

1 The ecological world of driver ants (*Dorylus*): a review

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Abstract

Driver ants (*Dorylus*) are among the most conspicuous and abundant predators in continental Africa. Their enormous surface-swarm raids and nomadic lifestyle have captivated naturalists for over 150 years, yet their ecology remains surprisingly poorly understood, especially compared to their Neotropical counterparts. Here, we review the ecology of African driver ants, synthesising knowledge of their taxonomy, evolution, life history, behaviour, trophic ecology, community effects, and ecological associates. Driver ants are formidable generalist predators extracting large quantities of prey from extensive areas. Their raids have long been hypothesised to create pronounced variable disturbances on the forest floor that may have a role in maintaining community structure and beta-diversity. At the same time, their nests and raids support an extraordinary diversity of organisms, including ant-following birds, vertebrate predators, myrmecophilous beetles, flies and other specialised associates. Such interactions suggest that driver ants influence tropical forest communities well beyond the direct and indirect effects of their raids. However, much of what we know of driver ants and their effects on African ecosystems remain based on natural history observations rather than quantitative or experimental evidence. In particular, we still lack a clear understanding of how driver ant raids alter arthropod community composition and diversity, details of their movement ecology, their vulnerability to anthropogenic change, and how strongly other organisms depend on driver ants. We critically evaluate the evidence for considering driver ants as 'keystone predators' and highlight the difficulties of applying this concept to nomadic superorganisms whose effects operate across multiple spatiotemporal scales. Finally, we identify emerging approaches that could pave the way to more comprehensively understanding the ecology of driver ants and their influence on African ecosystems. Our review highlights that driver ants are not simply abundant predators, but almost certainly ecologically central components of African rainforest ecosystems whose influence extends across trophic levels, spatial scales and biological communities. Understanding and quantifying these effects in detail is the next step to describing how driver ants fit into the wider ecosystem, and what might be lost in their absence.

Introduction

"It also drives everything before it capable of muscular motion, so formidable is it from its numbers and bite..." wrote the American naturalist Thomas S. Savage in 1847 during his medical mission in West Africa (Savage 1847). His fascination referred not to wild dogs, lions, or hyenas, but instead to what he considered an "important practical part in the economy of nature": the surface swarming army ants of the genus *Dorylus*. Savage continued, *"...in respect to the last fact it stands unique in its habits, and, in distinction from other species of this country, may well take for its vulgar name that of Driver."*, coining the term 'driver ants' (**Figure 1**). Driver ants are considered to be the dominant arthropod predators across African forests and conduct vast 'raids' in search of animal prey that they then overpower, butcher, and return to the nest (Hölldobler and Wilson 1990, Gotwald 1995, Franks et al. 1999). Surface swarming *Dorylus* army ants are endemic to tropical Africa and have a deep cultural importance to many groups of people across the continent, evidenced by their prominence in African folklore and language (Van Huis 2021). Driver ants are called 'zurkw' in the Fang language, 'siafu' in Swahili, and 'ijere' in Igbo, for example. The fascination people have for driver ants arises from their captivating behaviour, conspicuousness in the environment, and the potential or perceived threat they pose.

Whilst natural history studies have shed some light on driver ant biology, significant gaps in our knowledge remain, including in foundational aspects of their ecology, life history, movement biology, population dynamics, and conservation. Several general overviews of army ant biology and ecology exist and, although these are excellent resources for those wanting to learn about *Dorylus* driver ants, they are typically biased towards army ants in Central and South America (e.g., *Eciton* and *Labidus* spp.) because of the much greater quantity of research in the Neotropical system (Gotwald 1995, Kronauer 2009, 2020). In this review, we aim to 1) describe the current state of knowledge for driver ants and highlight key gaps in our understanding; 2) scrutinise the keystone species concept in the context of driver ants, and 3) present some emerging tools and future directions for studying driver ants.



Figure 1. Driver ants (*Dorylus nigricans* group). Panel A: cooperative prey transport of a large earwig (Dermaptera) by *Dorylus sjostedti*; Panel B: colony emigration of *Dorylus wilverthi* to a new nest site, showing brood transport; Panel C: defensive positioning of *D. sjostedti* at a nest entrance; Panel D: *D. wilverthi* workers form a ‘living archway’ to protect an emigration trail beneath; and Panel E: the beginning of a *D. wilverthi* raid at the nest, showing workers aggregating on vegetation. Photo credits: Panels A and C – NCJFV, Panel B – Ibon Malaxetbarria; Panel D – Sean Glynn; Panel E – MPTGT. All photos were taken in Equatorial Guinea.

Taxonomy, evolution, and biogeography

The taxonomy of *Dorylus* is long and confusing (Borowiec 2016), described by Gotwald (1995) as “a meandering stream cluttered by the flotsam of esoteric debate”. Briefly, Linnaeus originally described the genus as *Vespa helvola* – a type of wasp – from a male collected in South Africa (Linnaeus 1764). Fabricius later created the genus *Dorylus* for the same species (Fabricius 1793) and, for about 85 years, males were referred to as *Dorylus* and workers as *Anomma* and *Typhlopone*. Thomas S. Savage then observed males and females together in the field and realised they were the same species (Savage 1849), naming one of the species *Anomma arcens*, Westwood 1847, collected from Liberia. In Gabon, Savage also described *Anomma rubella* Savage, 1849. This species performed similar conspicuous raids to other current *Anomma* species and the common ‘driver ant’ name was established for species that performed any sort of conspicuous raid in the leaf litter or vegetation. Species that perform raids in only the leaf litter and do not climb vegetation are not today typically thought of as true driver ants (Schöning et al. 2005a, 2011). *Anomma* was eventually demoted to a subgenus of *Dorylus* and included all conspicuous raiding species. Not all species in the *Anomma* subgenus are driver ants, however, as several only perform raids epigaeically. The true driver ants that perform large surface swarm raids and climb into the vegetation form a clade, and the intermediate ‘above-ground hunting’ species are more closely related to the subgenus *Dorylus sensu stricto* (Kronauer et al. 2007b). The classification of *Dorylus* into subgenera did not support the known phylogenetic relationships within the genus and was subsequently abandoned in favour of informal species groups. The true driver ants are now referred to as the *Dorylus nigricans* group (Borowiec 2016, Schöning et al. 2026). Borowiec (2016) provides a history and modern overview of the taxonomy of *Dorylus*, and a more in-depth discussion of this historical taxonomic saga is detailed in Gotwald (1995) and again more recently in Schöning et al (2026). Driver ants make up only a small portion of the approximately 220 species of *Dorylus*, most of which form comparatively small colonies that live almost entirely subterranean lives (Gotwald 1995).

The higher-level phylogeny of the Dorylinae is better understood, with the crown doryline ants diversifying in the Late Cretaceous around 74 million years ago (Ma) in the final stages of the breakup of the Gondwana supercontinent (Kronauer et al. 2007b, Borowiec 2019). Divergence estimates suggest that the crown doryline ants split 16 times in the first 20 Ma, indicating a rapid ancient radiation (Borowiec 2019). The most recent common ancestor of New World army ants dates to approximately 60 Ma, with the Old World army ant clade sharing a common ancestor similarly at ~58 Ma, around when the Old World army ant lineages *Aenictus* and *Dorylus+Aenictogiton* split (Borowiec 2019). *Dorylus* emerges ca. 16 Ma, but surface swarming driver ants are remarkably young in evolutionary terms, diversifying only within the last 5-6 Ma (and, interestingly, their analogues in the Neotropics appear independently around the same time) (Borowiec 2019). Phylogenetic reconstruction and biogeographic analyses suggest the doryline ants originated in the Old World, with an ancestral range in the Afrotropics (Borowiec 2019). Some of these estimates have a high level of uncertainty because the phylogeny of the entire Dorylinae army ant clade were calibrated using only seven fossil records with one located in the New World clade (Borowiec 2019).

Driver ants are endemic to tropical Africa and do not overlap geographically with other surface swarming army ants possessing large colony sizes. There are approximately eight recognised species and subspecies of ‘true’ driver ants (**Figure 2**), some of which are currently classified as subspecies of *Dorylus nigricans* but may be given full species status with additional genetic

information (Schöning et al. 2026). The formal (sub)species-level description of driver ants is still not completely clarified. A conspicuous *Dorylus* species exists in Asia (*Dorylus laevigatus*), which can be locally common in Borneo and Malaysia (Berghoff et al. 2002), but this species does not form similarly large surface swarm raids and has a relatively small colony size compared to driver ants, totalling around 325,000 workers (Berghoff et al. 2002, 2003).

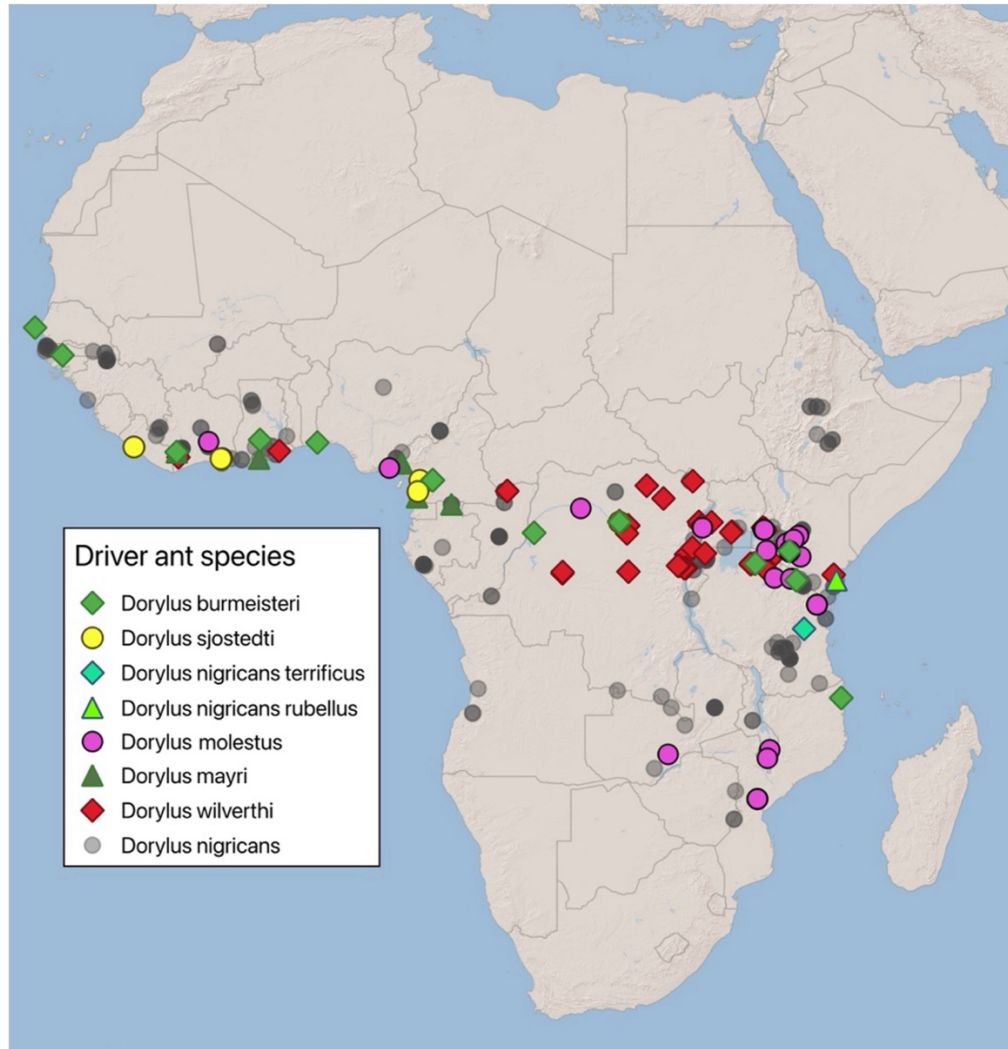


Figure 2. Records of different driver ant species across Africa. Data downloaded from GBIF under CCBY 4.0; DOI: [10.15468/dl.np8n9b](https://doi.org/10.15468/dl.np8n9b).

The taxonomic confusion within *Dorylus* has been a significant barrier to the study of this extraordinary group of social insects (Schöning et al. 2008a). However, new genetic approaches and phylogenetic analyses provide a clear path towards resolving the taxonomic issues that have persisted for over a century (Kronauer et al. 2007b, Schöning et al. 2008a, 2026, Brady et al. 2014, Borowiec 2016, 2019).

Life history and behavioural ecology

Driver ants are a type of army ant and therefore possess several life history traits common to the 'army ant behavioural syndrome' (Kronauer 2009). Namely, these include obligate collective foraging for animal prey, nomadism, and specialised permanently wingless queens (Wilson 1958, Gotwald 1995, Kronauer 2009). Driver ants exemplify this suite of behavioural

169 traits and form the largest colonies and swarm raids of all army ants (Hölldobler and Wilson
170 1990).

171 *Swarm raiders*

172 Driver ants forage for food in impressive surface swarms, also called ‘raids’ – the principal
173 behaviour that has captivated naturalists for centuries and written army ants into African
174 folklore (Gotwald 1995, Van Huis 2021). The swarm raids of driver ants begin when a mass of
175 ants collects outside the nest. From this mass arises order in the form of several anastomosing
176 columns moving together in one direction. The increasingly orderly mass eventually moves
177 away from the nest and a large column of ants coalesces to feed the swarm (Gotwald 1995).
178 The swarm then begins to divide, fanning out into a more clearly definable ‘raid front’ in the
179 foraging area; many small branches link the raid front and the main column. Vertebrates and
180 invertebrates alike flee from the raid front if they can, but often run or jump the wrong way, or
181 fall into the swarm from vegetation above, where they are overpowered and killed by workers.
182 Ants that have obtained prey head back in the direction of the nest. The raid eventually
183 terminates as the raid front diminishes and recoils back into the main column, which slowly
184 dissolves as the remaining ants return to the nest (Gotwald 1995). A raid can last for 48 hours
185 or more, but more commonly persist for between 9 to 27 hours (Raignier and van Boven 1955,
186 Gotwald 1995).

187 Different driver ant species form raids somewhat differently from the process described above,
188 which is based on a *D. wilverthi* raid. *Dorylus nigricans* observed in the Ivory Coast, for
189 example, form a more distinct fan-shaped sheet at the initial stage of the raid, and raids rarely
190 form without this structure (Leroux 1977). Compared to the slowly expanding mass of workers
191 in *D. wilverthi*, the raids of *D. nigricans* may reach their final functional shape more quickly,
192 with a clearly defined raid front. It is unclear how interspecific variation in raid formation affects
193 the foraging ecology of driver ant species, but it may have important consequences for how
194 rapidly raids form and how quickly a colony can respond to its nutritional requirements (e.g.,
195 of larvae).

196 Raids can be enormous, representing significant ecological events for animals dwelling in and
197 around the forest floor, and advance as rapidly as 20 m per hour (Gotwald 1995). In Equatorial
198 Guinea, *D. wilverthi* raids have been measured at 30 m wide and 200 m long, which
199 theoretically covers an area of ~6,000 m² (Tercel et al, unpublished data), similar to records in
200 other regions that have measured raids over 25 m wide and 150 m long for both *D. wilverthi*
201 and *D. nigricans* (Raignier and van Boven 1955, Leroux 1977, Gotwald 1995, Schöning et al.
202 2005b). The average length of raids is somewhat shorter, about 125 m long for *D. wilverthi*
203 and *D. nigricans* (Leroux 1977). Moreover, many *D. nigricans* raids are much shorter, with 63
204 % measured between 26 – 75 m in the Ivory Coast (Leroux 1977). Substantial variation of raid
205 geometry may exist between colonies of the same species (e.g., because of colony size) and
206 across driver ant species and regions.

207 The geometry of driver ant raids is not well known, but one of the most promising avenues to
208 describe how sympatric driver ant species separate their niches is the verticality of raids. Some
209 driver ant species, such as *D. wilverthi* can climb over 10 metres into the trees to apprehend
210 prey, and *D. sjostedti* similarly climbs into trees several metres high (Tercel and Huber,
211 unpublished data). The efficacy of climbing vegetation is impressive: as driver ants climb

upward through the vegetation and understorey, the raid front on the ground continues to advance. When animals high on the vegetation leap to the forest floor to flee from the ants, every surface is carpeted in ants, and the prey are quickly overwhelmed and killed. The ants themselves also eventually leap off the vegetation in their thousands to efficiently return to the forest floor (Gotwald 1995). Some driver ant species appear to dig for prey more readily during raids, e.g., *D. molestus* digging for annelid prey (Schöning et al. 2008c). Identifying vertical stratification of raids between sympatric driver ant species might illuminate niche differences that have been otherwise overlooked thus far.

The colony and division of labour

Driver ants have the same fundamental caste structure as the vast majority of other ant species: queens, males, and workers. The queens of driver ants are the largest of all ants, measuring approximately 5 cm long, and are permanently wingless, possess a greatly enlarged gaster measuring >50 % of total body length, and strong legs that are important during colony emigrations (Gotwald 1995). Colony reproduction is the primary function of the queen, and her egg-laying productivity is truly extraordinary, surpassing that of all other ant species. Raignier and van Boven (1955) estimate that a single *D. wilverthi* queen can lay 3 – 4 million eggs per month, with an annual yield of 36 – 48 million. For *D. wilverthi*, such a vast number is necessary because colonies can total 20 million ants or more (Raignier and van Boven 1955, Gotwald 1995). Using these data, we can roughly approximate that the average life span of workers equates to 20 – 25 weeks, though there is likely to be substantial variation to this rough estimate because of seasonality, intraspecific variation, and colony age.

New driver ant colonies form through colony fission, whereby one colony with a functional queen divides following the emergence and insemination of a new queen. This is unlike most ants, where new colonies are formed by individual queens after performing a nuptial flight, but is seen in some unicolonial ants and other Hymenoptera, such as honeybees. In driver ants, colony division begins when the mother queen and up to half the workers and brood emigrate to find a new nesting location, leaving the unmated queens with the remaining workers (Raignier and van Boven 1955). The new queens can be in any form – larval, pupal, recently emerged, or fully sclerotised – and they can number up to several dozen (Raignier and van Boven 1955). All but one of these new unmated queens are killed by the daughter colony workers once fission is complete. Raignier & van Boven (1955) found up to 56 unmated queens killed in a single nest after colony fission. It is not known how this selection process takes place. In *D. nigricans*, males are produced 2-3 weeks after new queens and begin their journey to mate with them soon after (Leroux 1982). Driver ant queens perform some of the highest mate frequencies of all ants, mating with between 17-18 different males (Kronauer et al. 2004). Queens store hundreds of millions of sperm cells from these males in a spermatheca for the rest of their reproductive life – a specialised sperm-storage organ many female insects possess (Kronauer et al. 2007a). The mother colony after fission in *D. nigricans* will emigrate more frequently and over longer distances than usual, with over half of the nest occupations lasting only 1-4 days (Leroux 1982). Presumably this is to avoid competition with the new daughter colony.

When the queen dies, the colony ultimately fails as a distinct reproductive and ecological unit but workers may try to merge with nearby conspecific colonies (Kronauer et al. 2010). Workers will retrace previous emigration trails, which probably evolved as a behaviour to recover the

queen if separated from the colony and/or remerge to a daughter colony if fission recently took place (Schneirla 1949, Schneirla and Brown 1950, Kronauer et al. 2010). There are many interesting evolutionary nuances and implications to workers merging with other colonies that are discussed at length elsewhere (see Schneirla and Brown 1950; Kronauer et al. 2010).

Males in most ant species are short-lived, and their sole mission is to mate with a queen from a conspecific colony – the same is true of driver ant males. Driver ant males are quite large and are only slightly smaller than queens in size (Gotwald 1995), which deviates from the general pattern in ants where males are relatively small. The key mission of driver ant males is to take flight from the parent colony, locate a conspecific colony, enter the new colony, run the gauntlet towards the queen whilst beset by aggressive workers, and ultimately mate with the colony's queen. Males need to pacify or avoid the workers of the foreign colony to reach the queen, and Franks and Hölldobler (1987) suggest that the convergent (or homological) morphology and exocrine glands between queens and males in army ants facilitates this trickery. It also presents the interesting conclusion that workers in a sense 'choose' which males are able to mate with the queens (Franks and Hölldobler 1987, Gotwald 1995). Males have little to live for after successfully mating with a queen; they offer no benefit to the colony and die soon after. Males typically fly from their parent nest at dusk or night but the exact hourly timing of this is species-specific. In fact, there is strong evidence showing that different *Dorylus* species (including but not restricted to driver ants) partition male flight timings throughout the night (Haddow et al. 1966). *Dorylus* males are produced year-round but have a seasonal peak that is synchronised across *Dorylus* species, presumably to oversaturate predators and increase survival likelihood (Leston 1979). However, it is completely clear why such strong interspecific nightly partitioning of male flight times exists, given that there is minimal risk of hybridisation in *Dorylus*. The males take flight at night, detect a newly emerged queen and locate the nest or column through species-specific pheromones, and therefore males only run the (small) risk of hybridising with very closely related species. Even if males of different species took flight at similar times, they would then presumably travel in the direction of the strongest conspecific pheromone plume. However, hybridisation can occur between different driver ant species (Kronauer et al. 2011), with as high as 2 % of all matings in *D. molestus* and *D. wilverthi* representing hybridisation in Kakamega Forest, Kenya (Butler et al. 2018), translating to ~1-2 % of the worker population. The ecological and genetic ramifications of hybridisation in driver ants are unclear but warrant further study in hybrid zones. Further empirical studies capturing and identifying males leaving their parent nest, navigating to conspecific colonies, and at light traps would help to better understand male flight and mating behaviour.

The vast majority of the biomass and abundance of a colony is made up of workers. Driver ant workers do not rigidly fall into different subcastes as some other ant groups do. Instead, workers lie on a size spectrum and the tasks they perform are correlated to their size (Raignier and van Boven 1955, Gotwald 1974, Braendle et al. 2003, Schöning et al. 2005a, Huber et al. 2026). Whilst all workers participate in all tasks, small workers are more likely to build gallery walls and other structures along raid columns (Gotwald 1995), whilst large workers are more likely to participate in defensive activities both close to and far from the nest (Braendle et al. 2003). Worker size is also correlated with prey retrieval. Large workers are more likely to carry prey items, and the size of the prey item is proportional to the size of the carrier (Huber et al. 2026). The relative load of workers carrying prey items is higher in small workers, who carry more relative to their body weight than do larger workers (Huber et al. 2026), following

classical laws of strength scaling. Small workers are also more likely to carry fluid food in their crops, presumably from the same origin as prey fragments carried by larger workers (Gotwald 1974, Schöning et al. 2008c). The size-correlated division of worker labour has implications for how colony demographics might influence the ecologies of different driver ant species and could be an underappreciated source of niche differentiation. If tangible demographic differences between species translate to raid-level predation behaviour, this might affect how frequently different prey types are selected in terms of taxonomic identity, size, and where they are found in the leaf litter or vegetation. This has been sorely understudied, but new research in central Africa shows that worker size distribution differs between *D. sjostedti* and *D. wilverthi* (Huber et al. 2026). The population of very large workers is sufficiently high in *D. wilverthi* that it represents an extra third worker size mode that is absent in *D. sjostedti* (**Figure 3**), whilst the overall range of worker sizes is not significantly different. It is not fully understood how such a demographic difference translates to the ecology of driver ant species, but Huber et al (2026) found that the extra size mode present in *D. wilverthi* allowed them to carry prey items that were on average 9.8% longer, 13.6 % wider and 21.8 % heavier than prey items carried by *D. sjostedti*. Further study in sites where multiple species of driver ants occur in sympatry could reveal the significance of these demographic differences in terms of driver ant ecology and speciation.

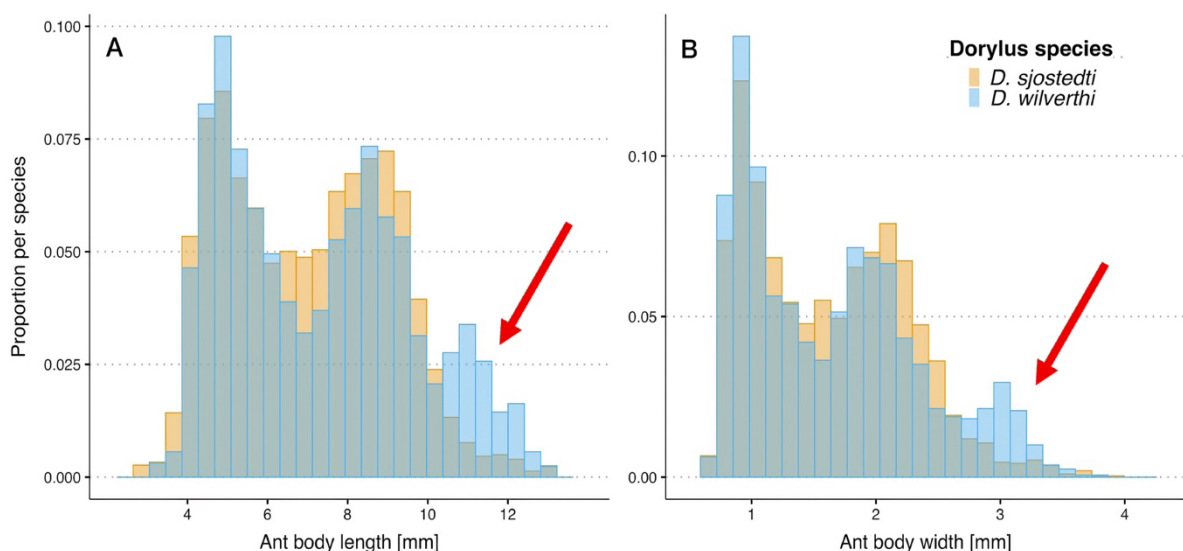


Figure 3. The demographic distribution of worker sizes in *Dorylus wilverthi* (blue) and *D. sjostedti* (orange), edited from Huber et al. (2026). The red arrows indicate the third size mode of larger workers occurring in *D. wilverthi*.

Cooperative transport by workers enables driver ants to carry very large or awkwardly shaped prey items, presumably allowing driver ants to efficiently exploit a wider range of food resources (Huber et al. 2026). In *D. wilverthi* and *D. sjostedti*, groups of driver ants carrying prey items are typically more heavily loaded than individual carriers when the total weight of a prey item is divided by the total number of ants carrying it (Huber et al. 2026). Cooperative prey transport therefore does not necessarily function primarily to reduce individual loading, but instead extends the upper weight limit of transportable prey (Huber et al. 2026), ensuring the largest prey items can make it back to the nest.

Nomadism in driver ants

Nomadism is broadly defined as a highly mobile lifestyle whereby an animal's survival strategy relies on constant frequent movement. Across the animal kingdom, this could be for a range of reasons, such as following weather patterns and seasonal shifts in foodplant availability (e.g., bison), courtship, mating and reproduction (e.g., young male lions), or predator avoidance (e.g., banded stilts). Although nest relocation in ants is not uncommon, for example in *Formica*, *Aphaenogaster*, *Tapinoma*, *Pogonomyrmex*, *Leptothorax*, and *Temnothorax* (Wilson 1958, Hölldobler and Wilson 1990, Tschinkel 2014, Yan and Prebus 2024), species that exhibit nest relocation behaviour are not necessarily nomadic (Wilson 1958). In army ants, however, nomadism defines their biology.

It is thought that nomadism in army ants evolved in parallel with group predation behaviour to avoid local food depletion (Wilson 1958, Gotwald 1995, Schöning et al. 2011). Through their raids, army ants are assumed to deplete prey communities surrounding their temporary residence (Kaspari et al. 2011) and, theoretically, colonies should maximise prey intake by avoiding areas that have recently been raided (Franks and Fletcher 1983), unless prey communities can swiftly recover to pre-raid levels. The ultimate cause of colony emigration in army ants is therefore principally assumed to be when food availability in the surrounding area decreases past a certain threshold, when the colony then journeys to a new area with higher prey populations in order to optimise foraging efficiency (Wilson 1958). Several army ant species raid in orderly and predictable ways that strongly support this idea. An *Eciton burchellii* colony in the Neotropics, for example, performs raids radiating out predictably from their bivouac that have minimal overlap with one another, and an emigration is precisely timed to accommodate both the phasic nature of their brood production and at the point a previously raided patch would be raided a second time (Franks and Fletcher 1983, Gotwald 1995). So-called phasic army ants precisely time their raids and emigration behaviour to align with brood development. By comparison, the nomadism of driver ants appears erratic.

Unlike the highly predictable emigration cycle of phasic army ants, African driver ants can remain at a nest site from anywhere between 1 – 125 days (Raignier and van Boven 1955). Whilst this range is extreme, driver ant colonies are much more likely to emigrate every 10-20 days, although the exact average appears to be species- and region-specific (Raignier and van Boven 1955, Leroux 1982, Gotwald 1995, Schöning et al. 2005b, 2011). Emigrations by driver ant colonies can last several days, with a mean duration of 56 hours in *D. nigricans* (Raignier and van Boven 1955). Emigration columns are usually more enclosed than raid columns, with earthen walls erected by workers to form a complete or partial tunnel through which the column moves; tunnels can also be made from the workers themselves as 'living archways', and can be performed across terrains of all types, including small rivers and streams (**Figure 4**). These walls are often adorned by plant fragments and other debris, and the function is presumably both for camouflage against predators and protection from the sun and rain (Schöning et al. 2005b). Emigration columns typically travel more rapidly than foraging columns – up to 30 m per hour (Raignier and van Boven 1955) – and can travel a distance of more than 200 m (Raignier and van Boven 1955). Several early studies of driver ant movement conducted over months and years in the field were bafflingly unable to find any clearly discernible pattern or proximal cause of emigrations (Raignier and van Boven 1955, Leroux 1982). The seemingly erratic and unpredictable nature of driver ant emigrations appeared inconsistent with the theory that army ants need to relocate their nests to avoid food depletion. However, Schöning et al. (2005b, 2011) unravelled some of the mystery by mapping

and following multiple *D. molestus* raids and emigrations over the landscape of Mount Kenya, in addition to conducting food supplementation experiments.



Figure 4. Emigration columns of driver ants. All panels show *Dorylus wilverthi*. Panel A: brood transport by various sized workers; Panel B: defensive positioning of large workers flanking the column; Panels C and D: colonies also emigrate over waterways by finding bridges or, in some cases, forming a ‘living bridge’ of many linked workers. All photos by Ibon Malaxetbarria in Equatorial Guinea.

In contrast to expectations, food supplementation did not affect the amount of time driver ants spent at nest sites, and colonies foraged normally in addition to collecting the supplemental food (Schöning et al. 2011). However, colonies supplemented with food emigrated 20 % shorter distances than control colonies (Schöning et al. 2011). Schöning et al. (2005b, 2011) also ruled out egg-laying cycles, compromised nest hygiene, and nest parasites as proximal causes of emigration in *D. molestus*. Nest attacks by predators – artificially simulated with a machete, or actual predation by pangolins – did result in rapid colony emigration within several hours and Schöning et al. (2011) suggest that predation may represent a major selection pressure on certain traits of driver ants. Unlike some other groups of army ants, such as *Eciton* spp., *Dorylus* lack powerful stings and do not nest openly in ‘bivouacs’, instead excavating underground nests and hidden tunnels for their foraging and emigration columns. Underground nest structures are harder to locate than an open nest and the queen is better protected (**Figure 5**); predators such as pangolins and chimpanzees consume many ants but driver ant colonies are so large that the primary danger is probably not predation per se, but a queen being inadvertently killed in the process of foraging by these mammalian predators. Relocating a nest prevents a predator from returning to the colony to feed again later. Direct predation of queens by subterranean army ants can, however, present a major risk to driver ant colonies, especially predation from other *Dorylus* species (e.g. *Dorylus (Typhlopone)* spp).

In the Ivory Coast, for example, attacks by subterranean army ants were the most frequent cause of colony death in *D. nigricans* (Leroux 1982). Driver ants participate in various defensive behaviours that act as an effective deterrence in many situations, though in cases where this strategy fails, swift colony relocation might prevent queen mortality and colony death.

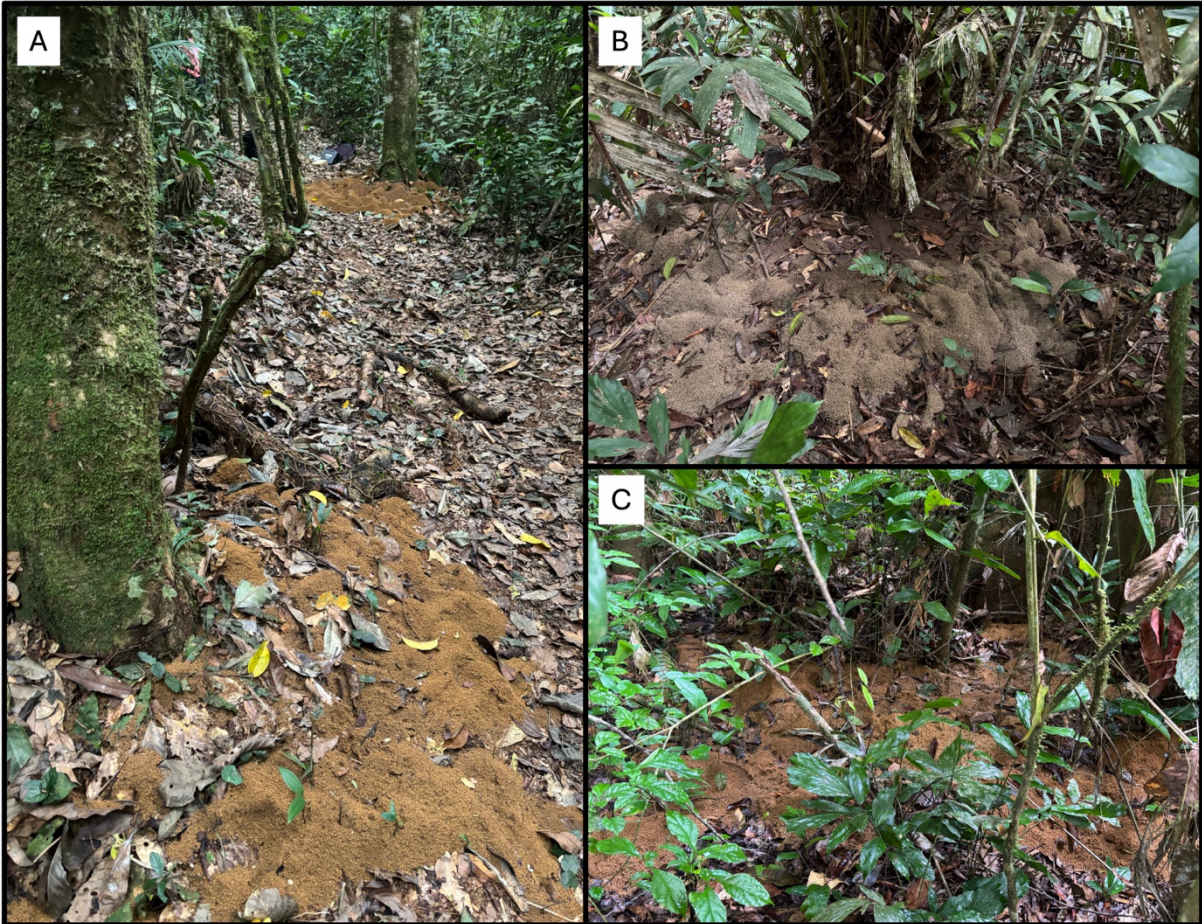


Figure 5. Driver ant nests are typically located at the foot of trees but can also be in the open. Panel A: two *Dorylus wilverthi* nests from the same colony in very close proximity; emigration to the nest in the foreground was stimulated after a student accidentally stepped on the far nest. Panel B: a *D. wilverthi* nest centred around a small palm tree. Panel C: a *D. sjostedti* nest formed beside the root buttresses of a large tree. All photos by MPTGT in Equatorial Guinea.

Although attacks by predators are an important proximal cause of some emigrations, these are relatively uncommon, and predation events do not explain the generally erratic emigration patterns in driver ants (Schöning et al. 2011). What then are the main factors explaining the nomadic movements of driver ants? Some evidence suggests that principles of optimal foraging combined with interactions between colonies might be the main proximal causes of emigration in terms of frequency, direction, and distance. For *D. molestus* in Keyna, Schöning et al (2005b) calculated that the average raid width was 10.3 m and each colony raided at least once per day. With raids radiating out from the nest systematically, they calculated that 51 % of the area within the mean foraging range of the nest (75 m) will have been raided within 17 days, which is the mean nest site stay duration. It is unlikely that colonies can forage in 100 % of the area around the nest because of the presence of other nearby colonies, which

presumably also raid within their potential foraging area. Schöning et al (2011) conclude that foraging by *D. molestus* colonies and their nearest neighbours depletes prey around the nest, and colonies that detect the presence of each other typically move directly away from each other in order to avoid competition for food (Schöning et al. 2005b, 2011). Indeed, colonies of *D. molestus* are significantly more likely to move in the opposite direction to their nearest neighbour than any other direction. What remains unclear is how colonies detect each other and how raid sites are selected. Raids from different colonies do not usually collide or reach one another's nests and therefore colonies do not normally determine one another's location from direct interaction, though in areas of high colony density, colliding raids can occur (Schöning et al. 2005b). In these circumstances, workers usually simply adjust their course to avoid significant contact and do not interact aggressively (Gotwald 1995, Schöning et al. 2005b). One possibility is that pheromones deployed by driver ants during raids persist in the environment for some time – perhaps at the scale of days or weeks. If persistent 'raid pheromones' are detectable by a different colony, a raid that intersects with a previous raid path of another colony would signal that the area may have suboptimal prey populations. Encountering multiple such intersections would suggest another colony is nearby and there may be increased chances of competition for prey in the direction of those intersections. Perhaps there is a threshold of raid pheromone intersections that, when surpassed, a colony is stimulated to emigrate. A similar process could also be true of a colony detecting their own raid path pheromones radiating from the nest over the last few days as a means to gauge how frequently the colony has raided in each direction and may stimulate an emigration, albeit with reduced urgency. Franks and Fletcher (1983) have a similar theory for *Eciton burchellii* in the Neotropics, where colonies use conspecific foraging trails to inform movement decisions; foraging trails in *E. burchellii* have been shown to persist for up to 31 days in the field (Schneirla and Brown 1950), and colony movement patterns provide some evidence that conspecific pheromones are being detected and used to avoid raiding areas that have recently been raided by another colony (Franks and Fletcher 1983, Schöning et al. 2005b). Ants possess extraordinarily sophisticated chemosensory apparatus that enable diverse and complex behaviours at individual- and colony-levels (Hölldobler and Wilson 1990, Lach et al. 2010). For example, trail intersection frequency is used in *Leptothorax* ants to measure the internal area of potential nest sites that is consistent with a 'Buffon's needle algorithm' (Mallon and Franks 2000). Driver ants may use an analogous pheromone intersection system for determining when to emigrate under normal circumstances (i.e., in lieu of attacks by predators or interested researchers). In each case – either through detecting their own raid pheromones or those of another colony – the proximal cause of an emigration is to maximise foraging efficiency by avoiding areas with depleted prey abundance. It is not clear how long driver ant pheromones persist in the environment and remain detectable to other colonies, but some laboratory evidence from *D. molestus* suggests they may be more short-lived than those of *Eciton* (Billen and Gobin 1996). Moreover, it is not clear how the higher colony density of driver ants compared to *E. burchellii* might influence these processes, or how these highly complex collective behaviours might be performed physiologically or neurologically at the individual- or colony-level.

The problem for scientists hoping to unravel the emigration dynamics of driver ants is two-fold: the spatial scale at which driver ants move and the importance of interactions between colonies. Driver ants can raid and emigrate at the scale of hundreds of metres and may do so unpredictably day or night. To understand how colony-colony interactions and other factors result in nest relocations, all driver ant colonies in a landscape and their raids and emigrations

need to be exhaustively mapped and followed over the course of months – this is no easy task. However, if driver ant colonies and their activity can be mapped across a landscape, points of raid intersection could be identified and used to test the above hypothesis. Identification of driver ant pheromones using standard methods in chemical ecology (e.g., gas chromatography mass spectrometry) could, in parallel, describe the chemosensory underpinnings of this quintessential driver ant behaviour. If successful, such patterns could be used as empirical ground truths to further explore the potential of predictive agent-based models of colony movement in a landscape using only colony location data, for example. Agent-based models could be a useful tool to predict the movement of driver ant colonies in different forest types, regions, and habitats, especially if driver ants are increasingly thought of as important for African rainforest ecosystems.

Habitat

Although driver ants are typically thought of as a group inhabiting rainforests, some species also occur in savannah, such as *Dorylus burmeisteri* (Gotwald 1974, Schöning et al. 2026) and *D. molestus* (Schöning et al. 2006, Peters et al. 2009). However, driver ant colony density in savannah is approximately four times lower than in closed-canopy forest for species that inhabit both habitats (Leroux 1977). Several driver ant species appear sensitive to desiccation and cease raiding behaviour in very dry conditions (Schöning et al. 2006), or do not emigrate across open habitats (Peters et al. 2009). Habitat preferences are poorly characterised across most driver ant species, though, in general, driver ants appear to attain highest densities in moist tropical rainforest, with some species appearing to be relatively tolerant of drier savannah or farmland habitats.

Diet and trophic ecology

Almost all army ants are formidable carnivores, but amongst the surface-swarming army ants, driver ants exploit the broadest dietary niche and take the largest prey (Gotwald 1974, 1995, Kronauer 2020). Anecdotes of driver ant diet are sometimes sensationalised or exaggerated, and are rarely quantified, but many extraordinary accounts nevertheless originate from reliable sources. Thomas Savage reported in the 1840s, for example, that driver ants killed a range of vertebrates around his residence in West Africa, including a snake ~1.2 m long that lived under the house, tied monkeys, pigs, and fowl, the Southern African rock python, and several other caged animals (Savage 1847). Referring to the attack of driver ants, Savage stated he “...may easily believe that it would prove fatal to almost any animal in confinement.”. Similarly, the highly respected British herpetologist Arthur Loveridge in 1922 provided an in-depth, if horrifying, account of driver ants besieging his house in Tanzania for five days (Loveridge 1922). He noted several reptiles being stripped to the bone by driver ants, including a caged crocodile. The various reports from academics are corroborated by the myriad similar observations made by local people living near driver ants, where anecdotes are given of driver ants preying on various animals in and around their homes and further into the forest. Several other army ant groups, such as *Eciton*, possess relatively blunt mandibles for holding and tearing pieces of arthropod integument apart (i.e., plier-like), whereas driver ant workers of all sizes possess sharp cutting mandibles that can effectively butcher a much broader range of prey (Kronauer 2020). Despite the numerous accounts of driver ants killing and consuming large vertebrates, many of these animals were domesticated and confined, and predation of vertebrates by driver ants in more natural settings is less common.

In general, the diet of driver ants is primarily of invertebrate origin and can vary substantially between regions and species in terms of which invertebrate groups are most frequently consumed (**Figure 6**; Gotwald 1974). For example, *D. molestus* around Mount Kenya mainly consume earthworms but also consume large numbers of insects when examined at higher altitude (Schöning et al. 2008c). In Uganda, *Dorylus wilverthi* mainly consume insects, which constitute over 90 % of prey biomass intake (Schöning et al. 2008c). The taxonomic informality of the *Dorylus nigricans* species group makes precise identification of the prey spectra of different driver ant species a challenge, but it appears exceptionally broad and mainly consists of arthropod prey (Gotwald 1995). Recent research conducted in Equatorial Guinea shows that *D. wilverthi* primarily consume insects, but other arthropods, such as spiders, make up a substantial portion of their total dietary intake, and small frogs and lizards are also naturally taken by the species (Huber et al. 2026). Huber et al (2026) also identified the diet of *D. sjostedti* for the first time, showing that the species similarly relies on arthropod prey (Huber et al. 2026). Interestingly, the diet composition of sympatric *D. wilverthi* and *D. sjostedti* in Equatorial Guinea appears remarkably similar, with almost complete dietary niche overlap at the order-level, though this could change substantially if prey intake was analysed at the family-, genus-, or species-levels (Huber et al. 2026). Other aspects of the species' niches could be divergent to minimise competition, but this has not yet been tested. Despite the many anecdotes of driver ant predatory behaviour, only a handful of studies – cited above – robustly quantify prey intake and identity, and our knowledge of the diet of driver ants is therefore based on a few studies in geographically isolated pockets.

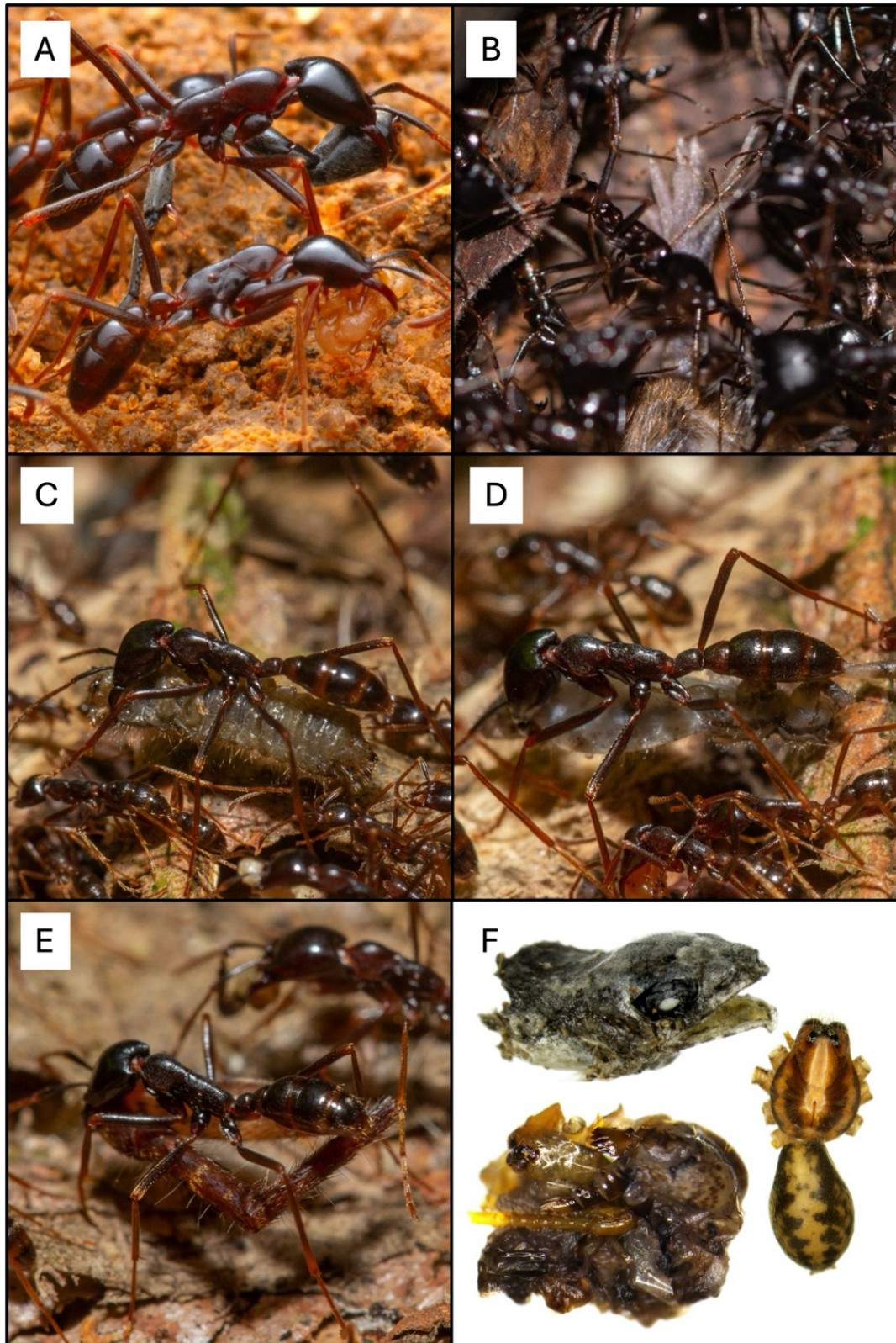


Figure 6. The prey of driver ants. Panel A: *Dorylus sjostedti* with ant prey; Panel B: *Dorylus wilverthi* butchering a small mammal; Panels C, D, E: *D. sjostedti* carrying a beetle larva, hemipteran nymph, and spider leg, respectively; Panel F: additional prey items found on driver ant columns include geckoes, balls of mashed up prey of different origin, and arthropod prey with extremities removed, like the spider pictured. Photo credits: Panel A – NCJFV; Panels B – E – Ibon Malaxetbarria; Panel F – SH. All photos were taken in Equatorial Guinea.

A few patterns emerge from these quantitative diet studies. Firstly, driver ants have very broad diets, but their diet composition often appears to be determined by the availability of prey in a given area, perhaps more than 'prey preferences' *per se*, though pairing of prey availability and prey intake has not been done quantitatively. Prey intake nevertheless varies substantially between different raids, probably resulting from different prey communities (Gotwald 1974, Schöning et al. 2008c, Huber et al. 2026). Some taxa also appear to be avoided by driver ants despite their abundance. Termites are among the most abundant insects in tropical forests but are seldom consumed by driver ants, and a similar pattern is true of adult beetles in the leaf litter (Gotwald 1974, Schöning and Moffett 2007, Schöning et al. 2008c, Huber et al. 2026). Presumably, termites are not an optimal prey group to exploit because of their robust nest structures and specialised combat tactics within them, putting driver ants at a disadvantage during confrontations. It is unclear why adult beetles may not be consumed as expected based on their abundance, but chemical deterrence and escape ability may allow beetles to reduce driver ant predation effectiveness. In most locations studied, other ants are only very rarely consumed by driver ants (Schöning et al. 2008c), but recent work in central Africa shows that 11.2 % of prey items taken by *D. wilverthi* are of other ants, rising to 14.1 % in *D. sjostedti* (Huber et al. 2026). The discrepancy in predation of ants between studies probably represents the difference in their availability as prey for driver ants in different regions and habitats. Several studies were conducted in higher altitude forest between 1000-2000 m a.s.l. where ant abundance was not particularly high, whereas the field sites in central Africa in more recent work are located at ~640 m a.s.l. and ants numerically dominate leaf litter communities. This level of predation may nevertheless still represent a lower frequency of consumption than expected based on the abundance of ants.

Whilst the very broad generalities of diet are known for most driver ant species, several aspects of their trophic ecology remain unclear. Principally, it is not well understood how diet varies between regions, habitats, and seasonally for the more widespread driver ant species such as *D. wilverthi*. Potential prey communities can be substantially different between forest and shrub, or high altitude moist montane forest or lowland deciduous rainforest; understanding how a given driver ant species responds to these differences is a major aspect of their trophic ecology that we do not fully understand. Moreover, diets have not been properly quantified for several members of the *D. nigricans* species group. Whilst this latter point is in part due to the persistent taxonomic confusion within driver ants, it would be worthwhile to quantify prey intake for each driver ant species to understand any similarities and differences. Perhaps most intriguingly, a recent study shows almost complete dietary overlap between *D. sjostedti* and *D. wilverthi*, presenting the question of how these species coexist (Huber et al. 2026). Diet analyses with higher taxonomic resolution of prey at the genus- or species-level, for example, could show dietary differences between the two species. Examining the trophic ecology of multiple coexisting species of driver ants at high taxonomic resolution can identify the components of the community that are most likely to be affected by their raids and how driver ants might partition the trophic niche space.

New molecular tools and statistical approaches can help answer longstanding questions in driver ant trophic ecology. By comparing invertebrate community abundance and prey intake frequency, powerful null networking analyses can determine which prey are disproportionately selected or avoided by predators (Vaughan et al. 2018, Tercel et al. 2026). This is useful to quantify the relative selection of prey by different driver ant species, and analyses can be run at different taxonomic levels to identify patterns at different scales. Moreover, molecular

approaches have revolutionised the field of trophic ecology (Alberdi et al. 2019) where dietary DNA metabarcoding (Cuff et al. 2023b, Tercel et al. 2024, 2025, 2026) and targeted prey barcoding (Hoenle et al. 2019, 2024) offer the tantalising opportunity to identify the prey of invertebrate predators to the species-level. These methods are particularly useful for army ants that dismember, dissect and otherwise destroy their prey, usually rendering them impossible to identify morphologically past order-level. Species-level prey identification could allow researchers to highlight how diets that appear similar at the order-level might diverge at greater taxonomic resolution. Furthermore, precise functional information can be assigned to prey species from family- or genus-level information using genetic assignments. These new statistical approaches and molecular tools are untapped in driver ant research and will undoubtedly further our understanding of driver ant trophic ecology if used effectively.

Impact of raiding

The immediate impact of raids and subsequent recovery of communities

A single colony of driver ants can raid thousands of square metres of forest each day, bringing vast quantities of animal biomass back to the nest. Would it therefore be reasonable to assume that their raids might impact a wide variety of animals over a large area of the forest (Gotwald 1995)? Perhaps; the cultural importance of driver ants across tropical Africa speaks to this assumption (Van Huis 2021) but, astonishingly, only a single study examines how driver ant raids affect animal communities. The study focussed on *D. molestus* on Mount Kenya, where it primarily consumes earthworms (about 50% of prey intake biomass) (Schöning et al. 2010). Across 25 raids, *D. molestus* reduced the number of earthworms but not the biomass of the earthworm community overall (Schöning et al. 2010). The authors state that the 307-fold range in individual earthworm biomass made these comparisons challenging. No studies have been published on how driver ant raids affect diverse communities of leaf litter arthropods. Although measuring community changes caused by driver ant raids might be a logical step to understand their role and impact in tropical forests, it is not easy. Tropical rainforests, where driver ants primarily inhabit (Gotwald 1995), are the most diverse ecosystems on Earth and harbour the majority of species (Ghazoul and Sheil 2010). Hyperdiverse invertebrate communities explain much of this diversity and, being the primary prey group of driver ants, studying them in the wake of raids has historically required taxonomic expertise in breadth and depth outside the remit of many projects. Moreover, high spatial variation in community composition and abundance can confound comparisons. Coarse taxonomic assortment and quantification of abundance might tell part of the story, but higher resolution taxonomic and trait-based information is required to describe how a raid impacts animal communities in terms of compositional and structural change, shifts in functional trait distributions, and the multiple dimensions of diversity that are affected once a raid sweeps through. Evidence from diet studies and observational or anecdotal evidence suggests that raids might exert heterogeneous pressure across a community, with some groups vulnerable to predation and others resilient or unchanged by raids. Insect larvae, particularly lepidopteran caterpillars, are slow moving and often recovered from raid columns (Gotwald 1974, Schöning et al. 2008c, Huber et al. 2026), whereas social insects such as termites and other ants appear to be rarely consumed despite their vast abundance in the leaf litter (Schöning and Moffett 2007, Huber et al. 2026). Similarly, some animals possessing powerful defences are almost never preyed upon by driver ants. MPTGT and SH observed a ~20 cm giant African olive millipede (*Telodeinopus aoutii*) walk onto a *D. sjostedti* raid column with no aggressive reaction from the ants; it was presumably avoided because of its noxious chemical secretions. Such

observations evidence the potentially strong heterogeneous impact of raids across a community that might lead to a substantial shift in community composition.

If compositional shifts do occur after a raid, it is not clear whether they persist over time, nor how quickly and in what form diverse invertebrate communities may recover after driver ant raids. As mentioned previously in the review, temporal aspects of invertebrate community recovery and the depletion of certain components of communities likely explain the nomadism of army ants – to avoid inefficiently revisiting recently raided areas (Gotwald 1974, 1995, Schöning et al. 2011). Presumably, driver ants extract significant biomass from components of the community that does not sufficiently recover before the next hypothetically optimal raid, but this has not been measured. It is possible that communities do recover to pre-raid biomass levels, but if driver ants preferentially select certain prey, this might not be enough to warrant re-raiding the area. For example, driver ants prey on caterpillars (Gotwald 1974, Schöning et al. 2008c, Huber et al. 2026) but this component of the community may not recover in time to energetically justify driver ants re-raiding an area. In this hypothetical scenario, the composition of the community may remain changed for quite some time.

The potential role of driver ants in supporting diversity

Raids can also be viewed as transient ecological disturbances that move through and disrupt communities. In this sense, army ants – including Neotropical army ants like *Eciton* and *Labidus* – have been hypothesised to generate diversity at the landscape-scale by creating a patchwork of communities at different stages of recovery (Franks and Fletcher 1983, Otis et al. 1986, Gotwald 1995, Kaspari et al. 2011, Schöning et al. 2011). Intermediate strength natural disturbances, such as tree falls, fires, other physical alternations of the environment, and the hunts of mobile social predators have long been hypothesised to promote biodiversity because they create opportunities for species that are different to those of the surrounding environment (Janzen 1970, Connell 1978, Denslow 1987, Whitmore 1989, Fortin et al. 2005), though this is not always well-supported by empirical evidence (Fox 2013, Moi et al. 2020). Raids by driver ants cover large areas of forest, removing individuals through predation, flushing out and subsequent predation by ant-following birds or predatory and parasitic insect associates, or through fleeing to a new area of forest away from the raid. Thus, raided communities may be quite different from communities found in the surrounding landscape. Scaling this up, the average level of dissimilarity between communities across a landscape with high raiding pressure may therefore be higher than one with low or no raiding pressure. In this way, raids might support high beta-diversity (Franks and Fletcher 1983, Gotwald 1995, Schöning et al. 2011). There is some evidence of this from *Eciton* in the Neotropical system, showing that their raids can substantially influence populations of social insects in the long term, whereas other prey populations recover quite quickly (Franks and Fletcher 1983, Otis et al. 1986). Further research is needed in the Neotropical system to properly test the theory. In general, communities experiencing an ecological disturbance pulse typically decrease in richness and abundance, then quickly recover due to the migration of new individuals into the area, but compositional change persists for substantially longer (Hillebrand and Kunze 2020). If raids perform ecologically like other pulse disturbances, it will support the hypothesis that raids promote community patchiness and beta-diversity (Peters et al. 2013). However, no published studies examine how compositional or functional compartments of communities shift and recover after raids by driver ants or any other swarm-raiding army ant. The hypothesis therefore remains untested empirically.

683 *Challenges in measuring the impact of raids*

684 Measuring how raids impact invertebrate communities in detail presents an extraordinary
685 challenge. Tropical communities are hyperdiverse: two communities in nearby patches of leaf
686 litter may vary in their richness and abundance by two orders of magnitude (Levings and
687 Franks 1982, Levings 1983, Levings and Windsor 1985, Yankelevich et al. 2006, Kaspari et
688 al. 2011), making comparisons between samples challenging. A way to overcome this is to
689 sample a large area of leaf litter, or sample and pool multiple smaller areas of leaf litter. A more
690 robust comparison can then be made between a raided and unraided area because samples
691 accommodate some of this spatial variation (Schöning et al. 2010, Kaspari et al. 2011).
692 Nevertheless, even with such samples, the abundance and diversity of organisms extracted
693 can be overwhelming for researchers. In one of the only studies quantifying the immediate
694 effect of army ant raids, Kaspari et al (2011) measured how *Eciton* and *Labidus* raids influence
695 invertebrate biomass, length, and density in the Neotropics. This was done by collecting 1.25
696 m² leaf litter samples (5 x 0.25 m²) before and after a raid has passed. Across 30 raids, they
697 extracted and processed a total of 119,619 litter invertebrates. Assigning species-level
698 information and functional traits to such a vast number of invertebrates requires a substantial
699 commitment in the lab that may not be supported by funding cycle timelines, personnel, or
700 institute infrastructure. It is also difficult to envisage how to minimise this work or find shortcuts
701 whilst properly answering the research question. Even in the age of high-throughput DNA
702 metabarcoding and efficient barcoding pipelines on a massive scale, critical dimensions of
703 community diversity would be lost if invertebrate communities are characterised solely using
704 these methods. For example, if communities were described only using bulk DNA
705 metabarcoding approaches, abundance and biomass could not be accurately computed within
706 or between taxa due to biases and stochasticity in the amplification of DNA using PCR primers
707 (Elbrecht et al. 2019, Tercel et al. 2021, Cuff et al. 2023a), and even PCR-free sequencing
708 approaches mask differences between taxa in field-collected community samples (Zhou et al.
709 2013, Thomas et al. 2016, Braukmann et al. 2019). The morphology and size of invertebrates
710 would also remain a mystery. Coarse data could be obtained by, for example, weighing all
711 specimens in a sample in bulk, but this would only provide coarse sample-level differences
712 and would not show heterogeneous effects between taxa that is expected to arise from raids.
713 These are crucial aspects of how a community might respond to driver ant raids, and losing
714 such data would prevent the calculation of informative dimensions of diversity necessary to
715 test the theory and understand the system overall.

716 Quantifying the indirect impact of driver ant raids is perhaps even more challenging. As
717 animals flee from raids, they may escape the advancing swarm only to be consumed by the
718 dozens of species of ant-following birds or predatory invertebrates commonly found at the raid
719 front. It should be stated that, by measuring invertebrate communities as outlined above, it
720 can describe the cumulative direct *and* indirect impact of army ant raids: invertebrates absent
721 from the litter after a raid may have been consumed by driver ants or their many associates,
722 or they may have simply fled. Quantifying the long-theorised effect of driver ant raids is not an
723 insurmountable challenge. Combining careful and rigorous application of conventional
724 methods in entomology and community ecology alongside new tools, such as DNA-based
725 approaches and videography, can begin to answer how driver ant raids alter animal
726 communities in African forests. For now, however, the true impact of driver ant raids remains
727 an enduring mystery.

Associates of driver ants

Colonies of driver ants attract a veritable menagerie of parasites and commensals that live within the nest, follow raids, and emigrate with the colony. These associations may be obligate or facultative and are seen across a range of taxa, including birds, mammals, reptiles, arachnids, worms and many orders of insect represented by over 500 described species (Kistner 1979, Kronauer 2020). Unfortunately, a comprehensive discussion of all of these groups is outside the remit of the current review. A large discrepancy in our ecological knowledge exists between different groups of associates and predators: whilst many of the vertebrates associated to driver ants have been relatively well-studied, we know very little or nothing of most of the myriad invertebrates that live within nests or follow raids. Throughout this section, we use the term ‘associate’ very broadly to refer to any species that benefits from direct interaction with driver ants, including facultative predators, parasites, and commensals from any taxon.

Vertebrates

Ant-following birds

Among the most iconic associates of driver ants are the ant-following birds (**Figure 7**). This diverse assemblage of species industriously follow driver ant raids to capture invertebrates fleeing the raid front. Explorer Paul du Chaillu published the first observations of ant-following behaviour in equatorial Africa in the mid-19th century:

“The bird is insectivorous; and when the bashikouay [driver ant] army routs before it the frightened grasshoppers and beetles, the bird, like a regular camp-follower, pounces on the prey and carries it off. I think it does not eat the bashikouay.” (du Chaillu 1861).

However, local people recognised ant-following behaviour long before European explorers arrived. For example, the Swahili name for *Neocossyphus* is “shesiafu”, meaning “the one of the driver ants” in Tanzania (Moreau 1942) and the Mbuti people of the Democratic Republic of the Congo have long noted the ant-following behaviour of Fire-crested Alethe, *Alethe castanea*, a specialised ant-follower (Ichikawa 1998). African ant-following birds do not appear to deliberately consume driver ants regularly (Willis and Oniki 1978). Although workers may be found in faecal samples, this probably represents accidental consumption, where a driver ant worker is attacking an insect that is then consumed by an ant-following bird.



Figure 7. African ant-following birds. Panel A: Fire-crested Alethe, *Alethe castanea*; Panel B: Brown-chested Alethe, *Chamaetylas poliocephala*; Panel C: Yellow-whiskered greenbul, *Eurillas latirostris*; Panel D: White-tailed Ant Thrush, *Neocossyphus poensis*. Photo credits: Panels A – C by Sean Glynn; Panel D by LLP.

Craig et al (2022), through a literature search, found 168 species of African birds from 36 families forage in association with driver ants, of which 116 are ‘occasional’ followers and 52 are ‘regular’ followers. Muscicapidae, Pycnonotidae, and Turdidae are particularly well represented among the ant-followers, comprising 38 of the 52 regular ant-followers (Craig 2022). Recent research conducted in central Africa detected a further 21 undocumented species and three additional families (Calyptomenidae, Cuculidae, and Oriolidae) attending driver ant raids (Rodrigues 2024). More new records will surely be found through further surveys in other parts of Africa. For most species found to be attending raids, it is not yet entirely clear how dependent they are on driver ants, i.e., where they exist on the obligate-facultative spectrum (Craig 2022). A handful of bird species, however, show predictable, strongly specialised ant-following behaviour. In Keyna, Peters et al (2008) found that five bird species attended raids much more often than predicted by their densities: White-tailed Ant Thrush (*Neocossyphus poensis*), Brown-chested Alethe (*Chamaetylas poliocephala*), Red-tailed Bristlebill (*Bleda syndactylus*), Gray-winged Robin (*Sheppardia polioptera*), and Equatorial Akalat (*Sheppardia aequatorialis*). Similarly, in central Africa, Rodrigues (2024)

found several species attending a high proportion of raids: Fire-crested Alethe (*Alethe castanea*, 95% of raids), Yellow-whiskered greenbul (*Eurillas latirostris*, 77% of raids), Brown-chested Alethe (*Chamaetylas poliocephala*, 72% of raids), White-tailed Ant Thrust (*Neocossyphus poensis*, 62% of raids), and Yellow-lored Bristlebill (*Bleda notatus*, 54% of raids). Several of the species listed above are thought to be obligate ant-followers (Peters et al. 2008, Craig 2022, Rodrigues 2024). Some bird species have also been shown to only breed in territories with active driver ant nests (e.g., *Chamaetylas fuelleborni*) (Dowsett-Lemaire 1987).

Some of these bird species also show additional distinctive behaviours that underpin their reliance on driver ants. Although bivouac-checking had previously been documented in Neotropical ant-following birds (Swartz 2001, O'Donnell et al. 2010), evidence of this behaviour in Africa was limited to anecdotal observations (Willis 1986). Using camera traps in Equatorial Guinea, Rodrigues (2024) recently provided the first definitive evidence that African ant-following birds also inspect driver ant nests, often arriving early in the morning, examining nests from nearby perches and then departing, presumably to locate active raids. Twelve species were recorded checking nests, and the frequency of this behaviour was strongly correlated with swarm attendance ($r_s = 0.9$), suggesting that it is particularly important among specialised ant-followers. These findings challenge the assumption that the subterranean nests and unpredictable movements of driver ants prevent African birds from evolving the sophisticated behavioural adaptations known in their Neotropical counterparts.

Chimpanzees and gorillas

Chimpanzees (*Pan troglodytes*) and mountain gorillas (*Gorilla beringei beringei*) facultatively prey upon driver ants. Most famously, wild chimpanzees feed on driver ants using tools (McGrew 1974, 2010, Schöning et al. 2008b). Opening the surface of *Dorylus nigricans* nests using their hands, chimps then dip a twig into the driver ant nest in an intricate process to recover and consume 17-20g of workers per feeding session on average (McGrew 1974). There is substantial cultural variation between chimp groups across their range and the process of feeding on driver ants is quite variable (McGrew et al. 1979, Koops et al. 2015), and some groups eat considerable quantities of driver ants, present in up to 40% of faecal samples (Sommer et al. 2017). Some groups of chimps use a stick to open the nest and a blade of grass is then used to acquire the ants rather than woody vegetation (McGrew et al. 2005). In contrast, some groups of chimps do not feed on sympatric driver ant colonies at all (Nishida and Hiraiwa 1982, Schöning et al. 2008b). Colonies attacked in this way probably emigrate soon after, and the main danger to the ants is the inadvertent killing of the queen as a chimp opens the nest and fishes for workers.

In contrast to chimps, gorillas only very rarely consume driver ants and do not use tools to do so, instead picking them up in their fingers (Watts 1989). Not all populations of gorillas consume driver ants, and the frequency of consumption can vary at small spatial scales; Ganas and Robbins (2004) found that two groups of gorillas within the same national park consumed driver ants at significantly different frequencies. Female and juvenile gorillas most frequently consume driver ants, whilst silverbacks very rarely do so (Watts 1989, Ganas and Robbins 2004). Differences in consumption between ape groups and populations may be cultural, though differences might arise as a function of driver ant colony density.

823 *Pangolins*

824 If driver ants possess a mortal enemy from the vertebrate realm, it is surely the pangolin. Using
825 their powerful front claws, pangolins dig up driver ant nests and consume workers using their
826 long tongues. Schöning et al (2005b) found that pangolin attacks on nests of *D. molestus* in
827 Kenya triggered colony emigrations, though these were quite rare, and observed only six times
828 in a 9-month period across ~45 colonies. Pangolin attacks on driver ant nests are probably
829 most frequently performed by the giant ground pangolin, *Smutsia gigantea*, but the smaller
830 semiarboreal species such as the white-bellied pangolin, *Phataginus tricuspis*, may also eat
831 driver ants (Bequaert 1922, Gotwald 1995). The stomach of one giant ground pangolin
832 contained 6 litres of driver ants in its hindgut (Bequaert 1922), representing by far the most
833 substantial record of a vertebrate preying on driver ants to date. The defensive response of
834 driver ants does nevertheless appear to cause some discomfort even to these well-armoured
835 foes, as written by Herbert Lang (in Bequaert, 1922):

836 “Sitting on its hind limbs and with its tail steadying its movements,
837 the fore part of the body was swung about freely. The claws of
838 the forelimbs were kept busy removing those of the fierce
839 assailants that, in spite of the oft repeated shivering movements
840 of the scaly armour, succeeded in gaining a hold. Lashing its
841 sticky tongue through the confused crowds, the ant-eater lost no
842 time in moving back and forth along the ant column as quickly as
843 the dense clusters vanished into its mouth. Its hunger satisfied, it
844 at once retreated, freeing itself of the few army ants that had
845 managed to dig their mandibles into the soft parts of its hide.”.

846 Not all pangolin individuals appear to immediately consume driver ants when encountered,
847 with some simply ignoring the columns (Bequaert 1922).

848 *Blind snakes*

849 Perhaps the most enigmatic vertebrate associate of driver ants are blind snakes (Typhlopidae)
850 – fossorial snakes that possess vestigial eyes and feed on social insects living in the soil. No
851 published studies exist on the life history, ecology, prevalence, or distribution of blind snakes
852 interacting with driver ants. It is also unclear whether these blind snakes are specialised on
853 driver ants or if there are multiple species interacting with driver ants. Schöning et al (2005b)
854 state that, in Kenya, *Afrotyphlops lineolatus* move in *D. molestus* emigration columns
855 alongside the ants as they find a new nest site. Gotwald (1995) never observed this behaviour
856 in blind snakes from over a decade of research in Africa, and found only one individual after
857 excavating an active driver ant nest in Ghana. Local people in Tanzania have also made these
858 observations, calling blind snakes the mkonko, or ‘cow of the driver ants’ (Loveridge 1949). A
859 widespread story describes blind snakes peacefully slithering alongside driver ants in their
860 columns protected by the soldiers, only to be killed and eaten by the ants when the colony is
861 short of food (Loveridge 1949, Gotwald 1995). Independent observations in Kenya, Tanzania,
862 and Ghana suggest blind snakes and driver ants interact throughout tropical Africa.
863 Videography during colony emigrations, and close to the nest, might help reveal the
864 prevalence of interactions between blind snakes and driver ants. The typical diet of blind
865 snakes consists of social insects living in the soil, and it is therefore assumed that blind snakes

interacting with driver ants probably parasitise colonies by consuming individuals whilst living in the nests. The obvious question is how these small snakes avoid being killed by driver ants. Similar to driver ants in Africa, blind snakes in the Neotropics (genus *Leptotyphlops*) have been found following columns and in the nests of the army ant *Neivamyrmex nigrescens* (Watkins et al. 1967). In lab experiments, ant workers did attack blind snakes, but this elicited a writhing and coiling response from the blind snakes where they quickly cover themselves in a pungent mixture of viscous liquid and faeces that repelled army ants (Watkins et al. 1967, 1969, Gehlbach et al. 1968). A similar chemical method may be used by African blind snakes to subdue driver ants but that, and all other aspects of their life-history, are poorly understood.

Other vertebrates

Various other vertebrates interact with driver ants as facultative predators. Joseph Bequaert (1922) listed driver ants being consumed by five species of *Bufo* toads and three genera of frogs (*Rana*, *Kassina*, *Hemisus*) across the Congo basin, and *Trachylepis affinis* forest skinks and the African mongoose *Bdeogale nigripes* also appear to consume workers on columns. Aardvarks have also been found to consume *Dorylus* (Patrizi 1946, Willis et al. 1992, Taylor et al. 2002), and aardwolf faeces sometimes contain *Dorylus* despite typically being a predator of termites (Kruuk and Sands 1972). The guinea fowl, *Phasidus niger*, also consumes driver ants (Chapin and Lang 1932), as do domestic chickens (Gotwald, 1972). Doubtless there are many more vertebrates that feed on driver ants opportunistically but, without specialised behavioural or physical adaptations to overcome the defensive response of driver ants, this may be short-lived or highly dependent on individual predator behaviour and their tolerance to bites.

Humans

Driver ants carry significant cultural value and utility in sub-Saharan Africa, and are not typically used as food by people (Van Huis 2021). In Cameroon, Kenya, Tanzania, Togo, and Nigeria, driver ants are instead (usually) welcomed into the home as a form of pest control, where they remove cockroaches, mice, snakes, scorpions, and termites (Van Huis 2021). In Nigeria, Yoruba people go a step further and collect driver ant soldiers to pour into snake burrows. The Mofu of Cameroon believe driver ants are 'jaglavak', the prince of insects (Seignobos et al. 1996), and collect majors with leaves of *Ficus abutilifolia*, releasing them into their homes to clear termites (Seignobos et al. 1996, Van Huis 2021). They even attempt to direct the ants using an ochre trail to parts of the house with infestations. But how does one prevent their house being raided when driver ants are not wanted? Fire is the main method mentioned in Benin and Nigeria, though spreading salt, ashes, kerosene, or petrol are variously used elsewhere in Africa (Van Huis 2021).

People across Africa also have several proverbs relating to driver ants. Yoruba people in Nigeria say, "it is not possible for the soldier driver ant to put on the trousers of a giant, but it is possible for the soldier driver ant to remove the trousers of a giant", meaning that driver ants are small but can cause damage (Van Huis 2021). In a similar vein, Yoruba people in Senegal say, "if they unite, ants can kill an elephant". A Swahili riddle, known as a kitendawili, goes, "I came across a long chain on the road but could not pick it up" and has two answers: the first is a path or trail, the second is a driver ant column (Van Huis 2021). There are also many varied beliefs and superstitions relating to driver ants; in general, these speak to the respect

909 people have for them and that they are considered powerful spiritually and ecologically (Van
910 Huis 2021).

911 *Invertebrates*

912 The enormous colonies and raids of driver ants present opportunities for a diverse assemblage
913 of invertebrates to exploit their nests, workers, prey, and middens. The best documented
914 associates are myrmecophilous beetles, particularly rove beetles (Staphylinidae), which can
915 occur within driver ant colonies and accompany their raids. The biology of the vast majority of
916 invertebrate associates is poorly understood. Much of what is known about driver ant
917 associations comes from taxonomic and natural-history studies conducted more than a
918 century ago, and many host records remain unresolved to species level (Parker 2016). This
919 is a major departure from the Neotropical army ant literature, where the ecology of associates
920 is far better understood (Rettenmeyer et al. 2011, Pérez-Espona et al. 2018, Von Beeren et
921 al. 2018, 2021).

922 *Facultative predators*

923 Despite their abundance, aggressive behaviour and enormous colony sizes, driver ants are
924 themselves attacked by a range of opportunistic predators. Among invertebrates, the African
925 weaver ant, *Oecophylla longinoda*, is the clearest example. Gotwald (1972) observed *O.*
926 *longinoda* workers successfully attacking driver ant workers on five separate occasions in
927 Ghana and considered the species to be a relatively common predator of driver ants (**Figure**
928 **8A**). Impressively, weaver ants were able to remove individual driver ants from foraging
929 columns without apparently triggering the widespread alarm response that normally
930 accompanies attacks on a driver ant column (Gotwald, 1972; pers. obs.). Other ants also prey
931 upon driver ants, including *Paltothyreus tarsatus* (Gotwald, 1972; pers. obs.), *Crematogaster*
932 (pers. obs.), and *Pheidole* (Gotwald 1995). Other army ants can also be a major source of
933 mortality. Leroux (1982), in a long-term study on *D. nigricans* conducted in the Ivory Coast,
934 concluded that attacks by subterranean *Dorylus* (*Typhlopone*) colonies were the most
935 important cause of colony death (**Figure 8B**). Spiders and other arthropod predators may
936 similarly exploit individual driver ants, particularly injured workers or males. For example, large
937 spiders have been observed capturing *Dorylus* males attracted to lights, but this represents a
938 very different interaction from predation on workers (Gotwald, 1995; Kronauer, 2020). The
939 apparent rarity of specialised invertebrate predators of driver ants is notable given the
940 enormous biomass concentrated in their colonies and the accessibility of workers during
941 surface raids. However, driver ants are highly mobile, aggressive, and possess large colonies,
942 potentially making sustained predation difficult.

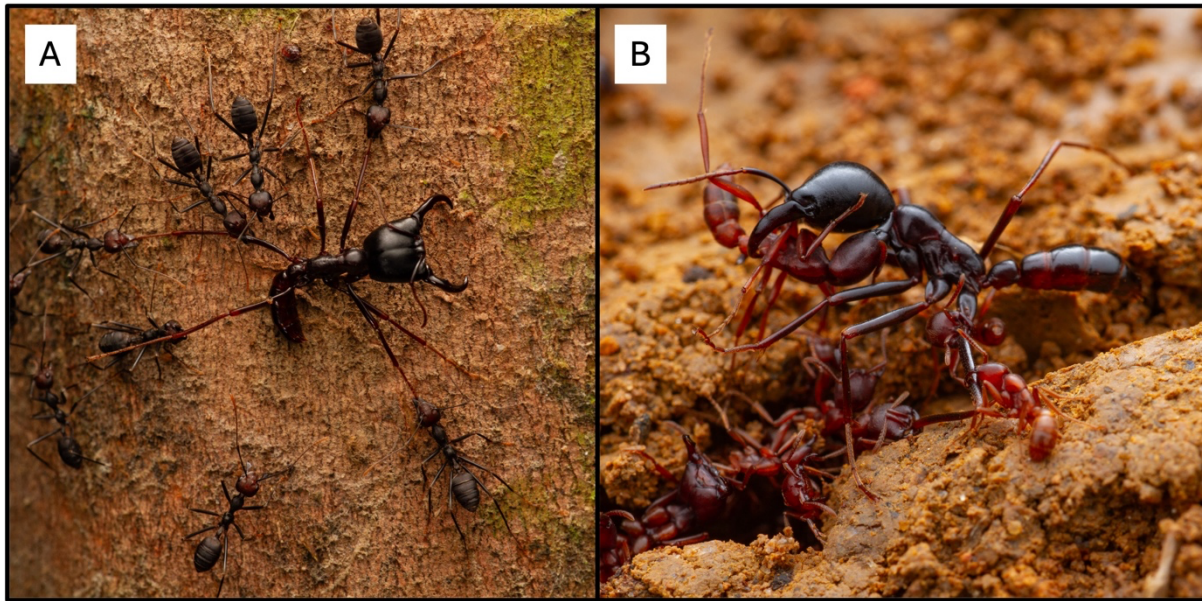


Figure 8. Other ants sometimes attack and kill driver ant individuals. Panel A: *Oecophylla longinoda* can be seen here with a large spreadeagled *Dorylus sjostedti* worker; Panel B: workers from a subterranean *Dorylus* sp. seen attacking a large *D. sjostedti* worker along a raid column. Both photos are by NCJFV in Equatorial Guinea.

Rove beetles (Coleoptera: Staphylinidae)

Early naturalists were amazed by the diversity of myrmecophilous rove beetles associated to driver ants, struck by the paradox that such a formidable predator could be accompanied by myriad beetles (**Figure 9**). Erich Wasmann documented more than 30 staphylinid species belonging to approximately 15 genera in *Dorylus wilverthi* colonies in the Congo (Wasmann 1900, 1912). Wasmann broadly classified myrmecophilous staphylinids into several morphological types, including ant mimics, more generalised 'protective' forms, and symphilic associates that appear to integrate closely into the host colony. Some species were observed travelling directly within driver ant columns, whilst others occupy the rear of the advancing army (Wasmann 1900, 1912). These exhibited a range of morphological and behavioural adaptations for life with driver ants, such as reduced tarsi and specialised body shapes (Wasmann 1912). For example, *Mimocete*, *Doryloxenus* and *Anommatoxenus* are all limuloid (rounded, like a *Limulus* horseshoe crab) in shape, which helps individuals slip through the mandibles of their host ants and find small crevices to hide (Kistner 1979). Attacks on beetle associates have been observed frequently, but their rounded shape usually allows individuals to escape (Kistner 1979, Parker 2016). Moreover, if a beetle is successfully arrested by its driver ant hosts, many species are capable of producing chemical defences that repel the ants (Kistner 1966a), e.g., in *Phyllodinarda* (Kistner 1965a).

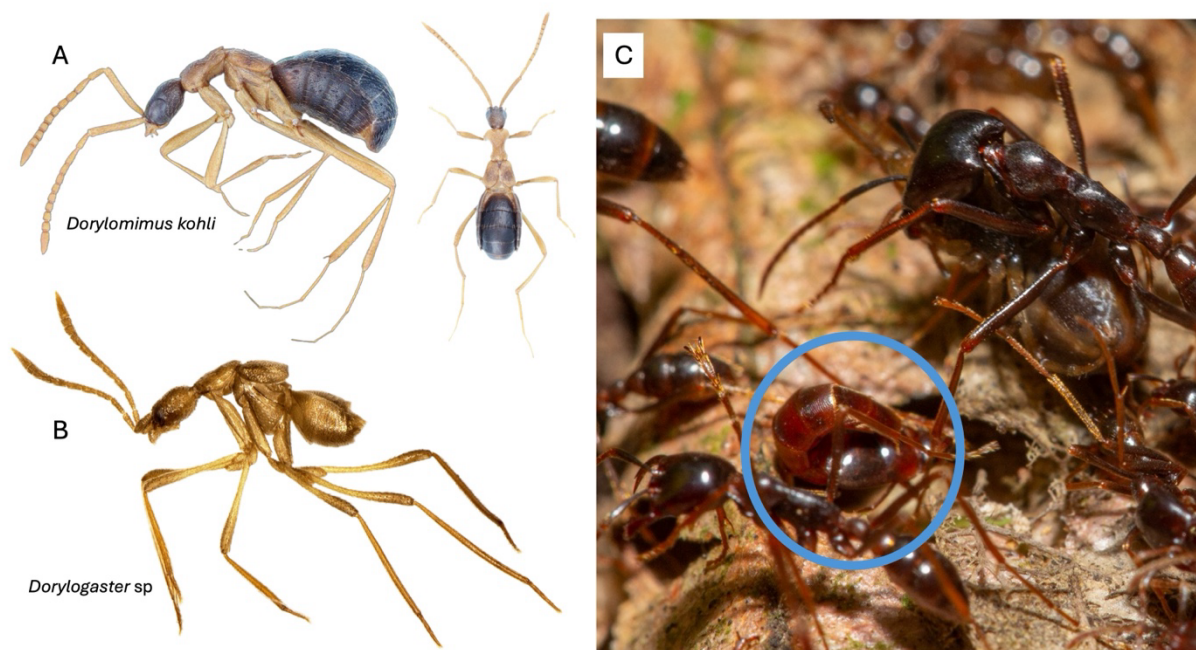


Figure 9. Staphylinid beetle associates of driver ants. Panels A and B show *Dorylomimus kohli* and *Dorylogaster* sp, respectively, edited from Figure S1 in Maruyama and Parker (2017). Panel C denotes a staphylinid beetle, highlighted with a blue circle, amidst a raid column alongside workers returning to the nest with prey; photo taken in Equatorial Guinea by Ibon Malaxetbarria.

Several ‘dorylophilic’ staphylinid genera possess highly specialised adaptations allowing them to exploit driver ant colonies. Wasmann (1912) observed *Doryloxenus* riding on the abdomen of driver ants, whilst later observations describe individuals repeatedly climbing onto workers and moving between the legs and thorax to avoid attempts by soldiers to dislodge them (Kistner 1965b, 1979), allowing them to avoid attacks by the ants (Wasmann 1912, Kistner 1979). The genus currently contains 52 described species distributed across Africa and Asia, but it is unclear how many species live within driver ant colonies and the strength of their host relationships; many host records are incomplete and most African species are recorded only from ‘*Dorylus* sp.’ without resolution to driver ants specifically (Kistner, 1965b, 1979).

Other staphylinids show even closer integration with driver ant colonies. *Sympolemon*, for example, was described by Wasmann as a true symphile of driver ants, with individuals occurring within the raid and exhibiting behaviour and morphology associated with close integration into the host colony and no aggression (Wasmann, 1900, 1912). Several genera classified as ant mimics, including *Dorylomimus*, *Dorylogaster* and *Dorylonia*, closely resemble their hosts and appear to gain access to the colony through morphological and behavioural mimicry (Kistner 1966a, 1966b, 1979). *Dorylogaster*, for example, has been observed using phoresy to move on individual ants, whereas species of *Dorylomimus* closely resemble their host workers and can move within the colony with little apparent disturbance (Kistner 1966a). Together, *Pygostenus*, *Anommatoophilus*, *Anommatoxenus*, and several other specialised genera illustrate the diversity of strategies by which rove beetles exploit driver ant colonies, ranging from active attachment to close integration within the colony and morphological mimicry. Most staphylinid associates of driver ants were recorded and described between 1900-1970, cumulatively representing an enormous sampling effort. However, the level of host specificity, mating and movement behaviour, diet, distribution,

996 longevity, and the exact nature of the relationship with their hosts has remained unstudied for
997 decades. Dietary DNA metabarcoding to determine their trophic interactions and methods in
998 chemical ecology determining how they integrate into driver ant colonies may help reveal their
999 ecology in more depth.

1000 *Diptera*

1001 Dipteran associates of driver ants are considerably less well documented than are the
1002 staphylinids but appear to exploit colonies and raids in a variety of ways. Phorid flies are
1003 particularly diverse: *Dorylus nigricans* has been recorded with at least seven species, including
1004 *Hexacanthrophora cohabitans*, three species of *Psyllomyia* and *Puliciphora karensis*,
1005 although the nature of most of these associations is unknown (Quevillon 2018). Other phorids
1006 appear to be more specialised parasitoids; two unidentified *Megaselia* species have been
1007 recorded as parasitoids of *D. nigricans*, with transmission occurring outside the nest, while
1008 *Aenigmatopoeus* species have been associated with several African driver ants, including *D.*
1009 *wilverthi*, *D. molestus* and *D. sjostedti* (Quevillon 2018). *Aenigmatopoeus* is a specialised
1010 genus of ant-parasitising phorids, although the precise biology of its associations with driver
1011 ants remains poorly known. Together, these records suggest that driver ant colonies may
1012 support dipterans ranging from relatively loose associates to highly specialised parasitoids,
1013 but the paucity of behavioural observations makes their ecological roles difficult to determine.

1014 Driver ant raids also create ephemeral feeding opportunities for flies that exploit the
1015 disturbance and prey exposed by the advancing raid, presenting the interesting conclusion
1016 that Diptera and ant-following birds have convergently evolved the same behaviours multiple
1017 times each. *Stylogaster* (Conopidae), for example, has been recorded over driver ant swarms,
1018 where females parasitise cockroaches and other insects fleeing the advancing ants, as well
1019 as other flies attracted to the swarm (Gotwald 1972, 1995). Some flies appear to exploit the
1020 ants themselves. *Bengalia* (Calliphoridae) has been observed flying around driver ant columns
1021 before darting towards individual workers and stealing prey or brood from them, effectively
1022 exploiting the ants as kleptoparasites and/or predators (Gotwald 1972). Similarly, *Tricylea*
1023 (Tachinidae) species have been observed ovipositing around driver ant nests, although this
1024 association with the ants remains poorly understood and may be commensal in nature (Engel
1025 and Cuthbertson 1937, Rognes 2011). Thus, rather than representing a single form of
1026 myrmecophily, dipteran associations with driver ants encompass parasitoidism, parasitism,
1027 kleptoparasitism, predation, and exploitation of the wider ecological disturbance generated by
1028 raids.

1029 *Middens*

1030 Driver ant middens may represent a further, largely overlooked resource for forest
1031 invertebrates. Driver ants accumulate and concentrate substantial quantities of prey remains
1032 and other refuse around their nests that appear to support diverse scavenging and predatory
1033 arthropods. Historical observations of African *Dorylus* middens noted particularly diverse
1034 assemblages of beetles, including numerous staphylinids (Collart 1934, Paulian 1948).
1035 However, the composition of these communities has received almost no systematic study.
1036 Work on Neotropical *Eciton* provides an indication of the potential importance of these
1037 deposits, with recent research showing that middens can provide food, breeding sites and
1038 nurseries for associated beetles (Von Beeren et al. 2018, 2021, 2021). Whether African driver-

1039 ant middens perform similar functions, and how their communities vary with colony size, prey
1040 composition or nest activity, remains unknown.

1041 *Other parasites and pathogens*

1042 Other parasites and pathogens of driver ants remain poorly documented. Several fungi,
1043 including entomopathogenic fungi, have been reported in *Dorylus*, but many records are not
1044 resolved to particular host species or to driver ants specifically (Quevillon 2018).
1045 Consequently, it remains unclear whether driver ants experience substantial parasite pressure
1046 comparable to that documented in many other social insects. This represents a notable gap
1047 given the enormous colony sizes, high densities of workers and frequent movement of driver-
1048 ant colonies. Parasite transmission may also be unusual in nomadic ants, where colonies
1049 repeatedly abandon and establish nests, but there is currently insufficient evidence to
1050 determine whether colony movement changes the dynamics of parasite transmission.

1051 Driver ant colonies are ecosystems in their own right, supporting a menagerie of associates
1052 that exploit the ants, their prey, their nests, and the disturbance generated by their raids. The
1053 diversity of these interactions is enormous and virtually unmatched by any other animal on
1054 Earth, save the far more intensely studied Neotropical army ant genus *Eciton* (Rettenmeyer
1055 et al. 2011). The diversity and abundance of myrmecophiles in a colony is directly proportional
1056 to the size of the host colony (Kistner 1979, Gotwald 1995, Rettenmeyer et al. 2011) and driver
1057 ant colonies can reach 9 million individuals in *D. nigricans* (Leroux 1982) and upwards of 20
1058 million in *D. wilverthi* (Raignier and van Boven 1955), i.e., 5-10 times the size of the largest
1059 *Eciton burchellii* colonies in terms of the number of individuals. It therefore appears likely that
1060 many more associates remain undiscovered in the driver ant system. Moreover, the literature
1061 is strongly biased towards conspicuous associations discovered by early naturalists, while the
1062 abundance, host specificity and nature of interaction for most associates still remains
1063 unknown. Modern molecular approaches, behavioural observations, and community sampling
1064 could reveal a much larger and more diverse assemblage associated with driver ants than is
1065 currently recognised. In this respect, driver ant colonies may represent not only major
1066 predators of tropical forest communities, but also mobile hotspots of biodiversity around which
1067 diverse assemblages of organisms are provisioned and structured.

1068 **Are driver ants keystone species?**

1069 Since its inception in the 1960s, the term 'keystone species' has been widely integrated into
1070 the lexicon of ecology and conservation science (Paine 1966, 1969, Mills and Doak 1993,
1071 Cottee-Jones and Whittaker 2012). But what does it actually mean? The term was originally
1072 used by Robert T. Paine in 1969 to describe a predator in the rocky intertidal zone, based on
1073 their work in 1966:

1074 *...the species composition and physical appearance were greatly*
1075 *modified by the activities of a single native species high in the*
1076 *food web. These individual populations are the keystone of the*
1077 *community's structure, and the integrity of the community and its*
1078 *unaltered persistence through time, that is, stability, are*
1079 *determined by their activities and abundances.*

There are two aspects of this original definition. The first is that keystone species maintain the structure and diversity of their ecological community. The second, more implicit aspect, is that this structuring force is great relative to other species in the community and depends on the abundance of the keystone species. Ecologists have iterated over this original definition for decades, but, in 1996, scientists working on keystone species produced a consensus definition (Power et al. 1996):

A keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance.

The type of community structuring and disproportionate effect implied by both the original and consensus definitions have very rarely been strictly demonstrated in nature, including in Paine's classic field study (Paine 1966). This is because the idea of proportionality, where a keystone species has a disproportionate influence on its community relative to its abundance or biomass, introduces a major conceptual and methodological hurdle to most natural ecological systems. To properly quantify and test whether a species formally qualifies as a keystone species, all the individuals of all the species in the community have to be counted, and/or the biomass of the suspected keystone species must be compared somehow to that of the entire community (Cottee-Jones and Whittaker 2012). Paine's own original field study did not adhere to properly testing these assumptions (Paine 1966), which took place within an 8 m strip of shoreline, the only species removed was the starfish *Pisaster ochraceus*, and it was not replicated (Paine 1966, Cottee-Jones and Whittaker 2012). Moreover, the vast majority of species are likely to have a very small comparative biomass/abundance relative to their entire community, and therefore most species and almost every top predator could conceivably be described as a keystone species. The keystone species concept therefore has a surprisingly weak empirical foundation (Paine 1966, Mills and Doak 1993, Power et al. 1996, Kotliar et al. 1999, Cottee-Jones and Whittaker 2012). Despite this, the term is very frequently invoked across a huge range of organisms and contexts, including for driver ants.

Driver ants have been called keystone predators since the 1980s (Sudd and Franks 1987) and 106 other published articles have linked the term keystone species to driver ants over the past 40 years (Google Scholar, search term: keystone "driver ants", October 1st, 2026). Driver ants have not undergone formal or informal tests of whether they conform to the consensus definition (or any other accepted definition) of keystone species, and we therefore struggle to see much support for continuing to use the term. We argue that the keystone species concept has little practical applicability to many species seemingly integral to the maintenance of communities and ecosystems, including driver ants. It appears insurmountable to formally test the keystone species concept in the driver ant system, and the critiques offered above also cast doubt on its conceptual underpinnings: almost any predator is likely to be deemed a keystone species when considered against the biomass of its entire community, and if every predator is a keystone species, does the term carry any meaning? This section and the wider review does not therefore conclude that driver ants lack importance, but rather the term itself lacks the practicality and ecological clarity to be applied in hypercomplex natural systems. Quite the contrary: with each new study and perspective, driver ants appear to be increasingly vital components of the diverse web of species present in Afrotropical rainforests, interacting with hundreds of other species as predators, prey, or hosts.

1124 **Conservation and anthropogenic change**

1125 *Habitat loss and fragmentation*

1126 Tropical Africa has lost an estimated 21.7% of its closed-canopy forest since 1900 (Aleman et
1127 al. 2017), and forest loss is predicted to continue as human populations grow and agricultural
1128 and industrial activities increase. Because of the unique biology and life history of driver ants,
1129 deforestation and forest fragmentation may have severe impacts on their populations.

1130 Good empirical evidence shows that forest fragmentation can substantially alter which species
1131 of driver ants are present in different forests. During four years of surveying for driver ants in
1132 the Kakamega Forest in Kenya, researchers showed that, as forest fragments got smaller, *D.*
1133 *wilverthi* became less abundant and was almost entirely absent from small fragments, whilst
1134 *D. molestus* increased in abundance, ultimately resulting in a remarkably consistent overall
1135 colony density and raid rate (Peters et al. 2009, Peters and Okalo 2009). *D. wilverthi* was
1136 almost entirely absent from small fragments (63 – 113 ha), whereas *D. molestus* colony
1137 density increased in small fragments compared to medium fragments (420 – 1370 ha) and the
1138 main forest (8235 ha). The decline of *D. wilverthi* in small fragments probably arises for several
1139 reasons: (1) a *D. wilverthi* colony can feature up to 20 million workers and requires large
1140 quantities of prey to sustain colony activity. Prey communities are probably replenished after
1141 a raid by the immigration of new individuals from the surrounding forest, and small fragments
1142 under high raiding pressure may be more limited in this way without a reservoir of new
1143 individuals from a larger forest. This might eventually nutritionally limit large *D. wilverthi*
1144 colonies, which can cover ~6,000 m² with a single raid. (2) *Dorylus wilverthi* appears to be
1145 strongly associated with rainforest and is rarely found in agricultural land or small forest
1146 fragments. In contrast, *D. molestus* is seen across the matrix of forest, savannah, and
1147 farmland. Colony emigration between fragments that involve stretches of open habitat may
1148 present a major physiological barrier for *D. wilverthi*, which could be more susceptible to
1149 desiccation than *D. molestus* (Peters et al. 2009). Although raid rates and colony densities
1150 were relatively uniform across fragment sizes, this does not necessarily mean the ecological
1151 roles of the two driver ant species are identical or fully compensated for by one another. With
1152 colony density being the same across fragments, the overall biomass of driver ants would still
1153 nevertheless decline due to the at least 3-fold larger colony size of *D. wilverthi* colonies
1154 compared to those of *D. molestus* (Raignier and van Boven 1955, Leroux 1982). Assuming
1155 density-dependent effects, the ecological role of driver ants in the forest would also therefore
1156 diminish in small fragments. Furthermore, only the decline of *D. wilverthi* was highly correlated
1157 with the decline of specialised ant-following birds, even after controlling for the effects of
1158 fragment size and other variables (Peters and Okalo 2009). A further study by Peters et al.
1159 (2011) estimated a ~52 % decline in *D. wilverthi* population size in western Kenya between
1160 1913 to 2003 based on colony density survey data and historical forest cover estimates. These
1161 studies suggest that large continuous areas of rainforest are needed to support *D. wilverthi*
1162 populations. Population responses to habitat loss or fragmentation remain unknown for all
1163 other driver ant species.

1164 *Climate change*

1165 Climate change represents an emerging but largely untested threat to driver ants. Temperature
1166 and humidity influence driver ant activity but responses are species-specific. For example,
1167 daytime raiding activity of *D. molestus* in rainforests was strongly associated with high

humidity, whereas *D. wilverthi* showed comparatively stable activity across humidity conditions (Peters and Okalo 2009). As described above, somewhat paradoxically, *D. molestus* also appears to persist in dry open savannahs and farmlands (Schöning et al. 2006). Increasing temperatures, altered rainfall patterns, and longer dry seasons may restructure driver ant communities rather than produce uniform declines. It is unclear how changing driver ant species composition influences the wider community. However, as above, the loss or reduction of certain species of driver ant, such as *D. wilverthi*, can lead to declines in specialist ant-following birds that are not compensated for by other species (Peters and Okalo 2009). The substantial differences in how different driver ant species respond to direct climate change-related effects requires further study across habitats and regions throughout Africa. Specifically, experiments quantifying the thermal and hydric limits of different driver ant species, alongside long-term monitoring of raid activity, would be valuable for predicting direct responses to climate change.

Driver ants may also be affected through the indirect effects of climate change on their prey communities. Insect populations across the tropics are facing declines (Harvey et al. 2023, Boyle et al. 2025), and increasing temperatures may severely affect lowland tropical insects because of a lack of thermal plasticity (Holzmann et al. 2026). Pervasive declines in lowland tropical insect communities could therefore potentially limit driver ant populations, which rely on abundant arthropod communities to fuel their large colonies. Whether declines in prey abundance translate into declines in driver ant populations remains untested.

Consequences of driver ant declines

As reviewed in the sections above, driver ants support an enormous array of associated species that would decline substantially or disappear locally from an area if driver ant populations decreased. Peters and Okalo (2009) showed a severe decline in ant-following bird abundance that was correlated with the decline of *D. wilverthi* despite colony density compensation by *D. molestus*, suggesting that driver ant species performing larger raids are a central part of the rainforest community. Moreover, several species of ant-following bird only breed in the presence of driver ant colonies (Dowsett-Lemaire 1987). The vast majority of intranidal invertebrate associates – the dozens of species of staphylinid beetles, for example – would be similarly lost from an area without driver ant colonies, along with other obligate associates. Facultative predators might also suffer population declines or fitness reductions if they are unable to draw on driver ant colonies as a resource (e.g., pangolins). The loss of driver ants from an ecosystem could therefore lead to substantial declines across communities of associated organisms, although the extent to which these represent broader extinction cascades remains unknown.

The effect of driver ant raids has long been hypothesised to maintain high community evenness and beta-diversity on the forest floor (Franks and Fletcher 1983, Gotwald 1995, Peters et al. 2013), as discussed in the section above. Declines in colony density could therefore lead to more homogenised leaf litter arthropod communities in rainforest ecosystems as highly competitive species dominate in the absence of driver ant predation pressure. Driver ants also excavate large quantities of soil and create new ground structures that may support a range of fossorial animals, though this has not been studied. Middens and frass represent the concentration of nutrients brought from the surrounding rainforest that may benefit

1211 detritivores, decomposers, and the plants that rely on the breakdown of biological tissues, but
1212 this process is likewise poorly understood.

1213 **Synthesis and future directions**

1214 Through their spectacular raiding behaviour, associations with hundreds of other species, and
1215 as conduits of energy flow, driver ants are the gravitational primary around which so many
1216 other species and processes appear to orbit across tropical Africa. But, as we hope this review
1217 has highlighted, the exact nature of the relationships between driver ants and the communities
1218 and ecosystems of which they are a part are still mostly obscured. Below are several of the
1219 research questions we believe are important to understand driver ant ecology heading into the
1220 future:

1221 *How do driver ant raids affect forest floor animal communities?*

1222 We still lack replicated, quantitative tests of how raids alter the abundance and composition of
1223 leaf litter communities taxonomically and functionally. Measuring the magnitude of the
1224 immediate effects of raids and how communities recover is important to understand to what
1225 degree driver ants are important agents of community-level change. This is not an easy task
1226 and will require the combination of species-level identifications and abundance measurement
1227 of raided communities and control communities (either in close proximity or before and after).
1228 High-throughput molecular tools can nevertheless help with species-level identifications from
1229 diverse morphospecies collections, for example, as a way of validating community data.

1230 *Do repeated raids maintain biodiversity?*

1231 This question has been ever-present in army ant ecological research for over 40 years but
1232 remains unanswered. Determining whether repeated raids increase community turnover, beta-
1233 diversity, and evenness, or simply repeatedly remove prey, would establish whether driver
1234 ants actively maintain biodiversity on the forest floor at potentially very large spatial scales
1235 within the African continent. Measurement of short-term raid impacts as per above, as well as
1236 identifying comparable areas with and without army ants and describing their arthropod
1237 communities on the forest floor, could together detect the short- and long-term effect of driver
1238 ant raids on community structure and diversity. Exclusion experiments might also be an
1239 effective tool to test whether driver ant raids maintain community evenness and beta-diversity,
1240 though non-target exclusion effects would need to be carefully considered.

1241 *What are the proximal determinants of raid location and colony emigration?*

1242 Driver ants move across the landscape, encountering neighbouring colonies or old conspecific
1243 raid pheromones, prey-depleted areas, and variable environmental conditions, yet the
1244 immediate stimuli governing driver ant movement decisions are poorly understood outside of
1245 disturbance at the nest. Combining colony tracking, mapping of conspecific (and congeneric)
1246 raid paths, and spatial modelling could comprehensively reveal the proximal colony-level
1247 decision-making process underpinning driver ant movement ecology. Agent-based models
1248 could potentially then be trained on these data and colony movement probabilities could be
1249 assessed solely based on colony locations across a landscape.

1250 *How do several driver ant species coexist?*

1251 Perhaps most mysteriously, we do not understand how multiple species of driver ants can
1252 seemingly coexist in the same place at the same time, often consuming similar prey and
1253 raiding in similar ways. Characterisation of the multidimensional niche space of sympatric
1254 driver ant species, e.g., through fine-scale comparisons of diet using DNA-based methods,
1255 prey size, foraging habitat, activity, colony size and seasonal behaviour, are needed to
1256 establish whether apparently similar species actually occupy distinct ecological niches.

1257 *Can we finally resolve the taxonomy of driver ants?*

1258 The taxonomy of African driver ants has been perpetually confusing, with historical species
1259 descriptions, uncertain synonymies, and limited sampling making it difficult to determine how
1260 many species exist and where they occur. Recent morphological and molecular work suggests
1261 that these problems are increasingly tractable (Schöning et al. 2026), but a comprehensive
1262 revision combining morphology, genomic data, and geographically extensive sampling is still
1263 needed. Resolving species boundaries and distributions would provide the necessary
1264 foundation for understanding the ecology and associates of different species of driver ants, as
1265 well as their coexistence.

1266 *What depends on driver ants?*

1267 Driver ants support a diverse menagerie of vertebrate and invertebrate associates, but the
1268 strength of these relationships are poorly characterised for all but a few species. Identifying
1269 the ecology of these associates (e.g., through dietary DNA metabarcoding), and how this
1270 relates to driver ants and their life-history, will reveal the level of reliance of different species
1271 interacting with driver ants. It will also highlight what might happen to these communities
1272 should driver ants decline or disappear and is therefore central to understanding their wider
1273 importance and conservation significance.

1274 *What determines the vulnerability of driver ants to habitat fragmentation and climate change?*

1275 The only studies examining driver ant responses to habitat loss and fragmentation observe
1276 divergent responses between two species. Nothing is known for other species of driver ant
1277 species nor for *D. wilverthi* or *D. molestus* outside of the single study area in Kenya. Replicated
1278 surveys across driver ant species distributions in different sized forest fragments and the wider
1279 landscape would help understand which species are sensitive to habitat degradation and the
1280 ecological underpinnings of this. Thermal and hydric experiments quantifying the limits of
1281 driver ant species alongside these surveys would be valuable for predicting declines for
1282 different driver ant species in response to climate change.

1283 *Summary*

1284 Driver ants are among the most conspicuous predators across tropical Africa, and their
1285 extraordinary biomass, voracious predation, and diverse ecological associations suggest they
1286 play an important role in shaping rainforest communities. Yet, despite more than a century of
1287 natural history observations, much of their ecology remains poorly understood. Unveiling their
1288 ecology will require moving beyond observations of their remarkable behaviour towards
1289 quantitative, experimental and molecular approaches that connect colony-level behaviour with
1290 their wider effects on the community and ecosystem. Driver ants are almost certainly important

1291 components of tropical African ecosystems, but understanding just how important they are,
1292 and what is lost when they disappear, remains a considerable challenge.

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1296 **References**

- 1297 Alberdi, A., O. Aizpurua, K. Bohmann, S. Gopalakrishnan, C. Lynggaard, M. Nielsen, and M.
1298 T. P. Gilbert. 2019. Promises and pitfalls of using high-throughput sequencing for diet
1299 analysis. *Molecular Ecology Resources* 19:327–348.
- 1300 Aleman, J. C., M. A. Jarzyna, and A. C. Staver. 2017. Forest extent and deforestation in
1301 tropical Africa since 1900. *Nature Ecology & Evolution* 2:26–33.
- 1302 Bequaert, J. 1922. The predaceous enemies of ants. *Bull. Am. Mus. Nat. Hist.* 45:271–331.
- 1303 Berghoff, S. M., U. Maschwitz, and K. E. Linsenmair. 2003. Influence of the hypogaeic army
1304 ant *Dorylus (Dichthadia) laevigatus* on tropical arthropod communities. *Oecologia*
1305 135:149–157.
- 1306 Berghoff, S. M., A. Weissflog, K. E. Linsenmair, M. Mohamed, and U. Maschwitz. 2002.
1307 Nesting habits and colony composition of the hypogaeic army ant *Dorylus*
1308 (*Dichthadia*) *laevigatus* Fr. Smith. *Insectes Sociaux* 49:380–387.
- 1309 Billen, J., and B. Gobin. 1996. Trail following in army ants. *Netherlands Journal of Zoology*
1310 46:272–280.
- 1311 Borowiec, M. L. 2016. Generic revision of the ant subfamily dorylinae (hymenoptera,
1312 formicidae). *ZooKeys* 2016:1–280.
- 1313 Borowiec, M. L. 2019. Convergent Evolution of the Army Ant Syndrome and Congruence in
1314 Big-Data Phylogenetics. *Systematic Biology* 68:642–656.
- 1315 Boyle, M. J. W., T. C. Bonebrake, K. Dias Da Silva, M. A. K. Dongmo, F. Machado França, N.
1316 Gregory, R. L. Kitching, M. J. Ledger, O. T. Lewis, A. C. Sharp, N. E. Stork, J.
1317 Williamson, and L. A. Ashton. 2025. Causes and consequences of insect decline in
1318 tropical forests. *Nature Reviews Biodiversity* 1:315–331.
- 1319 Brady, S. G., B. L. Fisher, T. R. Schultz, and P. S. Ward. 2014. The rise of army ants and
1320 their relatives: diversification of specialized predatory doryline ants. *BMC*
1321 *Evolutionary Biology* 14:93.
- 1322 Braendle, C., N. Hockley, T. Brevig, A. W. Shingleton, and L. Keller. 2003. Size-correlated
1323 division of labour and spatial distribution of workers in the driver ant, *Dorylus*
1324 *molestus*. *Naturwissenschaften* 90:277–281.
- 1325 Braukmann, T. W. A., N. V. Ivanova, S. W. J. Prosser, V. Elbrecht, D. Steinke, S.
1326 Ratnasingham, J. R. De Waard, J. E. Sones, E. V. Zakharov, and P. D. N. Hebert.
1327 2019. Metabarcoding a diverse arthropod mock community. *Molecular Ecology*
1328 *Resources* 19:711–727.
- 1329 Butler, I. A., M. K. Peters, and D. J. C. Kronauer. 2018. Low levels of hybridization in two
1330 species of African driver ants. *Journal of Evolutionary Biology* 31:556–571.
- 1331 du Chaillu, P. B. 1861. *Exploration and Adventures in Equatorial Africa*. First edition. John
1332 Murray, London.
- 1333 Chapin, J. P., and H. Lang. 1932. *The birds of the Belgian Congo*. American Museum of
1334 Natural History., New York.
- 1335 Collart, A. 1934. Collart, A. "Notes de chasse au sujet de quelques Coléoptères du Congo
1336 Belge. *Bulletin & Annales de la Société Entomologique de Belgique* 28:84–85.
- 1337 Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs: High diversity of
1338 trees and corals is maintained only in a nonequilibrium state. *Science* 199:1302–
1339 1310.

1340 Connell, J. H. 1980. Diversity and the Coevolution of Competitors, or the Ghost of
1341 Competition Past. *Oikos* 35:131.

1342 Cottee-Jones, H. E. W., and R. J. Whittaker. 2012. perspective: The keystone species
1343 concept: a critical appraisal. *Frontiers of Biogeography* 4.

1344 Craig, A. J. F. K. 2022. African birds as army ant followers. *Journal of Ornithology* 163:623–
1345 631.

1346 Cuff, J. P., J. J. N. Kitson, D. Hemprich-Bennett, M. P. T. G. Tercel, S. S. Browett, and D. M.
1347 Evans. 2023a. The predator problem and PCR primers in molecular dietary analysis:
1348 Swamped or silenced; depth or breadth? *Molecular Ecology Resources* 23:41–51.

1349 Cuff, J. P., F. M. Windsor, M. P. T. G. Tercel, J. R. Bell, W. O. C. Symondson, and I. P.
1350 Vaughan. 2023b. Temporal variation in spider trophic interactions is explained by the
1351 influence of weather on prey communities, web building and prey choice. *Ecography*
1352 2023:e06737.

1353 Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation
1354 of favoured races in the struggle for life. John Murray, London.

1355 Denslow, J. S. 1987. TROPICAL RAINFOREST GAPS AND TREE SPECIES DIVERSITY.
1356 *Annual Review of Ecology and Systematics* 18:431–451.

1357 Dowsett-Lemaire, F. 1987. On the distribution, ecology and voice of two Alethe species in
1358 Malawi. *Scopus* 11:25–32.

1359 Elbrecht, V., T. W. A. Braukmann, N. V. Ivanova, S. W. J. Prosser, M. Hajibabaei, M. Wright,
1360 E. V. Zakharov, P. D. N. Hebert, and D. Steinke. 2019. Validation of COI
1361 metabarcoding primers for terrestrial arthropods. *PeerJ*.

1362 Engel, E. O., and A. Cuthbertson. 1937. On the biology of some Rhodesian Diptera, together
1363 with descriptions of three species of Asilidae new to science. *Transactions of the*
1364 *Rhodesia Scientific Association*:1–15.

1365 Fabricius, J. C. 1793. *Entomologia systematica emendata et aucta. Secundum classes,*
1366 *ordines, genera, species, adjectis synonymis, locis observationibus, descriptionibus.*
1367 C. G. Proft, Hafniae [= Copenhagen].

1368 Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves
1369 influence elk movements: behavior shapes a trophic cascade in Yellowstone National
1370 Park. *Ecology* 86:1320–1330.

1371 Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. *Trends in*
1372 *Ecology & Evolution* 28:86–92.

1373 Franks, N. R., and C. R. Fletcher. 1983. Spatial patterns in army ant foraging and migration:
1374 *Eciton burchelli* on Barro Colorado Island, Panama. *Behavioral Ecology and*
1375 *Sociobiology* 12:261–270.

1376 Franks, N. R., and B. Hölldobler. 1987. Sexual competition during colony reproduction in
1377 army ants. *Biological Journal of the Linnean Society* 30:229–243.

1378 Franks, N. R., A. B. Sendova-Franks, J. Simmons, and M. Mogie. 1999. Convergent
1379 evolution, superefficient teams and tempo in Old and New World army ants.
1380 *Proceedings of the Royal Society of London. Series B: Biological Sciences*
1381 266:1697–1701.

1382 Ganas, J., and M. M. Robbins. 2004. Intrapopulation differences in ant eating in the
1383 mountain gorillas of Bwindi Impenetrable National Park, Uganda. *Primates* 45:275–
1384 278.

1385 Gehlbach, F. R., J. F. Watkins, and H. W. Reno. 1968. Blind Snake Defensive Behavior
1386 Elicited by Ant Attacks. *BioScience* 18:784–785.

1387 Ghazoul, J., and D. Sheil. 2010. Tropical rain forest ecology, diversity, and conservation.
1388 Oxford university press, Oxford.

1389 Gotwald, W. 1974. Predatory Behavior and Food Preferences of Driver Ants in Selected
1390 African Habitats 1. *Annals of the Entomological Society of America* 67:877–886.

1391 Gotwald, W. 1995. *Army Ants*. Cornell University Press, Ithaca.

1392 Gotwald, W. H. 1972. *Oecophylla Longinoda* , an Ant Predator of *Anomma* Driver
1393 *Ants*(Hymenoptera: Formicidae). *Psyche: A Journal of Entomology* 79:348–356.

1394 Haddow, A. J., I. H. H. Yarrow, G. A. Lancaster, and P. S. Corbet. 1966. Nocturnal flight cycle
1395 in the males of African doryline ants (Hymenoptera: Formicidae). *Proceedings of the*
1396 *Royal Entomological Society of London. Series A, General Entomology* 41:103–106.

1397 Harvey, J. A., K. Tougeron, R. Gols, R. Heinen, M. Abarca, P. K. Abram, Y. Basset, M. Berg,
1398 C. Boggs, J. Brodeur, P. Cardoso, J. G. De Boer, G. R. De Snoo, C. Deacon, J. E.
1399 Dell, N. Desneux, M. E. Dillon, G. A. Duffy, L. A. Dyer, J. Ellers, A. Espíndola, J.
1400 Fordyce, M. L. Forister, C. Fukushima, M. J. G. Gage, C. García-Robledo, C. Gely,
1401 M. Gobbi, C. Hallmann, T. Hance, J. Harte, A. Hochkirch, C. Hof, A. A. Hoffmann, J.
1402 G. Kingsolver, G. P. A. Lamarre, W. F. Lurance, B. Lavandero, S. R. Leather, P.
1403 Lehmann, C. Le Lann, M. M. López-Urbe, C. Ma, G. Ma, J. Moiroux, L. Monticelli, C.
1404 Nice, P. J. Ode, S. Pincebourde, W. J. Ripple, M. Rowe, M. J. Samways, A. Sentis, A.
1405 A. Shah, N. Stork, J. S. Terblanche, M. P. Thakur, M. B. Thomas, J. M. Tylianakis, J.
1406 Van Baaren, M. Van De Pol, W. H. Van Der Putten, H. Van Dyck, W. C. E. P. Verberk,
1407 D. L. Wagner, W. W. Weisser, W. C. Wetzels, H. A. Woods, K. A. G. Wyckhuys, and S.
1408 L. Chown. 2023. Scientists' warning on climate change and insects. *Ecological*
1409 *Monographs* 93:e1553.

1410 Hillebrand, H., and C. Kunze. 2020. Meta-analysis on pulse disturbances reveals differences
1411 in functional and compositional recovery across ecosystems. *Ecology Letters*
1412 23:575–585.

1413 Hoenle, P. O., N. Blüthgen, A. Brückner, B. Fiala, D. A. Donoso, C. V. Beeren, D. J. C.
1414 Kronauer, M. A. Smith, and B. Ospina. 2019. Species - level predation network
1415 uncovers high prey specificity in a Neotropical army ant community:1–18.

1416 Hoenle, P. O., C. Merkel, D. A. Donoso, A. A. Argoti, N. Blüthgen, and C. Von Beeren. 2024.
1417 Hunting habits die hard: Conserved prey preferences in army ants across two distant
1418 neotropical rainforests. *Ecosphere* 15:e4812.

1419 Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Page Harvard University Press. Springer-
1420 Verlag, Cambridge.

1421 Holzmann, K. L., T. Schmitzer, A. Abels, M. Čorkalo, O. Mitesser, M. Kortmann, P. Alonso-
1422 Alonso, Y. Correa-Carmona, A. Pinos, F. Yon, M. Alvarado, A. Forsyth, A. Lopera-
1423 Toro, G. Brehm, A. Keller, M. Otieno, I. Steffan-Dewenter, and M. K. Peters. 2026.
1424 Limited thermal tolerance in tropical insects and its genomic signature. *Nature*
1425 651:672–678.

1426 Huber, S., L. L. Powell, and M. P. T. G. Tercel. 2026. Comparative prey transport behaviour,
1427 demographics, and diet of two sympatric driver ant species in a central African
1428 rainforest. *Ecology, EcoEvoRxiv*.

1429 Ichikawa, M. 1998. *The Birds as Indicators of the Invisible World: Ethno. African Study*
1430 *Monographs*:105–121.

1431 Janzen, D. H. 1970. Herbivores and the Number of Tree Species in Tropical Forests. *The*
1432 *American Naturalist* 104:501–528.

1433 Kaspari, M., S. Powell, J. Lattke, and S. O'Donnell. 2011. Predation and patchiness in the
1434 tropical litter: do swarm-raiding army ants skim the cream or drain the bottle?:
1435 Predation and patchiness in the tropical litter. *Journal of Animal Ecology* 80:818–823.

1436 Kistner, D. H. 1965a. Kistner, David H. "A revision of the species of the genus *Phyllodinarda*
1437 *Wasmann* with notes on their behavior. *he Pan Pacific Entomologist* 2:121–132.

1438 Kistner, D. H. 1965b. New Species and New Records of *Pygostenini* from Liberia, Ivory
1439 Coast, and Cameroun (Coleoptera: Staphylinidae). *Journal of the Kansas*
1440 *Entomological Society* 38:325–351.

1441 Kistner, D. H. 1966a. A Revision of the Myrmecophilous Tribe *Deremini* (Coleoptera:
1442 *Staphylinidae*)1 Part I: the *Dorylopora* Complex and Their Behavior. *Annals of the*
1443 *Entomological Society of America* 59:341–358.

1444 Kistner, D. H. 1966b. A Revision of the African Species of the Aleocharine Tribe *Dorylomimini*
1445 (Coleoptera: Staphylinidae).1 II. The Genera *Dorylomimus*, *Dorylonannus*,
1446 *Dorylogaster*, *Dorylobactus*, and *Mimanomma*, with Notes on Their Behavior. *Annals*
1447 *of the Entomological Society of America* 59:320–340.

1448 Kistner, D. H. 1979. Kistner, David H. "Social and evolutionary significance of social insect
1449 symbionts. Page Social insects. Academic Press, New York.

1450 Koops, K., C. Schöning, W. C. McGrew, and T. Matsuzawa. 2015. Chimpanzees prey on
1451 army ants at Seringbara, Nimba Mountains, Guinea: Predation patterns and tool use
1452 characteristics. *American Journal of Primatology* 77:319–329.

1453 Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A Critical Review of
1454 Assumptions About the Prairie Dog as a Keystone Species. *Environmental*
1455 *Management* 24:177–192.

1456 Kronauer, D. J. C. 2009. Recent advances in army ant biology (Hymenoptera : Formicidae).
1457 *Myrmecol News* 12:51–65.

1458 Kronauer, D. J. C. 2020. Army ants: nature's ultimate social hunters. Harvard University
1459 Press, Cambridge, Massachusetts.

1460 Kronauer, D. J. C., R. A. Johnson, and J. J. Boomsma. 2007a. The evolution of multiple
1461 mating in army ants. *Evolution* 61:413–422.

1462 Kronauer, D. J. C., C. Schöning, P. d'Ettorre, and J. J. Boomsma. 2010. Colony fusion and
1463 worker reproduction after queen loss in army ants. *Proceedings of the Royal Society*
1464 *B: Biological Sciences* 277:755–763.

1465 Kronauer, D. J. C., C. Schöning, J. S. Pedersen, J. J. Boomsma, and J. Gadau. 2004.
1466 Extreme queen-mating frequency and colony fission in African army ants. *Molecular*
1467 *Ecology* 13:2381–2388.

1468 Kronauer, D. J. C., C. Schöning, L. B. Vilhelmsen, and J. J. Boomsma. 2007b. A molecular
1469 phylogeny of *Dorylus* army ants provides evidence for multiple evolutionary
1470 transitions in foraging niche. *BMC Evolutionary Biology* 7:56.

1471 Kronauer, D. J., M. K. Peters, C. Schöning, and J. J. Boomsma. 2011. Hybridization in East
1472 African swarm-raiding army ants. *Frontiers in Zoology* 8:20.

1473 Kruuk, H., and W. A. Sands. 1972. The aardwolf (*Proteles cristatus* Sparrman) 1783 as
1474 predator of termites*. *African Journal of Ecology* 10:211–227.

1475 Lach, L., C. L. Parr, and K. L. Abbott. 2010. Ant ecology. Oxford university press, Oxford.

1476 Leroux, J. M. 1977. FORMATION ET DEROULEMENT DES RAIDS DE CHASSE
1477 D'ANOMMA NIGRICANS ILLIGER (HYM. DORYLINAE) DANS UNE SAVANE DE
1478 COTE D'IVOIRE. *Bull. Soc. Zool. Fr.* 102.

1479 Leroux, J. M. 1982. Ecologie des populations de dorylines *Anomma nigricans* dans la région
1480 de Lamto (Côte d'Ivoire). Publications du Laboratoire de Zoologie. Ecole Normale
1481 Supérieure, Paris, France.

1482 Leston, D. 1979. Dispersal by Male Doryline Ants in West Africa. *Psyche: A Journal of*
1483 *Entomology* 86:63–77.

1484 Levings, S. C. 1983. Seasonal, Annual, and Among-site Variation in the Ground Ant
1485 Community of a Deciduous Tropical Forest: Some Causes of Patchy Species
1486 Distributions. *Ecological Monographs* 53:435–455.

1487 Levings, S. C., and N. R. Franks. 1982. Patterns of Nested Dispersion in a Tropical Ground
1488 Ant Community. *Ecology* 63:338–344.

1489 Levings, S. C., and D. M. Windsor. 1985. Litter Arthropod Populations in a Tropical
1490 Deciduous Forest: Relationships between Years and Arthropod Groups. *The Journal*
1491 *of Animal Ecology* 54:61.

1492 Linnaeus, C. 1764. Museum S:ae R:ae M:tis Ludovicae Ulricaе Reginae Svecorum,
1493 Gothorum, Vandalorumque. Page 720 In quo animalia rariora, exotica, imprimis.
1494 Insecta and Conchilia describuntur and determinantur. Prodrumi instar. Holmiae
1495 [Stockholm]: Laur. Salvii.

1496 Loveridge, A. 1922. Account of an Invasion of "Siafu" or Red Driver-Ants—*Dorylus* (*Anomma*)
1497 *nigricans* Illig. *Transactions of the Royal Entomological Society of London* 5:33–46.

1498 Loveridge, A. 1949. Many Happy Days I've Squandered. Scientific Book Club, London.

1499 Mallon, E. B., and N. R. Franks. 2000. Ants estimate area using Buffon's needle.
1500 *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267:765–
1501 770.

- Maruyama, M., and J. Parker. 2017. Deep-Time Convergence in Rove Beetle Symbionts of Army Ants. *Current Biology* 27:920–926.
- McGrew, W. C. 1974. Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution* 3:501–508.
- McGrew, W. C. 2010. Chimpanzee Technology. *Science* 328:579–580.
- McGrew, W. C., J. D. Pruetz, and S. J. Fulton. 2005. Chimpanzees Use Tools to Harvest Social Insects at Fongoli, Senegal. *Folia Primatologica* 76:222–226.
- McGrew, W. C., C. E. G. Tutin, and P. J. Baldwin. 1979. Chimpanzees, Tools, and Termites: Cross-Cultural Comparisons of Senegal, Tanzania, and Rio Muni. *Man* 14:185.
- Mills, L. S., and D. F. Doak. 1993. The Keystone-Species Concept in Ecology and Conservation. *BioScience* 43:219–224.
- Moi, D. A., R. García-Ríos, Z. Hong, B. V. Daquila, and R. P. Mormul. 2020. Intermediate Disturbance Hypothesis in Ecology: A Literature Review. *Annales Zoologici Fennici* 57:67.
- Moreau, R. E. 1942. Bird-nomenclature in an East African Area. *Bulletin of the School of Oriental and African Studies* 10:998–1006.
- Nishida, T., and M. Hiraiwa. 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution* 11:73–99.
- O'Donnell, S., A. Kumar, and C. Logan. 2010. Army Ant Raid Attendance and Bivouac-Checking Behavior by Neotropical Montane Forest Birds. *The Wilson Journal of Ornithology* 122:503–512.
- Otis, G. W., E. S. C., D. L. Crawford, and M. L. Higgins. 1986. The Effect of Foraging Army Ants on Leaf-Litter Arthropods. *Biotropica* 18:56.
- Paine, R. T. 1966. Food Web Complexity and Species Diversity. *The American Naturalist* 100:65–75.
- Paine, R. T. 1969. A Note on Trophic Complexity and Community Stability. *The American Naturalist* 103:91–93.
- Parker, J. 2016. Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. *Myrmecological News* 22:65–108.
- Patrizi, S. 1946. Stomach contents of a female ant-eater from Nairobi. *J. East Afr. Nat. Hist. Soc.* 19:67–68.
- Paulian, R. 1948. Paulian, Reynaud. "Observations sur les Coléoptères commensaux d'*Anomma nigricans* en Côte d'Ivoire. *Annales des Sciences Naturelles* 10:79–102.
- Pérez-Espona, S., W. P. Goodall-Copestake, S. M. Berghoff, K. J. Edwards, and N. R. Franks. 2018. Army imposters: diversification of army ant-mimicking beetles with their *Eciton* hosts. *Insectes Sociaux* 65:59–75.
- Peters, M. K., G. Fischer, F. Hita Garcia, T. Lung, and J. W. Wägele. 2013. Spatial Variation in Army Ant Swarm Raiding and its Potential Effect on Biodiversity. *Biotropica* 45:54–62.
- Peters, M. K., G. Fischer, G. Schaab, and M. Kraemer. 2009. Species compensation maintains abundance and raid rates of African swarm-raiding army ants in rainforest fragments. *Biological Conservation* 142:668–675.
- Peters, M. K., S. Likare, and M. Kraemer. 2008. EFFECTS OF HABITAT FRAGMENTATION AND DEGRADATION ON FLOCKS OF AFRICAN ANT-FOLLOWING BIRDS. *Ecological Applications* 18:847–858.
- Peters, M. K., T. Lung, G. Schaab, and J. W. Wägele. 2011. Deforestation and the population decline of the army ant *Dorylus wilverthi* in western Kenya over the last century: Deforestation and army ants. *Journal of Applied Ecology* 48:697–705.
- Peters, M. K., and B. Okalo. 2009. Severe declines of ant-following birds in African rainforest fragments are facilitated by a subtle change in army ant communities. *Biological Conservation* 142:2050–2058.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the Quest for Keystones. *BioScience* 46:609–620.

1557 Quevillon, L. E. 2018. Quevillon, Lauren E. The ecology, epidemiology, and evolution of
 1558 parasites infecting ants (Hymenoptera: Formicidae). PhD, The Pennsylvania State
 1559 University.
 1560 Raignier, A., and J. K. A. van Boven. 1955. Etude taxonomique, biologique et biométrique
 1561 des *Dorylus* du sous-genre *Anomma* (Hymenoptera: Formicidae). *Ann. Mus. R.*
 1562 *Congo Beg.* 2:1–359.
 1563 Rettenmeyer, C. W., M. E. Rettenmeyer, J. Joseph, and S. M. Berghoff. 2011. The largest
 1564 animal association centered on one species: The army ant *Eciton burchellii* and its
 1565 more than 300 associates. *Insectes Sociaux* 58:281–292.
 1566 Rodrigues, P. F. 2024. The Behavioral Specialization of African Ant-following Birds on
 1567 *Dorylus* Driver Ants. PhD, Louisiana State University, Baton Rouge.
 1568 Rognes, K. 2011. A review of the monophyly and composition of the Bengaliinae with the
 1569 description of a new genus and species, and new evidence for the presence of
 1570 Melanomyinae in the Afrotropical Region (Diptera, Calliphoridae). *Zootaxa* 2964.
 1571 Savage, T. S. 1847. I. *On the Habits of the “Drivers” or Visiting Ants of West Africa.*
 1572 *Transactions of the Royal Entomological Society of London* 5:1–15.
 1573 Savage, T. S. 1849. The driver ants of western Africa. *Proceedings of the Academy of*
 1574 *Natural Sciences of Philadelphia* 4:195–200.
 1575 Schneirla, T. C. 1949. Army-ant life and behavior under dry- season conditions. 3. The
 1576 course of reproduction and colony behavior. *Bull. Am. Mus. Nat. Hist.* 94:1–82.
 1577 Schneirla, T. C., and R. Z. Brown. 1950. Army-ant life and behavior under dry-season
 1578 conditions. 4. Further investi- gation of cycle progresses in behavioral and
 1579 reproductive functions. *Bull. Am. Mus. Nat. Hist.* 95:263–354.
 1580 Schöning, C., C. Csuzdi, W. Kinuthia, and J. O. Ogutu. 2010. Influence of driver ant swarm
 1581 raids on earthworm prey densities in the Mount Kenya forest: implications for prey
 1582 population dynamics and colony migrations. *Insectes Sociaux* 57:73–82.
 1583 Schöning, C., W. H. Gotwald Jr., D. J. C. Kronauer, and L. Vilhelmsen. 2008a. Taxonomy of
 1584 the African army ant *Dorylus gribodoi* Emery, 1892 (Hymenoptera, Formicidae) - new
 1585 insights from DNA sequence data and morphology. *Zootaxa* 1749.
 1586 Schöning, C., T. Humle, Y. Möbius, and W. C. McGrew. 2008b. The nature of culture:
 1587 Technological variation in chimpanzee predation on army ants revisited. *Journal of*
 1588 *Human Evolution* 55:48–59.
 1589 Schöning, C., W. Kinuthia, and J. J. Boomsma. 2006. DOES THE AFROTROPICAL ARMY
 1590 ANT *DORYLUS* (*ANOMMA*) *MOLESTUS* GO EXTINCT IN FRAGMENTED
 1591 FORESTS? *Journal of East African Natural History* 95:163–179.
 1592 Schöning, C., W. Kinuthia, and N. R. Franks. 2005a. Evolution of allometries in the worker
 1593 caste of *Dorylus* army ants. *Oikos* 110:231–240.
 1594 Schöning, C., and M. W. Moffett. 2007. Driver Ants Invading a Termite Nest: Why Do the
 1595 Most Catholic Predators of All Seldom Take This Abundant Prey? *Biotropica* 39:663–
 1596 667.
 1597 Schöning, C., W. Njagi, and W. Kinuthia. 2008c. Prey spectra of two swarm-raiding army ant
 1598 species in East Africa. *Journal of Zoology* 274:85–93.
 1599 Schöning, C., W. M. Njagi, and N. R. Franks. 2005b. Temporal and spatial patterns in the
 1600 emigrations of the army ant *Dorylus* (*Anomma*) *molestus* in the montane forest of Mt
 1601 Kenya. *Ecological Entomology* 30:532–540.
 1602 Schöning, C., L. Shepard, A. Sen, W. Kinuthia, and J. O. Ogutu. 2011. Should I stay or
 1603 should I go now? Patch use by African army ant colonies in relation to food
 1604 availability and predation. *Insectes Sociaux* 58:335–343.
 1605 Schöning, C., R. Weniger, W. Gotwald Jr., L. Vilhelmsen, J. J. Boomsma, and D. J. C.
 1606 Kronauer. 2026. Taxonomy of African driver ants (Hymenoptera, Formicidae, *Dorylus*
 1607 *nigricans* species group) west of the Dahomey Gap. *ZooKeys* 1290:185–226.
 1608 Seignobos, C., J. P. Deguine, and H.-P. Aberlenc. 1996. Les Mofus et leurs insectes. *ournal*
 1609 *d’agriculture traditionnelle et de botanique appliquée* 38:125–187.

- Sommer, V., U. Buba, G. Jesus, and A. Pascual-Garrido. 2017. Sustained myrmecophagy in Nigerian chimpanzees: Preferred or fallback food? *American Journal of Physical Anthropology* 162:328–336.
- Sudd, J. H., and N. R. Franks. 1987. Ant Ecology. Pages 161–187 *The Behavioural Ecology of Ants*. Springer Netherlands, Dordrecht.
- Swartz, M. B. 2001. Bivouac Checking, A Novel Behavior Distinguishing Obligate from Opportunistic Species of Army-Ant-Following Birds. *The Condor* 103:629–633.
- Taylor, W. A., P. A. Lindsey, and J. D. Skinner. 2002. The feeding ecology of the armadillo *Oryzomys azer*. *Journal of Arid Environments* 50:135–152.
- Tercel, M. P. T. G., J. P. Cuff, W. O. C. Symondson, R. J. Moorhouse-Gann, T. R. Bishop, N. C. Cole, E. Jolin, B. Govier, J. Chambon, R. Mootoocurpen, M. Goder, and I. P. Vaughan. 2025. Threatened endemic arthropods and vertebrates partition their diets with non-native ants in an isolated island ecosystem. *Ecology* 106:e70158.
- Tercel, M. P. T. G., J. P. Cuff, I. P. Vaughan, W. O. C. Symondson, M. Goder, S. Matadeen, V. Tatayah, and N. C. Cole. 2024. Ecology, natural history, and conservation status of *Scolopendra abnormis*, a threatened centipede endemic to Mauritius. *Endangered Species Research* 54:181–189.
- Tercel, M. P. T. G., W. O. C. Symondson, and J. P. Cuff. 2021. The problem of omnivory: A synthesis on omnivory and DNA metabarcoding. *Molecular ecology* 30:2199–2206.
- Tercel, M. P. T. G., W. O. C. Symondson, J. P. Cuff, N. C. Cole, M. Goder, K. Ruhomaun, V. Tatayah, and I. P. Vaughan. 2026. Intraguild Interactions Drive the Dynamics of a Complex Community of Globally Invasive Ant Species. *Molecular Ecology* 35:e70464.
- Thomas, A. C., B. E. Deagle, J. P. Eveson, C. H. Harsch, and A. W. Trites. 2016. Quantitative DNA metabarcoding: Improved estimates of species proportional biomass using correction factors derived from control material. *Molecular Ecology Resources* 16:714–726.
- Tschinkel, W. R. 2014. Nest Relocation and Excavation in the Florida Harvester Ant, *Pogonomyrmex badius*. *PLoS ONE* 9:e112981.
- Van Huis, A. 2021. Cultural aspects of ants, bees and wasps, and their products in sub-Saharan Africa. *International Journal of Tropical Insect Science* 41:2223–2235.
- Vaughan, I. P., N. J. Gotelli, J. Memmott, C. E. Pearson, G. Woodward, and W. O. C. Symondson. 2018. econullnetr: An R package using null models to analyse the structure of ecological networks and identify resource selection. *Methods in Ecology and Evolution* 9:728–733.
- Von Beeren, C., N. Blüthgen, P. O. Hoenle, S. Pohl, A. Brückner, A. K. Tishechkin, M. Maruyama, B. V. Brown, J. M. Hash, W. E. Hall, and D. J. C. Kronauer. 2021. A remarkable legion of guests: Diversity and host specificity of army ant symbionts. *Molecular Ecology* 30:5229–5246.
- Von Beeren, C., A. Brückner, M. Maruyama, G. Burke, J. Wieschollek, and D. J. C. Kronauer. 2018. Chemical and behavioral integration of army ant-associated rove beetles – a comparison between specialists and generalists. *Frontiers in Zoology* 15:8.
- Wasmann, E. 1900. Neue Dorylinengäste aus dem neotropischen und dem athiopischen Faunengebiet. (114 Beitrag zur Kenntniss der Myrmekophilen und Termitophilen). *Zoologische Jahrbücher*. 14:215–290.
- Wasmann, E. 1912. The ants and their guests. Pages 455–475 *Board of Regents of Smithsonian Institution*. Government Printing Office, Washington, DC.
- Watkins, J. F., F. R. Gehlbach, and R. S. Baldrige. 1967. Ability of the Blind Snake, *Leptotyphlops dulcis*, to Follow Pheromone Trails of Army Ants, *Neivamyrmex nigrescens* and *N. opacithorax*. *The Southwestern Naturalist* 12:455.
- Watkins, J. F., F. R. Gehlbach, and J. C. Kroll. 1969. Attractant-Repellent Secretions of Blind Snakes (*Leptotyphlops Dulcis*) and Their Army Ant Prey (*Neivamyrmex Nigrescens*). *Ecology* 50:1098–1102.
- Watts, D. P. 1989. Ant eating behavior of mountain gorillas. *Primates* 30:121–125.

1664 Whitmore, T. C. 1989. Canopy Gaps and the Two Major Groups of Forest Trees. *Ecology*
1665 70:536–538.

1666 Willis, C. K., J. D. Skinner, and H. G. Robertson. 1992. Abundance of ants and termites in
1667 the False Karoo and their importance in the diet of the aardvark *Orycteropus afer*.
1668 *African Journal of Ecology* 30:322–334.

1669 Willis, E. O. 1986. West African thrushes as safari ant followers. *Le gerfaut* 76:95–108.

1670 Willis, E. O., and Y. Oniki. 1978. Birds and army ants. *Annual Review of Ecology and*
1671 *Systematics* 9:243–263.

1672 Wilson, E. O. 1958. The Beginnings of Nomadic and Group-Predatory Behavior in the
1673 Ponerine Ants. *Evolution* 12:24.

1674 Yan, J. L., and M. Prebus. 2024. Variability of nest relocation behavior among acorn ant
1675 species. *Insectes Sociaux* 71:49–60.

1676 Yankelevich, S. N., C. Fragoso, A. C. Newton, G. Russell, and O. W. Heal. 2006. Spatial
1677 Patchiness of Litter, Nutrients and Macroinvertebrates during Secondary Succession
1678 in a Tropical Montane Cloud Forest in Mexico. *Plant and Soil* 286:123–139.

1679 Zhou, X., Y. Li, S. Liu, Q. Yang, X. Su, L. Zhou, M. Tang, R. Fu, J. Li, and Q. Huang. 2013.
1680 Ultra-deep sequencing enables high-fidelity recovery of biodiversity for bulk
1681 arthropod samples without PCR amplification. *GigaScience* 2:4.
1682