



## TECHNIQUES &amp; METHODOLOGY

# ***GlobalAnts*: a new database on the geography of ant traits (Hymenoptera: Formicidae)**

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**Abstract.** 1. In recent years the focus in ecology has shifted from species to a greater emphasis on functional traits. In tandem with this shift, a number of trait databases have been developed covering a range of taxa. Here, we introduce the *GlobalAnts* database.

2. Globally, ants are dominant, diverse and provide a range of ecosystem functions. The database represents a significant tool for ecology in that it (i) contributes to a global archive of ant traits (morphology, ecology and life history) which complements existing ant databases and (ii) promotes a trait-based approach in ant and other insect ecology through a broad set of standardised traits.

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3. The *GlobalAnts* database is unique in that it represents the largest online database of functional traits with associated georeferenced assemblage-level data (abundance and/or occupancy) for any animal group with 9056 ant species and morphospecies records for entire local assemblages across 4416 sites.

4. We describe the structure of the database, types of traits included and present a summary of data coverage. The value of the database is demonstrated through an initial examination of trait distributions across subfamilies, continents and biomes.

5. Striking biogeographic differences in ant traits are highlighted which raise intriguing questions as to the mechanisms generating them.

**Key words.** Assemblages, ecology, functional trait, morphology, online database.

## Introduction

One of the central goals in ecology is to understand how diversity varies in time and space (Rosenzweig, 1995; Whittaker *et al.*, 2001). Although much consideration has been given to the diversity and composition of communities and regions, functional aspects of community structuring have received greater attention in recent years. This wider lens is not new. The study of the biogeography of plant and animal traits has a long history, dating to J.R. Forster (1729–1798). Traits are well-defined, quantifiable properties of organisms, usually measured at the individual level and used comparatively across species: functional traits are those that strongly influence an organism's performance (McGill *et al.*, 2006). However, it is only lately with the compilation of sufficient data that formal and quantitative study of the diversity and distribution of traits within higher taxa, such as plants (Kattge *et al.*, 2011), has been possible. As a result of emerging datasets, researchers are increasingly exploring the role of functional traits of species in structuring assemblages (Cadotte *et al.*, 2011), at regional (e.g. Siefert *et al.*, 2013; Lamanna *et al.*, 2014) and even global spatial scales (e.g. Swenson *et al.*, 2012; van Bodegom *et al.*, 2014; Mouillot *et al.*, 2014).

It is very difficult to draw generalisations about how ecosystems are structured and how they function based solely on species composition because species are unique and geographically restricted. For species-rich groups such as insects, incomplete taxonomic knowledge can be a huge barrier to ecological understanding (Diniz-Filho *et al.*, 2010). The use of functional traits can therefore be valuable as it enables the identification of sets of organisms with common features and allows focus on measurable traits of organisms without reliance on (or need to generate) a robust species-level taxonomy. Relating function to measurable traits should allow for a predictive framework for ecology ranging from individuals through community patterns (McGill *et al.*, 2006) to ecosystems (e.g. Díaz *et al.*, 1999).

Trait data provide a promising basis for a more quantitative and predictive ecology, and global change science (Kattge *et al.*, 2011), whether in the context of forecasting

future assemblages or understanding the origin of current ones. Although a trait approach has perhaps been most widely used in vegetation ecology (e.g. Westoby & Wright, 2006; Cornwell *et al.*, 2008; Adler *et al.*, 2014), there are a growing number of studies on animal groups, at local or continental scales (e.g. fish, Logez *et al.*, 2013; birds, Ding *et al.*, 2013; beetles, Barton *et al.*, 2011; ants, Silva & Brandão, 2010).

With increasing focus on functional traits in ecology, a number of online databases have been developed that allow traits to be considered among habitats, regions and continents. One of the earliest and most successful is the global database of plant traits (TRY) that was initiated in 2007, and now contains 750 traits of 1 million individual plants, representing 69 000 plant species (Kattge *et al.*, 2011). The use of this trait database has, for example, enabled the understanding of variation in plant life-history strategies (Adler *et al.*, 2014), facilitated the prediction of invertebrate foliar herbivory (Loranger *et al.*, 2012) and helped improve predictions of how global change will affect terrestrial biodiversity (McMahon *et al.*, 2011). Trait databases have also been developed for a number of faunal groups including birds, fish and mammals, as well as insects and other invertebrates (e.g. carabids, see [www.carabids.org](http://www.carabids.org), Homburg *et al.*, 2014; soil invertebrates, see Pey *et al.*, 2014), including ants (see Bertelsmeier *et al.*, 2013).

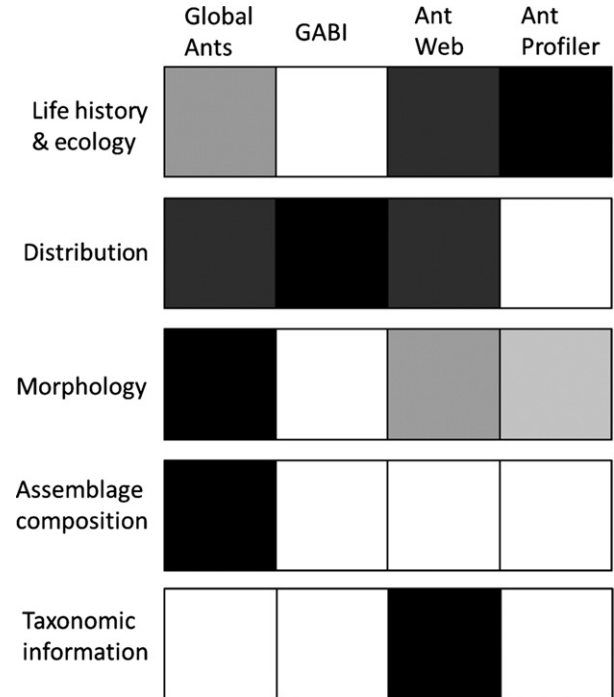
Ants (Hymenoptera: Formicidae) are globally successful and conspicuous. They occur throughout all continents except Antarctica, are ecologically dominant and diverse (estimated 30 000 species globally) and fulfil a variety of ecological roles as scavengers, specialist predators and seed harvesters and dispersers (Lach *et al.*, 2010). As with many other animals, body size and trophic groups have been the ant traits most commonly considered by ecologists. For example, ant body size was found to predict the dispersal distance of seeds (Ness *et al.*, 2004) and non-native ants tend to be smaller than related native genera (McGlynn, 1999).

In addition, a number of studies have examined how ant morphological traits respond to environmental gradients at local, regional (e.g. Kaspari & Weiser, 1999; Bihn

*et al.*, 2010; Wiescher *et al.*, 2012; Arnan *et al.*, 2014; Silva & Brandão, 2014; Gibb *et al.*, 2015a) and continental (e.g. Cushman *et al.*, 1993; Kaspari, 2005) scales, but only two studies have approached these questions at a global scale (Gibb & Parr, 2013; Gibb *et al.*, in review). These studies have used a limited subset of traits and focussed predominantly on body size measures, such as Weber's length and the body size index (Sarty *et al.*, 2006; Data S1). A few have included trophic measures (e.g. Bihn *et al.*, 2010; Wiescher *et al.*, 2012; Gibb & Cunningham, 2013), while physiological measures, such as Critical Thermal Maximum (e.g. Diamond *et al.*, 2012; Wiescher *et al.*, 2012) are gaining popularity as a result of predicted strong relationships with climate. While the main purpose of these studies has been to understand the relationship between traits and the environment, Silva and Brandão (2010) used morphological traits to develop a globally applicable method to allocate species to functional groups. Recently, the relationship between traits and phylogenies has been explored in ant communities (Donoso, 2014; Blaimer *et al.*, 2015), and this promises to be a fruitful area of research.

Current ant databases include AntProfiler ([www.antprofiler.org](http://www.antprofiler.org)) which focuses on life-history traits and ecology (e.g. colony information, behaviour, habitat, nesting, diet, invasiveness status and minimum and maximum body size) (Bertelsmeier *et al.*, 2013) and The Global Ant Biodiversity Informatics (GABI) Project, a comprehensive global database of ant species distributional records (see Guénard *et al.*, 2012) linked to [www.antmaps.org](http://www.antmaps.org), which is a tool for visualising and interacting with GABI. There are also a number of image databases including AntWeb ([www.antweb.org](http://www.antweb.org)); this is the largest online database of images, specimen records and natural history information on ants. These current databases focus on complementary datasets (Fig. 1): Ant Profiler focuses on ecology and life-history information, GABI focuses on distribution records and AntWeb principally on taxonomic information.

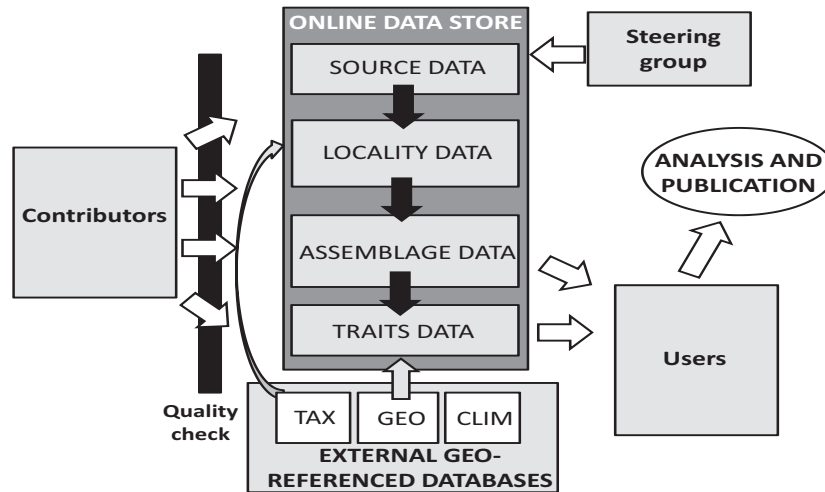
Our database (*GlobalAnts*: [www.globalants.org](http://www.globalants.org)) is distinct from these other ant databases, and is a significant advance on other trait databases, as it contains not only trait data for individual species but also data for whole assemblages with accompanying abundance data (Figs 1 and 2). Abundance data allow us to quantify assemblage structure; indeed data on abundance linked to traits are essential for examining many key questions in ecology. Data on assemblage structure are necessary to quantify the relative prevalence of traits when exploring trait–environment interactions, but this type of data tends to be rare. In addition, because most trait databases do not link to local assemblages, they only provide average trait values, not individual or location-specific ones; this can be problematic because aggregated information from regional databases does not always reliably reflect onsite trait values or local variation between sites (Cordlandwehr *et al.*, 2013). Our new database contains data on local assemblages and linked traits, which means we can understand what is going on in real communities with real



**Fig. 1.** Summary of types of data within each database. The database with the greatest focus on a data type is shown in the darkest colour. White (no fill) represents no coverage of a data type within a database. GABI = Global Ant Biodiversity Informatics.

interactions among species, rather than relying on regional abundance data or species range distributions. The availability of both species traits and abundance data also allows us to use exciting new analytical techniques that link traits with the environment through the abundances of species; the new predictive fourth corner analysis is one example (Brown *et al.*, 2014; Gibb *et al.*, 2015a). Finally, an additional consideration is that our database, through the inclusion of georeferenced assemblage data, means there is scope for intra-specific studies, in addition to the standard inter-specific ones. Georeferenced data should help us understand better to what extent, and why, trait values differ from location to location by enabling the addition of information about drivers of difference in traits (e.g. NPP, temperature).

In this study, we (i) introduce this new ant trait database and describe a set of standardised traits for use in ant functional ecology work, (ii) present a summary of current data coverage with respect to different traits and their availabilities among subfamilies, biomes and continents, (iii) examine initial relationships among measured traits and (iv) present an initial set of patterns in need of explanation; patterns that seem to have gone unnoted, but that become obvious in the light of even a cursory consideration of the geography of particular traits (e.g. pilosity, eye size). Although for this initial data exploration, we focus on a few selected traits (ranging from



**Fig. 2.** The *GlobalAnts* Database functions via the contribution of data which are uploaded online or emailed to the Database Managers. All data must have source and locality information. Data quality and formatting is checked prior to integration into the database. Contributors can include species' abundances (assemblage data) and species' traits data, but it is not necessary to have both. External georeferenced databases can be linked to either the locality or traits data as these both include information on site location. Data within the online data store are available to users for analysis and publication via a data sharing agreement. TAX = taxonomic data, GEO = geographic data (e.g. biome, land use), CLIM = climate data.

core traits to less well-known ones); overall the database includes a diverse suite of traits. Many of the traits we include are measures already used by taxonomists (as standardised descriptive measures) and are thought to represent key evolutionary traits. The traits included are also useful ecologically and therefore can inform us about the functions the ants perform, how ants interact with their environment and how assemblages are structured.

### The *GlobalAnts* Database

Below, we detail a new functional trait database for ants that builds on a global ant diversity database. Initiated in 2006, the ant diversity database focused on species richness (i.e. alpha diversity) for sites globally (Dunn *et al.*, 2007), and was subsequently expanded to contain assemblage-level data for sites worldwide (i.e. species and their abundances for different assemblages) (see, e.g. Gibb *et al.*, 2015b). Data were compiled from voluntary contributions from ant researchers worldwide. As a result, the database grew to contain data on ant assemblages from over one thousand locations worldwide and has enabled collaboration of over fifty researchers from around the world. These collaborations have resulted in a number of publications investigating drivers of species richness and abundance at a global scale (e.g. Dunn *et al.*, 2009; Weiser *et al.*, 2010; Jenkins *et al.*, 2011; Gibb *et al.*, 2015b).

In a significant advance, the *GlobalAnts* database includes trait data which are linked to assemblage abundance data, thus facilitating examination of the functional properties of communities. The *GlobalAnts* database

contains 9056 species and morphospecies with the data for 4416 assemblages covering all continents in which ants are found (Table 1). The *GlobalAnts* database therefore now represents the most comprehensive database linking insect species richness, abundance, composition and functional traits at the community level.

Although the long-term focus of the database is on traits linked to specific assemblages, the database also includes species traits not associated with specific assemblages (i.e. trait data are linked to a locality but there are no associated assemblage data), as well as a trait data for species where we have no specific locality (Table 1). We have chosen to include these data because they are useful for large-scale macrostudies, studies at a higher taxonomic order (e.g. comparisons across genera or subfamilies) and there are no current databases that incorporate them.

Data are uploaded via an online portal ([www.globalants.org](http://www.globalants.org)), and are available, through a data sharing agreement, to researchers who have contributed data. The database will be made open access by 2018 with similar Intellectual Property Guidelines to the TRY database ([https://www.try-db.org/TryWeb/TRY\\_Intellectual\\_Property\\_Guidelines.pdf](https://www.try-db.org/TryWeb/TRY_Intellectual_Property_Guidelines.pdf)), thus facilitating data sharing through open access while also providing for contributors. The development of this database is a significant task, but the sum of the collective parts will enable us to address global-scale questions in a way that, to date, has not been possible. All contributions are welcome, but especially those with abundance and species composition data associated with species traits (Fig. 2, see Data S1 for a template with examples for data entry).

**Table 1.** Summary of data type combinations and associated number of species and morphospecies included in the *GlobalAnts* database (as of February 2016). X – data are available.

Trait data	Assemblage data	Locality	Source	Georeferenced	No. species with associated trait data*	No. of assemblages
X	X	X	X	X	9056	444
X	–	–	X	–	2765	–
X	–	–	–	X	133	–
X	–	–	–	–	93	–
–	X	X	X	–	N/A	4416

\*Includes species and morphospecies.

## Ant traits

Here, we present a set of standardised trait measures that are used for the *GlobalAnts* database (Tables 2 and 3, Appendix S1). In an effort to facilitate comparisons between disparate studies, we advocate the widespread use of these traits for trait-based studies; these measures are standardised by providing guidelines on the method of quantification. Natural selection can operate at both an individual and colony level for ants (Keller, 1995), so ant functional traits may be quantified at both the level of the individual worker and that of the colony. Accordingly, the database contains individual-level traits (e.g. morphology)

and also some colony-level traits (e.g. colony size, type and founding), although data on colony-level traits are more challenging to collect. We have not classified these standardised trait measures into trait types (e.g. performance traits or response traits, Violle *et al.*, 2007) because often this distinction is dependent on the question being posed (Petchey & Gaston, 2006). Instead we simply detail whether these traits relate to morphological, life-history or ecological characteristics (Tables 2 and 3). Many of the morphological traits we include are standard taxonomic measurements used for species descriptions (Table 2; e.g. head length, scape length, hind femur length; www.antwiki.org) and thus relatively easy to obtain. We have also

**Table 2.** List of standardised morphological traits used in the *GlobalAnts* database, their hypothesised functions and unit of measurement. Priority assigned from 1 (high) to 3 (low), based on likely significance and correlation with other traits. Figures in Appendix S1 illustrate the morphological trait measures.

Trait	Hypothesised trait function or environmental response	Measure	Priority	Figure
Morphological – continuous				
Head width across the eyes	Size of gaps through which worker can pass (Sarty <i>et al.</i> , 2006); mandibular musculature (Kaspari, 1993). Also indicative of worker body size.	mm	1	S2a,b
Head length	May be indicative of diet; longer head length may indicate herbivory. Also indicative of worker body size.	mm	1	S3a
Clypeus length	Clypeus linked to sucking ability and liquid-feeding behaviour (Davidson <i>et al.</i> , 2004)	mm	2	S3b
Mandible length	Length of mandibles relates to diet (Fowler <i>et al.</i> , 1991): longer mandibles = more predatory (Gibb & Cunningham, 2013)	mm	1	S4
Tibia length	Indicative of foraging speed, which reflects the complexity of the habitat (Feener <i>et al.</i> , 1988); thermoregulatory strategy (Sommer & Wehner, 2012)	mm	3	S5
Femur length	Indicative of foraging speed, which reflects the complexity of the habitat (Feener <i>et al.</i> , 1988); thermoregulatory strategy (Sommer & Wehner, 2012)	mm	1	S6
Scape length	Sensory abilities: longer scapes facilitate following of pheromone trails (Weiser & Kaspari, 2006)	mm	2	S7
Weber's length	Indicative of worker body size (Weber, 1938), which correlates with metabolic characteristics	mm	2	S8
Pronotum width	Size of gaps through which worker can pass (Sarty <i>et al.</i> , 2006).	mm	2	S9
Inter-ocular width	Related to hunting method (Fowler <i>et al.</i> , 1991) or the component of the habitat occupied (Gibb & Parr, 2013); Eye position = residual of (Head width – I-O width) with head length	mm	1	S10
Max eye width	Eye size is indicative of food searching behaviour and activity times (Weiser & Kaspari, 2006)	mm	1	S11
Whole body length	Size of gaps through which worker can pass (Sarty <i>et al.</i> , 2006); also linked to metabolic characteristics	mm	3	S12

**Table 3.** List of standardised non-continuous morphological traits and ecological and life-history traits used in the *GlobalAnts*, their hypothesised functions and unit of measurement. Descriptions of how to obtain these measures are provided in Appendix S1.

Trait	Hypothesised trait function or environmental response	Measure	Priority	Figure
Morphological – count/ordinal/categorical				
Sculpturing	Thickened, structured cuticles may increase dehydration tolerance	Ordinal ranking: 0 = no markings, shiny; 1 = fine network of marks; cell-like shallow ridges; 2 = deeper dimples and ridging; 3 = surface heavily textured with ridges, grooves or pits	2	S13
Pilosity	Hairs may increase tolerance to dehydration or may relate to mechanoreception (Wittlinger <i>et al.</i> , 2007)	Count of hairs crossing mesosoma profile	2	S14
Number of spines	Spines may act as an antipredation mechanism (Michaud & Grant, 2003)	Count (mesosoma & petiole separate)	2	S15
Dominant colour - head - mesosoma - gaster	Thermal melanism (Clusella-Trullas <i>et al.</i> , 2007); environmental stress (Hiyama <i>et al.</i> , 2012); camouflage/predation risk (Garcia <i>et al.</i> , 2009); mimicry	Based on a colour wheel (Appendix I) and RGB codes	2	S16a, b
Polymorphism	Different worker castes perform different tasks within the colony, allowing greater specialisation (Wilson, 1953)	Categorical: Monomorphic, dimorphic and polymorphic	2	–
Ecology				
Nest site	–	Categorical: Hypogaecic, under stones, dead wood, litter, arboreal	2	–
Activity time	–	Categorical: Diurnal, crepuscular, nocturnal, hypogaecic	2	–
Diet	–	Categorical: Generalist predator, specialist predator, generalist, seed harvester, seed harvester & generalist, sugar feeder & generalist	2	–
Invasive	–	Categorical: Invasive, Native	2	–
Life history				
Queen number	–	Categorical: Monogyny, polygyny, both monogyny and polygyny	3	–
Worker number	–	Count	3	–
Colony type	–	Categorical: Monodomous, polydomous, both monodomous and polydomous, supercolony	3	–
Colony founding	–	Categorical: Dependent, claustral independent, non-claustral independent, facultative dependent, social parasite	3	–

included a range of other morphological traits that, to date, have received little attention; these include spinosity, pilosity and colour (Table 3). Exact measures and examples of some of these categorical traits are shown in the online supplementary material (Appendix S1). Spinosity may relate to defence, whereas the degree of pilosity may be related to thermoregulation (Shi *et al.*, 2015), desiccation tolerance or sensory ability. Colour of ectotherms is receiving increasing research attention as interest in the effects of climate change grows (e.g. Zeuss *et al.*, 2014; Bishop *et al.*, 2016). We separate ant body colour into dominant colours for the head, mesosoma and gaster; two colour wheels are provided to standardise classification, with one focusing on variation among the browns and

yellows (Appendix S1). These data can then be converted into R:G:B or HSV classification for subsequent analysis.

Where possible we ask contributors to measure six individuals of each monomorphic species, whereas for dimorphic species we ask for 6 individuals for both minors and majors and 10 individuals for each polymorphic species; these data also provide exciting opportunities to explore patterns in intra-specific variation.

Given the large number of potential traits per individual, we chose to rank the importance of the traits for the *GlobalAnts* database to enable contributors who are pressed for time to focus on what we consider to be a subset of the most essential traits (Tables 2 and 3). Of course, any number and combination of these traits can

be used, but the significance ranking allows for prioritisation for the *GlobalAnts* database. We acknowledge that collecting data on some traits is more challenging than others (e.g. colony data vs. measuring head length – see Tables 4 and 5), thus the database is weighted towards those traits that are more readily obtainable. Ideally in the future it would be desirable to work to increase data on important life-history and ecological traits such as colony size, number of queens or trophic position (measured using isotopes).

We are confident that many of the traits we have chosen to include in our trait scheme represent the hypothesised function. For example, Weber's length correlates closely with body size (Weber, 1938), and therefore reflects total energy consumption (i.e. Kleiber's Law). Some of the other functional traits have been proposed by various authors, but many require further verification and testing. For example, as many relate to diet or trophic position, stable isotope work will be particularly useful tool: Gibb *et al.* (2015a) found a positive relationship between mandible length and  $\delta^{15}\text{N}$ , suggesting predatory ants have larger mandibles.

### Database structure

Contributions to the *GlobalAnts* database include 'Source', 'Locality', 'Observation' and 'Traits' data (Fig. 2, Data S1). A Notes page provides an explanation of all terms (Data S1). Each file is linked by the code name of the source or locality. The 'Source' data describe the contributor, source type and publication status, year of publication and source citation. The 'Localities' data link to the 'Source' data through the source and include the detail of specific localities ('Locality ID'), including georeferencing, detail on political regions, summaries of abundances and species richness, trapping technique details, habitat descriptions and disturbance categories (e.g. Gibb *et al.*, 2015b). The 'Observations' data link to the 'Localities' page through the Locality ID and list the abundance and/or occurrence of ant species in each locality. The 'Traits' data link to the 'Locality' or 'Observations' data through the Locality ID and include detail on different traits (e.g. morphological, ecology and life history). For traits data not linked to assemblage data, georeferencing is included if possible. The online portal ([www.globalants.org](http://www.globalants.org)) highlights data that do not conform to the accepted format, allowing the contributors to make corrections before the data are uploaded.

### Current traits data coverage and trait patterns

As of January 5<sup>th</sup> 2016, the *GlobalAnts* database contained 82 910 trait entries for 9056 ant species and morphospecies across 4416 localities that include the entire 'Source', 'Locality', 'Observation' and 'Traits' information. Trait data are available for some species, but not all

data are georeferenced (Table 1). Data are most comprehensive for continuous morphological traits (Table 4) with 92% of localities having some form of traits data (providing data for any particular continuous trait) and are least comprehensive for life-history and ecological traits. For traits associated with assemblage data, the majority of measures have been taken from individuals described to genus and morphospecies (53%), with the remainder from specimens identified to species.

The localities from which traits data have been collected cover a broad range of climatic conditions, with mean annual temperatures from 0 to 30 °C and mean annual rainfall from 0 to 3000 mm (Fig. 3). A data gap at high precipitation and low temperature reflects an absence of those climates on earth. The distribution of data for major morphological traits is comprehensive, although some traits, such as pilosity, cover a more limited climatic range at present.

Kernel density plots, which illustrate the probability density function of a variable (Parzen, 1962), were used to represent the distribution of data for biomes, continents and subfamilies in R ('density' function, R Development Core Team 2014). Selected traits included head length, mandible length, femur length, eye width, eye position (residual of head width minus inter-ocular distance with head length, Gibb & Parr, 2013) and pilosity. The availability of data across subfamilies roughly reflects their relative species richnesses (Table 4). An overview of the density distribution of the six selected traits shows some differences among the four most speciose subfamilies (Myrmicinae, Formicinae, Ponerinae and Dolichoderinae) (Fig. 4a). For example, eye position (high values indicate more dorsally positioned eyes) tends to be greatest for dolichoderine and formicine ants, whereas mandible length tends to be greatest for ponerines.

The availability of data varies among continents and biomes. Although there are data from all continents on which ants occur, most measurements from species associated with assemblage data come from sites in Central and South America and Oceania (Table 5). Not all major biomes (e.g. deserts) are represented in the dataset yet; the most prevalent biomes being tropical, reflecting the distribution of species richness. Our preliminary analysis indicates that there is strong biogeographic variation in traits. Data density distributions for size-related traits suggest that body size tends to be larger in Europe and Oceania, whereas mean eye width is highly uniform across continents (Fig. 4b). For biomes, temperate ecosystems appear to support larger species on average, mandibles appear smaller in tropical biomes, whereas forested biomes seem to have ants with smaller eyes (Fig. 4c).

### Considerations

One limitation of using some of the data beyond the assemblages within which it was collected is that morphospecies are used extensively. Morphospecies are particularly prevalent in datasets from outside Europe and

**Table 4.** Summary of data availability in terms of localities and numbers of species across traits in the database (as of January 2016) for ant subfamilies and minimum, median, mean and maximum values for continuous and ordinal traits.

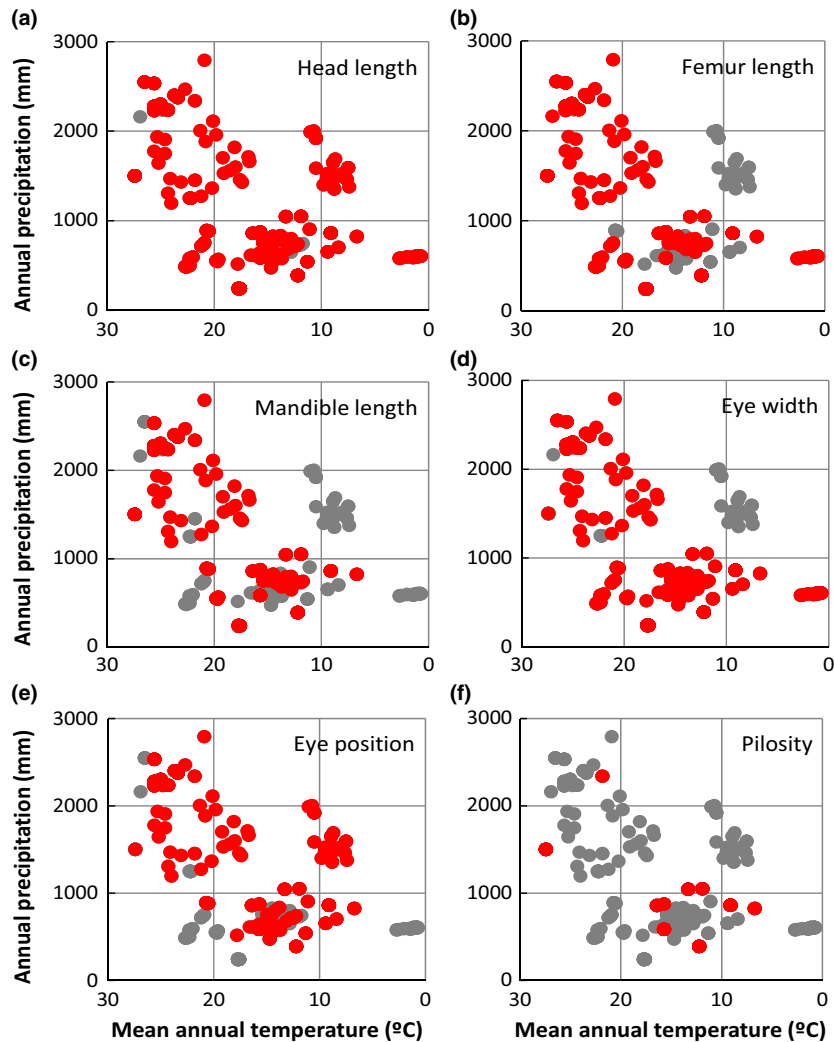
Trait	Localities	Species records	% species	Agroecomyrmecinae	Amblyoponinae	Dolichoderinae	Dorylinae	Ectatomminae	Formicinae	Heteroponerinae	Leptanillinae	Myrmecinae	Myrmecillinae	Myrmicinae	Paraponerinae	Ponerinae	Proceratinae	Pseudomyrmecinae	Minimum	Median	Mean	Maximum
Head width across eyes	265	1463	67	1	11	74	31	53	218	7	1	0	824	0	0	221	14	8	0.22	0.72	0.90	4.94
Head length	407	1850	68	1	12	118	54	68	328	9	1	8	1001	1	1	223	12	14	0.22	0.61	0.75	4.10
Clypeus length	236	1305	71	0	9	77	38	51	220	7	1	3	711	0	0	173	7	8	0.02	0.17	0.21	0.94
Mandible length	284	1525	72	0	12	104	44	58	291	11	1	12	794	0	0	182	8	8	0.09	0.38	0.50	5.16
Hind femur length	339	1913	71	0	14	126	55	71	346	11	1	12	1015	1	1	236	12	14	0.10	0.70	0.98	6.90
Scape length	391	1618	71	0	13	107	49	58	311	11	1	12	846	0	0	194	8	8	0.14	0.60	0.82	5.87
Weber's length	363	1861	73	1	12	122	50	68	377	11	1	12	963	0	0	221	13	10	0.27	0.89	1.22	9.50
Pronotum width	274	1244	69	1	9	73	34	51	210	7	1	3	669	0	0	170	8	8	0.15	0.43	0.54	2.38
Inter-ocular width	284	1513	72	0	12	104	37	58	291	11	1	12	792	0	0	180	7	8	0.05	0.54	0.65	3.78
Max eye width	393	1838	70	1	14	124	44	70	336	11	1	12	984	1	1	216	10	14	0.00	0.12	0.16	1.33
Whole body length	112	666	56	0	7	17	11	38	74	7	0	0	421	0	0	84	3	4	1.06	3.05	3.63	15.83
Sculpturing	242	866	72	1	4	65	21	30	179	2	1	5	426	0	0	119	9	4	0	2	2	3
Pilosity	113	418	48	1	1	21	10	21	80	0	0	0	232	0	0	45	5	2	0	9	14	115
Number of Spines	208	821	67	1	5	64	19	29	165	2	1	5	402	0	0	115	9	4	1	2	3	16
Dominant colour head*	119	429	47	1	1	21	10	21	84	0	0	0	239	0	0	45	5	2	0	0	1	2
Dominant colour mesosoma*	119	429	47	1	1	21	10	21	84	0	0	0	239	0	0	45	5	2	1	17	-	24
Dominant colour gaster*	119	429	47	1	1	21	10	21	84	0	0	0	239	0	0	45	5	2	1	17	-	24
Polymorphism	153	653	60	1	3	39	20	26	133	0	0	5	356	0	0	63	5	2	1	1	-	3
Worker number	8	17	0	1	0	1	0	0	7	0	0	0	8	0	0	0	0	0	10	1300	9724	100000
Colony type	52	260	37	1	1	6	3	17	35	0	0	0	163	0	0	29	5	0	1	1	-	3
Colony founding	6	10	0	0	0	0	0	0	6	0	0	4	0	0	0	0	0	0	1	2	-	3
Invasive	52	265	36	1	1	6	3	17	38	0	0	0	165	0	0	29	5	0	1	2	-	2
Diet	52	265	36	1	1	6	3	17	35	0	0	0	163	0	0	29	5	0	0	2	-	2
Nest site	46	256	37	1	1	6	3	17	38	0	0	0	165	0	0	29	5	0	0	2	-	2
Activity	52	260	37	1	1	6	3	17	34	0	0	0	160	0	0	29	5	0	0	2	-	2
Queen number	52	264	36	1	1	6	3	17	37	0	0	0	165	0	0	29	5	0	1	1	-	2

\*Colour codes are as follows: 1: black (Red: 0; Green: 0; Blue: 0); 17: yellow-brown (R: 212; G: 138; B: 6); 18: pale yellow-brown (R: 215; G: 172; B: 95); 24: dark brown (R: 41; G: 27; B: 13); further detail about colour is provided in Appendix I.



**Table 5.** Summary of data availability (as of August 2015) in terms of numbers of species across traits in the database for continents and biomes.

Trait	Africa	Asia	Europe	North America	Oceania	Central & South America	Boreal Forests/ Taiga	Mediterranean Forests, Woodlands, and Scrub	Temperate Broadleaf and Mixed Forests	Temperate Coniferous Forests	Temperate Grasslands, Savannas, and Shrublands	Tropical and Subtropical Grasslands, Savannas, and Shrublands	Tropical and Subtropical Moist Broadleaf Forests
Head width across eyes	221	367	66	144	94	597	9	57	1	37	0	419	1020
Head length	228	296	77	167	325	785	9	168	112	60	67	629	949
Clypeus length	154	296	57	60	199	556	0	163	0	0	0	352	868
Mandible length	155	296	57	65	415	556	0	163	192	0	67	353	871
Hind femur length	228	367	66	77	415	784	9	163	192	0	67	629	992
Scape length	228	296	77	65	415	556	9	168	209	0	66	425	872
Weber's length	155	559	66	131	414	558	9	163	191	24	67	353	1176
Pronotum width	79	296	66	65	199	558	9	163	1	0	0	277	873
Inter-ocular width	152	296	57	60	409	556	0	163	189	0	67	347	868
Max eye width	218	296	77	77	409	784	9	168	206	0	67	616	921
Whole body length	0	0	66	60	0	555	9	57	0	0	0	104	571
Sculpturing	79	296	66	120	220	92	9	57	95	15	67	173	486
Pilosity	79	0	57	105	92	92	0	57	0	0	0	171	190
Number of Spines	79	296	66	105	190	92	0	57	114	0	0	173	486
Dominant colour head	79	0	66	105	94	92	0	57	17	0	0	173	190
Dominant colour mesosoma	79	0	66	105	94	92	0	57	17	0	0	173	190
Dominant colour gaster	79	0	66	105	94	92	0	57	17	0	0	173	190
Polymorphism	164	0	72	107	218	100	9	57	110	0	67	258	199
Worker number	0	0	16	0	0	1	0	0	16	0	0	0	1
Colony type	0	0	61	107	0	100	0	57	8	0	0	0	199
Colony founding	0	0	10	0	0	0	0	0	10	0	0	0	0
Invasive at that site	0	0	66	107	0	100	0	57	17	0	0	0	199
Diet	0	0	66	107	0	100	0	57	11	0	0	0	197
Nest site	0	0	63	107	0	100	0	57	17	0	0	0	199
Activity	0	0	63	105	0	99	0	57	0	0	0	0	199
Queen number	0	0	65	107	0	100	0	57	15	0	0	0	199



**Fig. 3.** Distribution of data in climate space (mean annual temperature and precipitation) for six selected traits: a) head length; b) femur length; c) mandible length; d) eye width; e) eye position (calculated from head width and inter-ocular distance) and f) pilosity. Each dot represents an assemblage locality. Grey dots represent the entire set of localities available (all traits); red dots represent the set of localities for which each selected trait is available. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

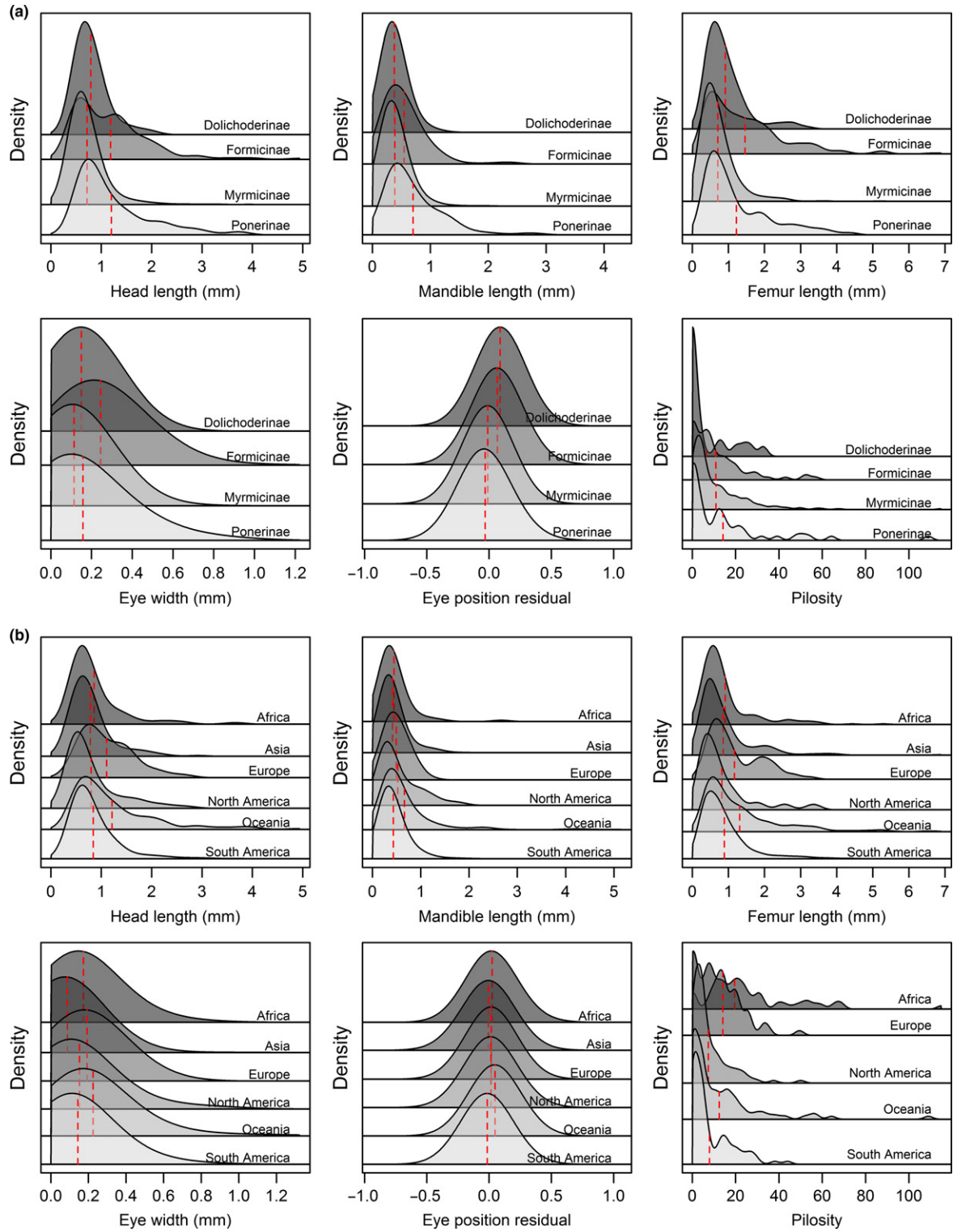
North America reflecting the paucity of knowledge about species from much of the world. It is possible that the same undescribed species is listed more than once under different morphospecies names, so overall species richness estimates from the database may be inflated, however, this issue does not affect analyses performed using the local assemblage as the study unit.

### Using the *GlobalAnts* database: Future Questions

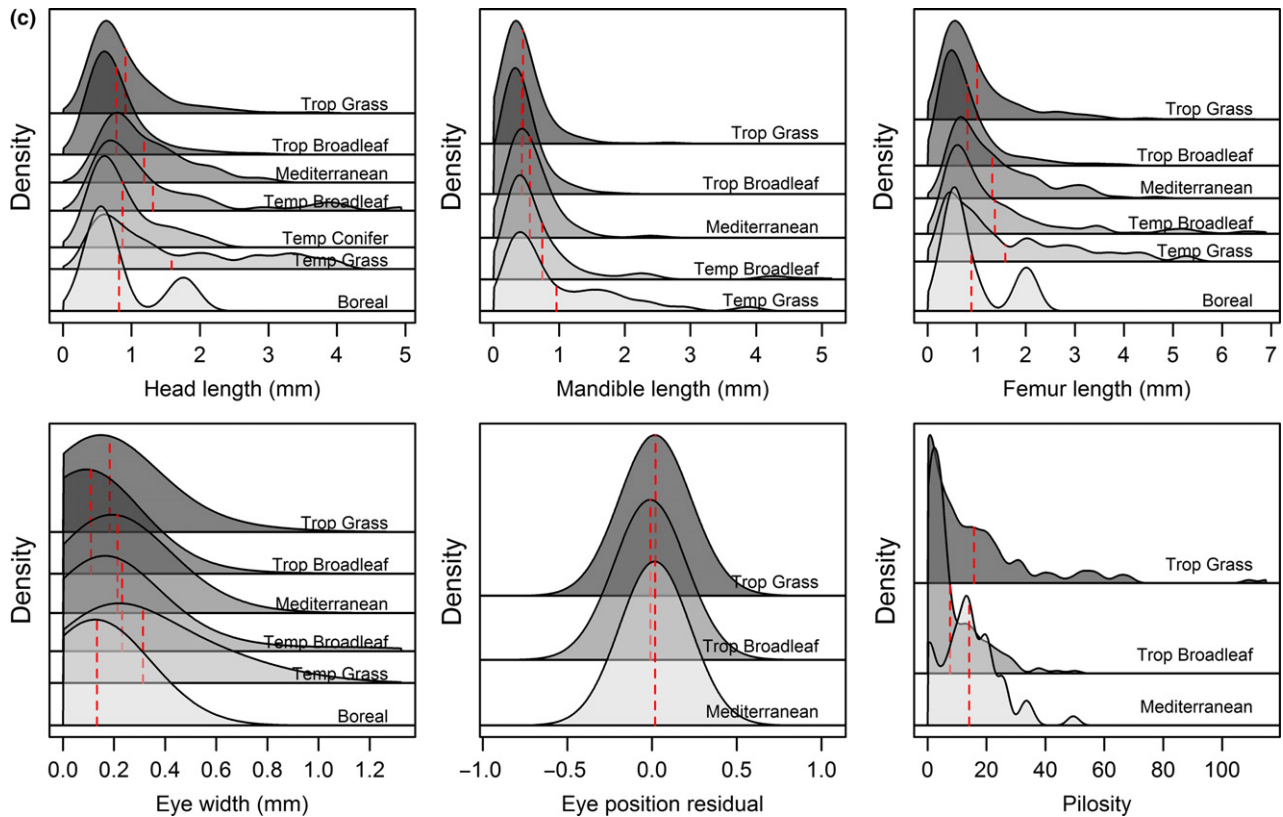
Initial examination of the data indicates broad global coverage in terms of biomes and climate space. When we consider these data even in a basic way, interesting differences in some ant morphological traits emerge among subfamilies (more than just differences in body size), and

there is clearly strong variation among continents and biomes. These intriguing variations in traits appear to be a mix of those associated with biogeographic region and climate, patterns which will be investigated further in future publications.

Immediately, one thing that these preliminary data make clear is that the first challenge we face is to develop better models and theories about how and why traits should differ among regions. No doubt this large-scale mensurative work will also inspire more experimental work investigating the mechanisms through which traits interact with their environment. For example, on initial examination of the data, there is a suggestion that ants may be hairier in open, warm environments (e.g. tropical grasslands); is this a true pattern and what is the driving mechanism? A second challenge, and one that we hope to



**Fig. 4.** Kernel density plots for six selected traits for (a) the four most speciose subfamilies, (b) main continents and (c) biomes. Traits are as follows: head length, femur length, mandible length, eye width, eye position (calculated from head width and inter-ocular distance) and pilosity. Biomes are based on the WWF terrestrial ecoregions classification. Mean = vertical red dashed line. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].



**Fig. 4.** Continued.

engage researchers in through this study, is to compile more data. Currently, there are regions of the world for which either we lack traits or trait data are limited. Filling in the gaps, particularly in areas with climate extremes, should be a priority; data from desert regions (both hot and cold) and areas that are cool and wet (0–15 °C and 1000–2000 mm) would be especially valuable (Fig. 3).

Specific key questions we hope to address with the database include:

- 1 At a global scale, which traits are independent of phylogeny? This is needed as a first step to reduce redundancy in future analyses.
- 2 Can we use the database to explore how traits relate to one another and explore their significance? Is there any redundancy in the traits? Broad patterns could inspire more detailed work testing the function of less well-understood traits and the mechanisms through which traits function.
- 3 How do ant traits evolve? For traits that are independent of phylogeny (e.g. colour, Bishop *et al.*, 2016), merging traits, communities and phylogenies could be a productive enterprise.
- 4 Can we identify global hotspots of ant functional diversity? Do they overlap with phylogenetic diversity? Can areas of functional redundancy be identified?
- 5 Multivariate analyses are highly dependent on the input variables which has hindered global and cross-study comparisons. Standardised ant traits will now enable multivariate analyses to be undertaken. To what extent is there always a fixed morphospace for any given assemblage? How does functional beta diversity vary globally (i.e., biogeographically, latitudinally, elevationally and among biomes – e.g. Bishop *et al.*, 2015)? Which types of trait combinations characterise different biomes?
- 6 How do broad-scale abiotic factors relate to different traits? How do climate, microclimate (e.g. Kearney *et al.*, 2014), latitude, habitat complexity and other environmental gradients affect the relative abundances of different traits? For example, how does ant colour vary latitudinally, but also what patterns are there in colour diversity and evenness?
- 7 How is the functional structure of communities influenced by anthropogenic disturbances and how consistent are phylogenetic and functional responses to disturbance? Can traits be used to predict species' vulnerability to anthropogenic disturbance (e.g. Senior *et al.*, 2013)? How does the relative dominance of different types of functions change?
- 8 Where data are available, how do responses differ intra-specifically, as well as inter-specifically? And how is variance in body size affected by environmental factors?

## Conclusions

The *GlobalAnts* database represents the most comprehensive coverage of global terrestrial invertebrate traits with associated assemblage data produced by any collaboration. The traits proposed here, if used broadly, will enable direct comparison across studies, facilitating understanding of general patterns and responses of communities. Furthermore, given access to online specimens (e.g. AntWeb) and the increasing interest in functional traits, there is much scope to build a significant resource for current and future myrmecologists. We also suggest that there is the potential for applications beyond ants; e.g. commonalities between ants and other epigeic fauna, or comparisons across different taxa at a global scale may be explored in future.

Use of the database has the potential to make a significant contribution to a new and rapidly expanding ecology based on traits and ecosystem functioning (Lavorel & Garnier, 2002; Gagic *et al.*, 2015). Uniquely, the database provides exciting opportunities to explore questions not only from a species-trait perspective but enables us to investigate the importance of abundance in influencing numerous processes and relationships.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12211:

**Data S1.** Template for data entry. [As Excel file].

**Appendix S1.** Guide to measurement of the traits included in the *GlobalAnts* database. [As PDF file].

## References

- Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M. (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Science USA*, **111**, 740–745.
- Arnan, X., Cerdá, X. & Retana, J. (2014) Ant functional responses along environmental gradients. *Journal of Animal Ecology*, **83**, 1398–1408.
- Barton, P.S., Gibb, H., Manning, A.D., Lindenmayer, D.B. & Cunningham, S.A. (2011) Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. *Biological Journal of the Linnean Society*, **102**, 301–310.
- Bertelsmeier, C., Luque, G.M., Confais, A. & Courchamp, F. (2013) Ant Profiler – A database of ecological characteristics of ants (Hymenoptera: Formicidae). *Myrmecological News*, **18**, 73–76.
- Bihn, J.H., Gebauer, G. & Brandl, R. (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology*, **91**, 782–792.
- Bishop, T.R., Robertson, M.P., Gibb, H., van Rensburg, B.J., Braschler, B., Chown, S.L., Foord, S.H., Munyai, T.C., Okey, I., Tshivhandekano, P.G., Werenkraut, V. & Parr, C.L. (2016) Ant assemblages have darker and larger members in cold environments. *Global Ecology & Biogeography*, **25**, 1489–1499.
- Bishop, T.R., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2015) Contrasting species and functional beta diversity in montane ant assemblages. *Journal of Biogeography*, **42**, 1776–1786.
- Blaimer, B., Brady, S.G., Schultz, T.R. & Fisher, B.L. (2015) Functional and phylogenetic approaches reveal the evolution of diversity in a hyper diverse biota. *Ecography*, **38**, 901–912.
- van Bodegom, P.M., Douma, J.C. & Verheijen, L.M. (2014) A fully traits-based approach to modelling global vegetation distribution. *Proceedings of the National Academy of Science USA*, **111**, 13727–13732.
- Brown, A.M., Warton, D.I., Andrew, N.R., Binns, M., Cassis, G. & Gibb, H. (2014) The fourth-corner solution – using predictive models to understand how species traits interact with the environment. *Methods in Ecology and Evolution*, **5**, 344–352.
- Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.
- Clusella-Trullas, S., van Wyk, J.H. & Spotila, J.R. (2007) Thermal melanism in ectotherms. *Journal of Thermal Biology*, **32**, 235–245.
- Cordlandwehr, V., Meredith, R.L., Ozinga, W.A., Bekker, R.M., van Groenendael, J.M. & Bakker, J.P. (2013) Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology*, **101**, 1365–2745.
- Cornwell, W.K., Westoby, M., Falster, D.S., FitzJohn, R.G., O'Meara, B.C., Pennell, M.W., McGlenn, D.J., Eastman, J.M., Moles, A.T., Reich, P.B., Tank, D.C., Wright, I.J., Aarssen, L., Beaulieu, J.M., Kooyman, R.M., Leishman, M.R., Miller, E.T., Niinemets, U., Oleksyn, J., Ordóñez, A., Royer, D.L., Smith, S.A., Stevens, P.F., Warman, L., Wilf, P. & Zanne, A.E. (2008) Plant traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.
- Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–38.
- Davidson, D.W., Cook, S.C. & Snelling, R.R. (2004) Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. *Oecologia*, **139**, 255–266.
- Diamond, S.E., Nichols, L.M., McCoy, N., Hirsch, C., Pelini, S.L., Sanders, N.J., Ellison, A.M., Gotelli, N.J. & Dunn, R.R. (2012) A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology*, **93**, 2305–2312.
- Díaz, S., Cabido, M., Zak, M., Martínez Carretero, E. & Aránibar, J. (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science*, **10**, 651–660.

- Ding, Z., Keeley, K.J., Wang, Y., Pakeman, R.J. & Ding, P. (2013) Patterns of bird functional diversity on land-bridge island fragments. *Journal of Animal Ecology*, **82**, 781–790.
- Diniz-Filho, J.A., De Marco JrP. & Hawkins, B.A. (2010) Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, **3**, 172–179.
- Donoso, D.A. (2014) Assembly mechanisms shaping tropical litter ant communities. *Ecography*, **37**, 490–499.
- Dunn, R.R., Agosti, D., Andersen, A.N., Bruhl, C.A., Cerdá, X., Ellison, A., Fisher, B.L., Fitzpatrick, M.C., Gibb, H., Gotelli, N.J., Gove, A.D., Guénard, B., Janda, M., Kaspari, M.E., Laurent, E.J., Lessard, J.P., Longino, J.T., Majer, J.D., Menke, S.B., McGlynn, T.P., Parr, C.L., Philpott, S.M., Pfeiffer, M., Retana, J., Suarez, A.V., Vasconcelos, H.L., Weiser, M.D. & Sanders, N.J. (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, **12**, 324–333.
- Dunn, R.R., Sanders, N.J., Fitzpatrick, M.C., Laurent, E., Lessard, J.-P., Agosti, D., Andersen, A.N., Bruhl, C., Cerdá, X., Ellison, A., Fisher, B., Gibb, H., Gotelli, N., Gove, A., Guénard, B., Janda, M., Kaspari, M., Longino, J.T., Majer, J., McGlynn, T.P., Menke, S., Parr, C.L., Philpott, S., Pfeiffer, M., Retana, J., Suarez, A.V. & Vasconcelos, H. (2007) Global ant biodiversity and biogeography - a new database and its possibilities. *Myrmecological News*, **10**, 77–83.
- Feener, D.H., Lighton, J.R.B. & Bartholomew, G.A. (1988) Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. *Functional Ecology*, **2**, 509–520.
- Fowler, H.G., Forti, L.C., Brandão, C.R.F., Delabie, J.H.C. & Vasconcelos, H.L. (1991) Ecologia nutricional de formigas. *Ecologia Nutricional De Insetos* (ed. by A.R. Panizzi & J.R.P. Parra), pp. 131–223. Manole, São Paulo, Brasil.
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I.S., Emmerston, M., Potts, S.G., Tschamtker, T., Weisser, V. & Bommarco, R. (2015) Functional identity and diversity of animals predicts ecosystem functioning better than species-based indices. *Proceedings of the Royal Society of London B*, **282**, 20142620.
- Garcia, T.S., Paoletti, D.J. & Blaustein, A.R. (2009) Correlated trait responses to multiple selection pressures in larval amphibians reveal conflict avoidance strategies. *Freshwater Biology*, **54**, 1066–1077.
- Gibb, H. & Cunningham, S.A. (2013) Restoration of trophic structure in an assemblage of omnivores, considering a revegetation chronosequence. *Journal of Applied Ecology*, **50**, 449–458.
- Gibb, H. & Parr, C.L. (2013) Does structural complexity determine the morphology of assemblages? An experimental test on three continents. *PLoS ONE*, **8**(5), e64005.
- Gibb, H., Sanders, N.J., Dunn, R.R., Watson, S., Photakis, M., Abril, S., Andersen, A.N., Angulo, E., Armbrrecht, I., Arnan, X., Baccaro, F.B., Bishop, T., Boulay, R., Castracani, C., Del Toro, I., Delsinne, T., Diaz, M., Donoso, D.A., Enriquez, M.L., Fayle, T.M., Feener, D.H., Fitzpatrick, M.C., Gomez, C., Grasso, D.A., Groc, S., Heterick, B., Hoffmann, B.D., Lach, L., Lattke, J., Leponce, M., Lessard, J.-P., Longino, J., Lucky, A., Majer, J., Menke, S.B., Mezger, D., Mori, A., Munyai, T.C., Paknia, O., Pearce-Duvel, J., Pfeiffer, M., Philpott, S.M., de Souza, J.L.P., Tista, M., Vasconcelos, H.L., Vonshak, M. & Parr, C.L. (2015b) Climate mediates the effects of disturbance on ant assemblage structure. *Proceedings of the Royal Society of London B*, **282**, 1808.
- Gibb, H., Stoklosa, J., Warton, D.I., Brown, A.M., Andrew, N.R. & Cunningham, S.A. (2015a) Does morphology predict trophic position and habitat use of ant species and assemblages? *Oecologia*, **177**, 519–531.
- Guénard, B., Weiser, M.D. & Dunn, R.R. (2012) Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. *Proceedings of the National Academy of Science USA*, **109**, 7368–7373.
- Hiyama, A., Taira, W. & Otaki, J.M. (2012) Color-pattern evolution in response to environmental stress in butterflies. *Frontiers in Genetics*, **3**, 15.
- Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. & Assmann, T. (2014) Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera: Carabidae). *Insect Conservation & Diversity*, **7**, 195–205.
- Jenkins, C.N., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerdá, X., Ellison, A.M., Fisher, B.L., Fitzpatrick, M.C., Gotelli, N.J., Gove, A.D., Lattke, J.E., Lessard, J.-P., McGlynn, T.P., Menke, S.B., Parr, C.L., Philpott, S.M., Sanders, N.J., Weiser, M.D. & Dunn, R.R. (2011) Diversity in light of climate change: the case of ants. *Diversity and Distributions*, **17**, 652–662.
- Kaspari, M. (1993) Body-size and microclimate use in Neotropical granivorous ants. *Oecologia*, **96**, 500–507.
- Kaspari, M. (2005) Global energy gradients and the regulation of body size: worker mass and worker number in ant colonies. *Proceedings of the National Academy of Science USA*, **102**, 5079–5083.
- Kaspari, M. & Weiser, M. (1999) Interspecific scaling in ants: the size grain hypothesis. *Functional Ecology*, **13**, 530–538.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C., Kerckhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.J., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

- Kearney, M.R., Isaac, A.P. & Porter, W.P. (2014) microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Scientific Data*, **1**, 140006.
- Keller, L. (1995) Social life: the paradox of multiple-queen colonies. *Trends in Ecology and Evolution*, **10**, 355–360.
- Lach, L., Parr, C.L. & Abbott, K.L. (eds) (2010) *Ant Ecology*. Oxford University Press, Oxford, UK.
- Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Simová, I., Donoghue, J.C. II, Svenning, J.-C., McGill, B.J., Boyle, B., Buzzard, V., Dolins, S., Jorgensen, P.M., Marcuse-Kubitza, A., Morueta-Holme, N., Peet, R.K., Piel, W.H., Regetz, J., Schildhauer, M., Spencer, N., Thiers, B., Wiser, S.K. & Enquist, B.J. (2014) Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Science USA*, **111**, 13745–13750.
- Lavelle, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Logez, M., Bady, P., Melcher, A. & Pont, D. (2013) A continental-scale analysis of fish assemblage functional structure in European rivers. *Ecography*, **36**, 80–91.
- Loranger, J., Meyer, S.T., Shipley, B., Kattge, J., Kern, H., Roscher, C. & Weisser, W.W. (2012) Predicting invertebrate herbivory from plant traits: evidence from 51 grassland species in experimental monocultures. *Ecology*, **93**, 2674–2682.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- McGlynn, T.P. (1999) Non-native ants are smaller than related native ants. *American Naturalist*, **154**, 690–699.
- McMahon, S.M., Harrison, S.P., Armbruster, W.S., Bartlein, P.J., Beale, C., Edwards, M.E., Kattge, J., Midgley, G., Morin, X. & Prentice, I.C. (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution*, **26**, 249–259.
- Michaud, J.P. & Grant, A.K. (2003) Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve a defence function? *Bulletin of Entomological Research*, **93**, 499–505.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L. & Bellwood, D.R. (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Science USA*, **111**, 13757–13762.
- Ness, J.H., Bronstein, J.L., Andersen, A.N. & Holland, J.N. (2004) Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. *Ecology*, **85**, 1244–1250.
- Parzen, E. (1962) On estimation of a probability density function and mode. *The Annals of Mathematical Statistics*, **33**, 1065.
- Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.
- Pey, B., Laporte, M.-A., Nahmani, J., Auclerc, A., Capowiez, Y., Caro, G., Cluzeau, D., Cortet, J., Decaëns, T., Dubs, F., Joimel, S., Guernion, M., Briard, C., Grumiaux, F., Laporte, B., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S., Santorufo, L. & Hedde, M. (2014) A thesaurus for soil invertebrate trait-based approaches. *PLoS ONE*, **9**(10), e108985. doi:10.1371/journal.pone.0108985.
- R Development Core Team (2014) *R: A Language and Environment for Statistical Computing V3.03*. Vienna, Austria. <ftp://cran.r-project.org/pub/R/doc/manuals/r-devel/fullrefman.pdf> 1st November 2016.
- Rosenzweig, M. (1995) *Species Diversity in Time and Space*. Cambridge University Press, Cambridge, UK, pp. 460
- Sarty, M., Abbott, K.L. & Lester, P.J. (2006) Habitat complexity facilitates co-existence in a tropical ant community. *Oecologia*, **149**, 465–473.
- Senior, M.J.M., Hamer, K.C., Bottrell, S., Edwards, D.P., Faye, T.M., Lucey, J.M., Mayhew, P.J., Newton, R., Peh, K.S.H., Sheldon, F.H., Stewart, C., Styring, A.R., Thom, M.D.F., Woodcock, P. & Hill, J.K. (2013) Trait-dependent declines of species following conversion of rain forest to oil palm plantations. *Biodiversity and Conservation*, **22**, 253–268.
- Shi, N.N., Tsai, C.-C., Camino, F., Bernard, G.D., Yu, N. & Wehner, R. (2015) Keeping cool: Enhanced optical reflection and radiative heat dissipation in Saharan silver ants. *Science*, **349**, 298–301.
- Siefert, A., Ravenscroft, C., Weiser, M.D. & Swenson, N.G. (2013) Functional beta diversity patterns reveal deterministic community assembly processes in eastern North American trees. *Global Ecology and Biogeography*, **22**, 682–691.
- Silva, R.R. & Brandão, C.R.F. (2010) Morphological patterns and community organization in leaf-litter ant assemblages. *Ecological Monographs*, **80**, 107–124.
- Silva, R.R. & Brandão, C.R.F. (2014) Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. *PLoS ONE*, **9**(3), e93049.
- Sommer, S. & Wehner, R. (2012) Leg allometry in ants: extreme long-leggedness in thermophilic species. *Arthropod Structure & Development*, **41**, 71–77.
- Swenson, N.G., Enquist, B.J., Pither, J., Kerkhoff, A.J., Boyle, B., Weiser, M.D., Elser, J.J., Fagan, W.F., Forero-Montana, J., Fyllas, N., Kraft, N.J.B., Lake, J.K., Moles, A.T., Patino, S., Phillips, O.L., Price, C.A., Reich, P.B., Quesada, C.A., Stegen, J.C., Valencia, R., Wright, I.J., Wright, S.J., Andelman, S., Jorgensen, P.M., Lacher, T.E. Jr, Monteagudo, A., Nunez-Vargas, P., Vasquez, R. & Noling, K.M. (2012) The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography*, **21**, 798–808.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional!. *Oikos*, **116**, 882–892.
- Weber, N.A. (1938) The biology of the fungus-growing ants. Part 4. Additional new forms. Part 5. The Attini of Bolivia. *Revista de Entomologia*, **7**, 154–206.
- Weiser, M.D. & Kaspari, M. (2006) Ecological morphospace of new world ants. *Ecological Entomology*, **31**, 131–142.
- Weiser, M.D., Sanders, N.J., Agosti, D., Cerdá, X., Ellison, A., Fisher, B.L., Gibb, H., Gotelli, N.J., Gove, A.D., Guénard, B., Janda, M., Kaspari, M.E., Lessard, J.P., Longino, J.T., Majer, J.D., Menke, S.B., McGlynn, T.P., Parr, C.L., Philpott, S.M., Retana, J., Suarez, A.V., Vasconcelos, H.L., Yanoviak, S.P. & Dunn, R.R. (2010) Canopy and litter ant assemblages share similar climate-species density relationships. *Biology Letters*, **6**, 769–772.
- Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.

- Wiescher, P.T., Pearce-Duvel, J.M.C. & Feener, D.H. (2012) Assembling an ant community: species functional traits reflect environmental filtering. *Oecologia*, **169**, 1063–1074.
- Wilson, E.O. (1953) The origin and evolution of polymorphism in ants. *Quaternary Review of Biology*, **28**, 136–156.
- Wittlinger, M., Wolf, H. & Wehner, R. (2007) Hair plate mechanoreceptors associated with body segments are not necessary for three-dimensional path integration in desert ants, *Cataglyphis fortis*. *Journal of Experimental Biology*, **210**, 375–382.
- Zeuss, D., Brandl, R., Brändle, M., Rahbek, C. & Brunzel, S. (2014) Global warming favours light-coloured insects in Europe. *Nature Communications*, **5**, 3874.

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