against MAP (mm) at the five observatories. Alpha diversity correlated negatively with abundance (r=-0.94) and MAP (r=-0.62) and positively with the CV of MAP (0.62)*

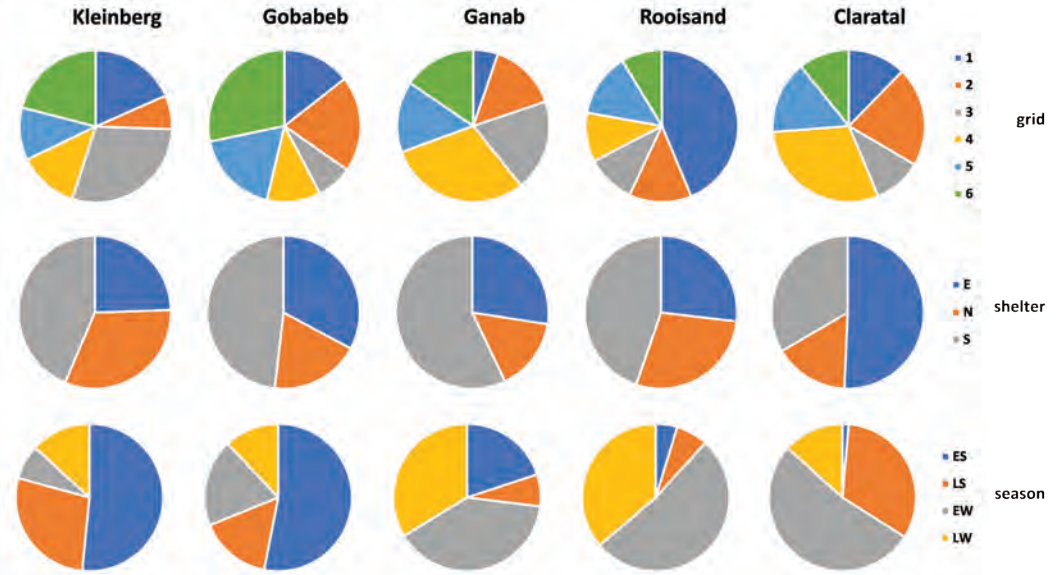

*Figure 7: Proportion of tenebrionid beetles collected in traps deployed in different grids (1–6 of each Observatory, Table 1), sheltered (S), near shelter (N), or fully exposed in the open (E), and in different seasons, early summer (ES: OND), late summer (LS: JFM), early winter (EW: AMJ), or late winter (LW: JAS)*

The seasonal capture rate differed between sites, with Kleinberg and Gobabeb recording over half of all abundance in early summer (Figure 7), which is the season with the highest occurrences of fog. At Ganab and Rooisand, in contrast, abundance was highest during early and late winter. At Claratal, abundance was highest during late summer and early winter, with 85% of the captures recorded.

Although a few widespread species occurred across the gradient (Table 5), the species composition differed considerably between observatories, with β-diversity ranging from 0.26 (between Gobabeb and Ganab) and 0.69 (between Gobabeb and Claratal, Table 4). While *Zophosis amabilis* was the most abundant species recorded during this study at Kleinberg and Gobabeb, only the fog-zone-associated *Cauricara eburnea* was co-dominant with *Zophosis* at Kleinberg. At Gobabeb, many other species were co-dominant, and diversity was high, although abundance was only a third of that recorded at Kleinberg. A different set of large-bodied species dominated at Ganab, while at Rooisand, the dominant set of species was relatively small-bodied and differed from Claratal (Table 5). β-diversity was high between Claratal and all other sites (Table 4), reflecting a vastly different beetle community on the highland plateau than in the lowland desert and adjacent escarpment (Table 5). Kleinberg was the next distinctive site, with high β-diversity to sites outside the fog zone (Table 4 & 5).

The full complement of species can be sorted into seven groups based on their affinity for the fog zone, the Namib interior, the escarpment, or the plateau (Table 5). Only five species occurred across the whole transect (with some gaps in the record), while a further seven appeared to be limited to below the plateau or below the escarpment (Table 5). Four species occurred mostly in the fog zone, which covers the first two sites, although only one (*C. eburnea*) was truly abundant (Table 5). Eight species were confined to the Namib interior and escarpment, essentially avoiding the fog zone (Table 5). Of the last six species, five occurred from the Namib interior up to the plateau, and one was recorded only on the plateau at Claratal (Table 5). The majority (19 out of 30) of the species were limited to the Namib and adjacent escarpment (Table 5).

## Discussion

Our datasets at two different scales showed that tenebrionid diversity increased across an east-to-west gradient of increasing aridity across the western half of southern Africa. This trend was especially pronounced across the Namib Desert, with tenebrionids being more diverse but less abundant within the desert than in the adjacent hinterland. Our estimate of endemism for the Namib Desert matches a previous estimate by Koch (1962) of about 200 endemic species, who had also included several other tribes in his study. This concentration of species indicates that the Namib Desert is a hotspot of tenebrionid diversity.

Over the past eight decades, the area between Namibia's capital city, Windhoek, and the country's main harbour at Walvis Bay has been intensively studied by scientists. This has provided valuable datasets for exploring the factors that might underlie the beetle biodiversity patterns across the Namib in this area. Over a distance of 300 km, MAP rises over 20-fold from Kleinberg near the coast to Claratal on the plateau, while the trend for variation in MAP goes in the opposite direction. Across this area, the number of tenebrionid species and all diversity indices increased from the foggy coast to the Namib interior (Gobabeb and Ganab) and decreased from there across the Great Escarpment to the Khomashochland (Table 4). Abundance had the opposite trend: declining from the western Namib to the middle zone (Gobabeb) and increasing over sixfold from there to the easternmost site (Claratal).

The coastal location (Kleinberg) fell out of the general longitudinal pattern. The regular occurrence of fog at this observatory supported an abundance of terricolous crustose and foliose lichens covering about half of the ground surface (Zedda and Rambold in Jürgens et al. (2010)) which increased the availability of water and food for tenebrionids (Lalley et al. 2006). The low eveness of diversity at Kleinberg was caused by particularly high abundances of two species, *Zophosis amabilis* and *Cauricara eburnea*, both known to feed on lichen (Wessels et al. 1979) with their populations tracking fog frequency (Seely et al. 2005; Henschel 2021). At Kleinberg, the numerous rare species would require considerably more trapping effort than the 18 traps deployed during 18 month-long trapping sessions to record the true species complement.

Coincident with the patterns in community structure, there were clear changes in composition over the transect, with high β-diversity indices between adjacent sites. The most marked difference between adjacent communities (ß = 0.57) was between the two sites located in the Thornbush Savanna, Rooisand at the foot of the escarpment, and Claratal, above the escarpment. The change in altitude thus had an even larger effect on species composition than the biome transition between Ganab and Rooisand (ß = 0.28). For many organisms, the mountainous terrain of the escarpment may act as a dispersal barrier, explaining abrupt changes in species composition seen along the escarpment (Barnard et al. 1998; Simmons et al. 1998; Mendelsohn et al. 2002; Jürgens et al. 2010). The mechanism behind the marked filtering effect that altitude plays on species pools is poorly understood for most invertebrate taxa beyond the general knowledge that species or their phenological and phenotypic characteristics often occur within very narrow climatic zones (Andrewartha & Birch 1954; Cheli et al. 2021; Lopez et al. 2021). These relationships with a range of micro and meso-climatic variables that vary with altitude are important to understand, as the fortunes of many species will be determined by the fine details of how aspects such as temperature and moisture levels will vary in the future (Roitberg & Mangel 2016; Figueroa et al. 2021; Tocco et al. 2021).

The trend in tenebrionid diversity from west to east is opposite to that of other taxa, a phenomenon that Koch had already noted during his surveys of Tenebrionidae across the arid west of southern Africa (Koch 1962). While species richness of other insects decreases with decreasing MAP from east to west, e.g. Lepidoptera (Mey 2010), tenebrionid richness increases. The taxonomic groups we included in our analysis of transect data represent only part of the tenebrionid species and did not include several species recorded close to the current observatories with different sampling methods that were continuous over decades (e.g., Henschel et al. 2003; Henschel 2021). Nevertheless, the west to east trend across the transect is similar to that previously recorded across the area (Table SM1). It is consistent with the overall picture of the 579 taxa for which distribution records were mapped across the AWSAR (Figure 3, SM1). However, there are many more tenebrionid species in the region. Alone in Namibia, some 743 known tenebrionid species or taxonomic entities are recorded from this family (Marais 1998; Irish 2012). Ongoing studies are identifying more tenebrionid taxa in the Namib Desert, including previously little-studied groups, e.g. Tentyriini (Schawaller 2012) and Cossyphodini (Schawaller 2013), and taxonomic revisions, e.g. Platynotina (Kamiński & Iwan 2013) and Molurina (Kamiński et al. 2021).

In sparsely vegetated areas, shelter appears to be premium, and our capture rates were higher at shelters such as shrubs or rocks. These provide some shade during the day and are places where locally generated or windblown detritus collects. The preference for open spaces at Claratal could perhaps be due to reduced predation risk away from structures where sit-and-wait predators lurk.

The seasonal patterns of tenebrionid abundance (activity) relate to the expected highest occurrence of moisture. At Kleinberg and Gobabeb, this would be when fog is most frequent, i.e., at the end of winter and the beginning of summer (September to December, Lancaster et al. (1984)). The occurrence of rains in late summer and early winter, driven by Tropical Temperate Troughs (Eckardt et al. 2013), and the resulting moderate temperatures and lingering soil moisture conditions during winter (Henschel 2021) could explain the relatively high activity of tenebrionids during winter at Ganab and Rooisand. At Claratal the tenebrionid activity was highest during the first half of the calendar year when most rains fell, and plant productivity was highest (Strohbach and Luther-Mosebach in Jürgens et al. (2010)).

Our finding that diversity correlates with the variability of MAP can possibly be explained by the intervals between rainfall events becoming longer with increasing aridity. This allows for dividing activity times more finely into temporal niches. Multiple successive time-niches used by populations of different tenebrionid species with divergent rates of growth and decline serially changes community composition, thus enhancing the coexistence of many species, resulting in the highest diversity at the driest location (Henschel 2021).

The extraordinarily high level of endemism in the desert is probably related to the great age of the Namib (Ward & Corbett 1990). As substrate specialists (Prendini 2001), isolated populations of tenebrionids are subject to geomorphological processes such as dune-field dynamics (Koch 1961; Endrödy-Younga 1982) or other changes in substrate configuration (Penrith 1979, 1986a). Divergence of isolated populations would lead to the speciation of endemics at local levels.

At a landscape level, the scale of ten to tens of km, an interplay of temporal and spatial rainfall variability may come into play. In the Namib, rainfall is highly variable over time (Table 2) and across space (Henschel et al. 2005), and in terms of rainfall, the Namib Desert is heterogeneous, irrespective of geophysical conditions. Therefore, populations of tenebrionids in adjacent landscapes could be in a very different status, e.g. irrupting in one area while crashing or in a bottleneck condition in another. This heterogeneity may constrain gene flow across the area and promote population differentiation even across geographically similar interconnected areas.

The increase of tenebrionid diversity with increasing aridity across the Namib Desert remains a fruitful topic for further research despite significant advances in understanding since Koch first noted it 60 years ago.

## Supplementary Material

This can be downloaded at:
http://data.sasscal.org/metadata/view.php?view=doc_data&id=7301

### Contents:

- **Figure SM1**: Number of tenebrionid species of focal taxa recorded in half-degree squares of latitude and longitude (HDS) across the western half of southern Africa between latitude 13-34.5°S and longitude 11.5-25.5°E.
- **Table SM1:** Tenebrionids recorded at five SASSCAL observatories and in their half-degree squares of latitude and longitude (HDS).
- **Figure SM2:** Total abundance (log N) of focal tenebrionids recorded at different SASSCAL observatories during month-long trapping sessions conducted at various times between April 2004 and March 2009.
- Site-specific overviews of tenebrionids recorded at west-to-east (WET) SASSCAL Observatories across the central Namib
- Files:
  - ○ Tenebrionid beetle data BIOTA-WET 2004–2009.
  - ○ Tenebrionid beetle metadata BIOTA-WET 2004–2009.

## Acknowledgements

This study was funded by the German Federal Ministry of Education and Research (BMBF) through the BIOTA programme, the Gobabeb Namib Research Institute, and the University of Hamburg. The Namibian Ministry of Environment and Tourism and the Ministry of Agriculture, Water and Forestry granted permission for this study. Norbert Jürgens facilitated this project and encouraged its completion. The farmers Heiko Freyer (Claratal) and Johannes Schmidt (Rooisand) gave permission to access their properties and kindly provided useful information. Field technicians Vilho Mtuleni, Olavi Makuti, Veronica Siteketa, Calvin Sisamu, Reginadia Hofnie, Taimi Kapalanga, Hiskia Mbura and Mycke Matengu managed the fieldwork and subsequent processing of collected material in the laboratory, assisted by paraecologists Justin Kham, Memory Dausas, Albertus

Kooitjie, Sebedeus Swartbooi, Jeannete Swartbooi. Research assistants Elsita Kiekebusch and Francois Becker facilitated the preliminary compilation of the Central Namib tenebrionid dataset. John Irish trained field technicians in identification and specimen management in the laboratory, and Ute Schmiedel provided training to the paraecologists. Karl-Eduard Linsenmair and Constanze Grohmann gave advice on fieldwork. Eugene Marais and Matilda Awases facilitated access to the beetle collection of the National Museum. The Namibian Meteorological Services, the Gobabeb Namib Research Institute and SASSCAL-Weathernet provided climatic data. Jens Oldeland kindly extracted and plotted MAP data from WorldClim.

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JOURNAL 69
Namibia Scientific Society / Namibia Wissenschaftliche Gesellschaft
Windhoek, Namibia 2022
ISSN: 1018-7677 ISBN: 978-99945-76-79-1

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### Theo Wassenaar

Theo Wassenaar has 30 years experience in various aspects of natural resource management and science, principally restoration and conservation ecology. He has participated in and led more than twenty large ecological impact assessments and ecological restoration projects for clients ranging from mines to regional government. Since 2011 he has led the Namib Ecological Restoration and Monitoring Unit (NERMU), established at Gobabeb to address the expected impacts to Namib biodiversity because of an upswing in mining activities. In 2018 Theo joined the Namibia University of Science and Technology as Associate Professor in Conservation Biology/Zoology but has maintained his ties with Gobabeb by continuing as Principal Investigator of the NERMU Project. His research focus is on land degradation and restoration ecology, and he has a special interest in the ecophysiology of arid zone organisms and how this relates to risks brought on by global change. He has published 40 scientific articles and book chapters, and numerous consultant reports.

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