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Does morphology predict trophic position and habitat use of ant species and assemblages?

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Abstract:	A functional traits-based theory of organismal communities is critical for understanding the principles underlying community assembly, and predicting responses to environmental change. This is particularly true for terrestrial arthropods, of which only 20% are described. Using epigaeic ant assemblages, we asked: 1) Can we use morphological variation among species to predict trophic position or preferred microhabitat?; 2) Does the strength of morphological associations suggest recent trait divergence?; 3) Do environmental variables at site scale predict trait sets for whole assemblages. We pitfall-trapped ants from a revegetation chronosequence and measured their morphology, trophic position (using C:N stoichiometry and isotope ratios) and characteristics of microhabitat and macrohabitat. We found strong associations between high trophic position (low C:N and high $\delta 15N$) in body tissue and morphological traits: predators were larger, had more laterally-positioned eyes, more physical protection and tended to be monomorphic. In addition, morphological traits were associated with certain microhabitat features, e.g., smaller heads were associated with the bare ground microhabitat. Trait-microhabitat relationships were more pronounced when phylogenetic adjustments were used, indicating a strong influence of recent trait divergences. At the assemblage level, our 4th corner analysis revealed associations between the prevalence of traits and macrohabitat, although these associations were not the same as those based on microhabitat associations. This study shows direct links between species-level traits and both diet and habitat preference. Trait-based prediction of ecological roles and community structure is thus achievable when integrating stoichiometry, morphology and phylogeny, but scale is an important consideration in such predictions.

Does morphology predict trophic position and habitat use of ant species and assemblages?

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Abstract

A functional traits-based theory of organismal communities is critical for understanding the principles underlying community assembly, and predicting responses to environmental change. This is particularly true for terrestrial arthropods, of which only 20% are described. Using epigaeic ant assemblages, we asked: 1) Can we use morphological variation among species to predict trophic position or preferred microhabitat?; 2) Does the strength of morphological associations suggest recent trait divergence?; 3) Do environmental variables at site scale predict trait sets for whole assemblages. We pitfall-trapped ants from a revegetation chronosequence and measured their morphology, trophic position (using C:N stoichiometry and isotope ratios) and characteristics of microhabitat and macrohabitat. We found strong associations between high trophic position (low C:N and high $\delta^{15}N$) in body tissue and morphological traits: predators were larger, had more laterally-positioned eyes, more physical protection and tended to be monomorphic. In addition, morphological traits were associated with certain microhabitat features, e.g., smaller heads were associated with the bare ground microhabitat. Trait-microhabitat relationships were more pronounced when phylogenetic adjustments were used, indicating a strong influence of recent trait divergences. At the assemblage level, our 4th corner analysis revealed associations between the prevalence of traits and macrohabitat, although these associations were not the same as those based on microhabitat associations. This study shows direct links between species-level traits and both diet and habitat preference. Trait-based prediction of ecological roles and community structure is thus achievable when integrating stoichiometry, morphology and phylogeny, but scale is an important consideration in such predictions.

Key words: Carbon to Nitrogen ratio; delta N; microhabitat; morphological traits; stoichiometry

Introduction

Trait-based approaches are becoming increasingly important in understanding community structure and species responses to global change (McGill et al. 2006; Westoby and Wright 2006; Bihn et al. 2010; Silva and Brandão 2010; Gibb and Parr 2013). Although phylogeny is an indicator of function, its value can be limited because of ecological divergences in some clades, and convergences among others. In contrast, the use of species traits allows us to examine commonalities across communities that differ in their evolutionary history, but which often include ecologically similar species performing similar roles. While the use of traits in understanding the ecology of plants is relatively well developed (Westoby and Wright 2006; Ackerly and Cornwell 2007; Cornwell et al. 2008), this approach is in its infancy in animal ecology. The ecology of many vertebrate species is well known, making predictive models of responses of individual species possible for many groups. However, our limited understanding of how species traits interact with the environment is particularly problematic for invertebrates because these taxa are poorly studied at the species level. Considerable interest in traits has resulted in the development of new statistical techniques that allow us to examine how species traits relate to the environment (e.g., Shipley et al. 2006; Brown et al. 2014; Stoklosa et al. 2014), and these techniques have the potential to rapidly advance our understanding of invertebrate trait-environment interactions.

A range of trait types may be considered useful for predicting the ecology of a species. To address questions related to global change, features of organisms that affect their likelihood of persistence in different environments are an obvious target. These include morphological, physiological, behavioural or life history traits that interact with structural elements of the environment (Sarty et al. 2006; Bihn et al. 2010; Wiescher et al. 2012; Gibb and Parr 2013), disturbance tolerance (e.g., Arnan et al. 2013; Yates et al. 2014) or climate (Chown 2012;

Diamond et al. 2012; Wiescher et al. 2012) or that favour success in the face of species invasions (Funk et al. 2008). Body size is probably the best-studied trait of animals, with evidence that it responds strongly to habitat disturbance and climate, both within and among species (Chown and Gaston 2010; Entling et al. 2010). However, a range of other, less well understood morphological traits are likely to be important in determining species responses to global change (e.g., eye position, Gibb and Parr 2013). Although many of these morphological traits have hypothesised functions (e.g., Table 1), there is usually little empirical testing of those functions.

Elemental stoichiometry is increasingly recognised as a means to determine the diet of species, another important trait. Predators have higher percentages of nitrogen in their tissues, possibly as a result of higher N in the predator diet, a requirement for more N-rich body parts (e.g., muscles, protein-rich cuticle) or to support N-based chemical weaponry (Fagan et al. 2002; Davidson 2005). A lower C:N ratio in body tissue is therefore interpreted as indicating a more predatory feeding profile. In addition, stable isotopes of carbon and nitrogen are informative because enrichment of the heavier isotopes of nitrogen and carbon occurs with each trophic level (DeNiro and Epstein 1979; DeNiro and Epstein 1981). The trophic position of species may therefore be characterised by chemical analyses of their tissues, which is a considerable improvement on previous observational approaches to understanding diet. There is also potential to link these continuous measures of trophic position with easily recorded traits, such as morphological traits.

Traits are, of course, also a product of phylogenetic history, such that more closely related species will, on average, have more similar traits (Felsenstein 1985; Harvey and Pagel 1991). For this reason many evolutionary studies use phylogenetic adjustments of the trait analysis to account for this non-independence of species (Freckleton 2009). In this study, we chose to examine correlations with trait values both with and without phylogenetic correction. This allows the possibility of detecting patterns in one or the other model, or both. If a trait correlation with an environmental variable is strongest without phylogenetic adjustment, this suggests trait divergences deeper in the phylogeny dominate, with more recent divergences not supporting the association. If a trait correlation is strongest with phylogenetic adjustment, then recent trait divergences are strongly contributing to the pattern, but the deeper phylogenetic divergences constrain the pattern. With evolutionary processes creating the underlying pattern of trait diversity, species assemblages are “filtered” by the abiotic environment and the milieu of species interactions is important in determining which species and therefore which traits persist or dominate in an assemblage (McGill et al. 2006; Wiescher et al. 2012).

In this study, we examine how traits change along a biotic gradient created through a revegetation chronosequence, where sites differ in the time since replanting, which corresponds to differences in a range of habitat structural measures. We address the following questions: 1) Can we use morphological variation among species to predict: a) trophic position; or b) preferred microhabitat?; 2) Does the strength of these morphological associations suggest recent trait divergence?; 3) Do environmental variables at site scale predict trait sets for whole assemblages of ants?

Material and Methods

Study sites description

The study was conducted in south eastern Australia, at 30 sites within 150 km of the city of Canberra (35°15’S 149°08’E), at altitudes 450 to 720 m above sea level (Fig. S1). The region experiences a relatively dry continental climate with warm to hot summers and cool to mild winters. The vast majority of native vegetation in the study area has been cleared for grazing, crops or urban development and the remaining vegetation is mainly open *Eucalyptus* woodlands. Government-assisted revegetation has been conducted on many properties in the study region since the early 1980s. Two methods were used: tube stock, where nursery-raised saplings were planted individually at distances between 2 and 5 m apart; and direct-seeding, where seeds were planted into ploughed furrows at higher densities. Both planting types were dominated by a mix of *Acacia* and *Eucalyptus* species.

To assess the relationship between ant morphological traits and changes in habitat characteristics across a successional gradient, five sites belonging to each of the following six categories were selected : 1) pastures without trees (“pastures”); 2) revegetated pastures planted with tube stock between 1998 and 2001 (“young tube stock”); 3) revegetated pastures planted by direct-seeding between 1998 and 2001 (“young direct-seeded”); 4) revegetated pastures planted with tube stock between 1989 and 1994 (“old tube stock”); 5) revegetated pastures direct-seeded between 1989 and 1994 (“old direct-seeded”); and 6) remnant areas (“remnants”) that had never been cleared and had been protected from heavy livestock grazing for a minimum of 10 years (Fig. S1). One of the remnant sites experienced occasional light grazing from cattle and evidence of kangaroos and rabbits was present in all sites. Remnant and revegetation patches were of similar sizes and sites of different categories were non-adjacent and spatially interspersed, but pastures were unavoidably part of a continuous matrix of agricultural land. Landform was distributed evenly amongst site categories. Although sites were selected because they fitted these specific categories, the variation in habitat structure variables among sites was relatively continuous.

Pitfall sampling

Epigaeic ants were sampled using pitfall traps, which were open for two eighteen-day sessions in each of the 30 sites in November 2007 and April 2008. Traps were left in place for a week before opening, in order to avoid digging in effects (Greenslade 1973). Traps were 7 cm in diameter and 8 cm in depth and were filled with 100 ml of propylene glycol. They were placed in two 2 x 2 m squares, with traps at each corner and one in the centre (n = 5 traps) (Fig. S1). These trap squares were placed halfway along the long edge of each site, with the first set of traps 20 m from the edge and the following set 50 m from the edge of the site. Pitfall traps were protected from direct rainfall by a black plastic plate (15 cm diameter), supported approximately 5 cm above ground level by pegs.

All specimens were identified to genus using Shattuck (1999). Morphospecies were verified, and some genera were identified to species level, by Dr Steve Shattuck (Australian National Insect Collection, CSIRO, Canberra, Australia). Assemblage analyses were conducted using ant ‘occurrences’, i.e., the number of traps per site in which a species occurred.

Micro- and macrohabitat characteristics

Habitat surveys were conducted in November 2007 at two scales: in association with pitfall traps and in 20 m x 20 m plots. Data associated with pitfall traps were used to characterise the microhabitats used by collected species. For microhabitat data, the percentage of bare ground and leaf litter and percentage canopy cover within a 1 m diameter circle, centred on each pitfall trap, was recorded.

Plot-scale data were used to characterise the thirty sites and were used in analyses at the assemblage level and we refer to this as macrohabitat. Two quadrats of 20 m x 20 m surrounding each of the two pitfall trap groups were marked at each site. The number of *Eucalyptus*, *Acacia* and other trees and shrubs in three height categories (0.5-2 m, 2-10 m and > 10 m) and diameter at breast height (DBH) and basal diameter (at 10 cm) for up to 10 trees in each of these categories was recorded. Trees were categorised as remnant, regrowth or planted in the revegetation process and aspect and slope recorded. In each quadrat, characteristics related to coarse woody debris (CWD) were noted. Whereas the usual definition for CWD includes debris with a minimum diameter of ≥ 10 cm (e.g., Gibb et al. 2005), our definition included debris of ≥ 5 cm diameter, in order to include fallen *Acacia* stems that commonly have smaller diameters. For lying CWD, we recorded maximum and minimum diameter, length, percent contact with the ground and decay state. For standing CWD, basal diameter, height and decay state were recorded. Decay state was classed into four categories: 1) outline of CWD intact and bark present; 2) outline of CWD intact, but bark lost from 50% of the surface; some bleaching; 3) Bark absent, outline of CWD less distinct; usually bleached; 4) CWD without clear outline; usually bleached and broken.

At the corners and centre of each of the 20 x 20 m quadrats, smaller, 1 m x 1 m quadrats were placed in which ground cover variables were recorded (a total of 5 replicates in each larger quadrat). In the smaller quadrats, the percentage cover of leaf litter, grass litter, bare ground, grass, moss and dead wood was estimated. In addition, the height of the tallest grass, the depth of leaf and grass litter and the presence and taxon of origin of animal dung were recorded.

Sampling for stoichiometry and stable isotope analyses

In March 2008, live ants were hand-collected from twelve study sites (4 pastures, 4 young tube stock and 4 remnant sites) to conduct chemical analysis, uncontaminated by pitfall trap preservatives. A species list is provided in Appendix I. All specimens were collected between 9 am and 6 pm. Our goal was to collect a representative sample of the diurnally-active ants in each site. Up to 30 workers of 8-17 ant species were collected by hand or aspirator at each site. For very small ant species, such as *Tapinoma* spp., 30 individuals were required to obtain sufficient mass for a single analysable sample. Smaller numbers were collected for larger ant species but samples always consisted of at least two individuals. Means for each species collected were calculated, based on a sample size of 2-3 (each sample contained 2-30 ants, depending on their size). Samples were stored on dry ice, then in a -20ºC freezer prior to analysis. Abdomens were removed before analysis to avoid complications related to gut contents (Blüthgen et al. 2003; Davidson 2005; Tillberg et al. 2006).

Soil samples were collected in April 2008 at all sites to use as a baseline for isotope values (Gibb and Cunningham 2011). Grass, leaf litter and the top centimetre of soil were removed and a 10 cm deep plug of soil (diameter 43 mm) was collected using an auger. Three samples were collected from a transect at each site, with 6 m spacing between samples. Soils were stored in a -20ºC freezer, and dried at 40ºC for 48 hrs prior to analysis.

Samples were analysed for total C and N content and for the ratio of the heavy to light isotopes of C and N. The analysis was performed using a Sercon Hydra 20-20 isotope ratio mass spectrometer (made in Crewe, UK) with an ANCA (automated nitrogen and carbon analyser) preparation system at CSIRO Black Mountain Laboratories (Canberra, Australia). Samples were dried in an oven at 60ºC, then approximately 1.0 mg of each sample was weighed into a tin capsule. Test and reference samples were used to correct for any drift or carry-over in the instrument. References were calibrated for total C% and N%. $^{15}N/^{14}N$ was measured relative to atmospheric N, while $^{13}C/^{12}C$ was measured relative to Vienna Pee Dee Belemnite. Sample ratios were compared to this element-specific standard and reported as δX, where $\delta X = [(R_{sample}/R_{standard})-1)] \times 1\,000$. R_{sample} and $R_{standard}$ are the ratio of heavy to light isotopes for the sample and standard, respectively. δ values are reported as “per mil” deviation from standards for the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotopic ratios of soil, herbivores, ants and predators.

The soil-corrected $\delta^{15}N$ for all individuals (ant $\delta^{15}N$ – soil $\delta^{15}N$ at the same site) was determined in order to eliminate differences in ant $\delta^{15}N$ resulting from site differences. The mean of the soil-corrected $\delta^{15}N$ across all samples within each species was used in analyses. Although the trophic position of ant genera may shift across restoration gradients (Gibb and Cunningham 2011), the *relative* position of species is generally constant (Ponsard and Arditi 2000; Gibb and Cunningham 2011), so it is appropriate to use a mean value across all sites in which a species was collected.

Morphological traits

Seven continuous morphometric measures and four ordinal measures were selected to describe species traits. Traits were selected because they had shown ecologically relevant associations in previous studies or because we had distinct hypotheses regarding their function (Table 1). Although colony size is considered a key measure of body size for ants, this trait was not available for species in this study and our emphasis was on traits of workers, rather than of colonies. Traits were measured on three individual workers of each species, which had been stored in ethanol. When species were morphologically dimorphic (*Pheidole* spp.) or clearly polymorphic (*Amblyopone* spp., *Camponotus* spp., *Melophorus* spp. and *Notoncus* spp.), only minors were used, although polymorphism was included as an ordinal trait (Table 1). For each ant, standard linear measurements were taken using an ocular micrometer mounted on a dissecting microscope, accurate to 0.01 mm. The positioning of species in trait-space using principal component analysis is shown in Appendix II.

Data analysis

For all analyses, habitat data was averaged across seasons because preliminary analyses showed that seasonal variation was low. For each site we pooled ant abundances across sampling events because composition remained similar between seasons.

Can we use morphological variation among species to predict trophic position or preferred microhabitat and does the strength of morphological associations suggest recent trait divergence?

For regression analyses, all continuous measures were log-transformed and regressed against $\log_e$ (Weber's length) to obtain residuals for analysis that did not depend on body size. Data for both sampling dates were pooled as they were significantly correlated (Environmental data: Pearson's correlation: $r^2 > 0.6$, $p < 0.001$; Species data: Mantel test: $p = 0.001$, Rho =

0.67). We used mean values per species for trait and isotope measures and mean measures of environmental variables across all locations at which a species occurred.

Consistent with previous studies (Blackburn and Gaston 1998; Garland et al. 1999), both phylogenetic and non-phylogenetic regression approaches were used to examine the relationship between species traits and predictors related to diet (n = 30 species) and microhabitat (n = 37 species). Non-phylogenetic regression analyses were conducted using the “lm” function on R (R Development Core Team 2013). Using phylogenetic independent contrasts (PICs) (Felsenstein 1985; Garland and Ives 2000) in the package ape (Paradis et al. 2004) on R allowed us to determine if present day patterns in trait associations are a result of a small number of large divergences across trait values in the evolutionary history of the species examined. An ant phylogeny derived from Moreau et al. (2006) was used to perform phylogenetic independent contrasts between morphological traits and microhabitat and diet variables. The phylogeny included only one or two examples from each genus, so species within genera were included as soft polytomies. Polytomies were resolved using the multi2di function on ‘ape’ to allow us to run phylogenetic independent contrasts and phylogenetic regressions.

If relationships were not phylogenetically independent, this did not necessarily mean that the trait-environment relationship was not meaningful. However, it did mean the relationship was more difficult to interpret as it may suggest either: 1) that environmental filtering of species by traits has resulted in related (and morphologically similar) species occurring in similar habitats or: 2) that the pattern is driven by other traits shared among related species.

Do environmental variables at site scale predict trait sets for whole assemblages of ants?

A new “4th corner” analysis “trait.mod” on R (R Development Core Team 2013) was used to determine the relationship between traits and the environment (Stoklosa et al. 2014), at the assemblage level. While analyses of associations between species traits and microhabitat described above used variables measured at each pitfall trap and related them to individual species, the fourth corner analysis related traits to site-level environmental variables using data on assemblage composition, which includes abundance data. The fourth-corner analysis considers conditional effects after accounting for all species abundances in the model, rather than examining species one-at-a-time. A fourth-corner problem can be thought of as one that involves using three tables describing environmental data (R), species abundances (L) and species traits (Q) to determine how species traits relate to the environment (D) (Brown et al. 2014). The analysis fits a predictive model for species abundances as a function of environmental variables, species traits and their interactions (Brown et al. 2014). This model-based approach uses generalized estimating equations (GEE) (Liang and Zeger 1986) to account for correlation between species observed at sites. Forward selection and the score information criterion (SIC) (Stoklosa et al. 2014) with a BIC-type penalty was used to select the most important environment-trait interactions. For this analysis, we used negative binomial regression because responses were count-based and a LASSO penalty, which has been shown to endow high predictive performance in species distribution models (Renner and Warton 2013).

Results

Can we use morphological variation among species to predict: a) trophic position; or b) preferred microhabitat?

Both standard and phylogenetic regressions revealed negative relationships between C:N of body tissue and Weber's length and sculpturing and positive relationships between C:N of body tissue and eye width and eye position (Table 2, Fig. 1). In addition, standard regressions showed a negative relationship between C:N and head width and mandible length and width. For phylogenetic regressions with $\delta^{15}N$, we detected positive relationships for eye position and pilosity and a negative relationship for polymorphism. Standard regressions revealed a significant positive relationship with mandible length. Although C:N and $\delta^{15}N$ might be expected to be negatively correlated if both are indicative of the same measure of trophic position, this relationship was not significant ($F_{(1,28)} = 0.15$, $p = 0.702$).

For microhabitat characteristics, phylogenetic regressions showed that bare ground was negatively related to head width, mandible length and width and spinosity, while canopy cover was negatively related to eye position and positively related to spinosity (Table 2, Fig. 2). Standard regressions revealed only a negative relationship between canopy cover and sculpturing.

Does the strength of morphological associations suggest recent trait divergence?

Similar patterns were observed for adjusted and unadjusted regressions on morphological traits and diet, suggesting that recent divergences were likely to be as important as deeper divergences in these relationships (Table 2). Surprisingly, accounting for phylogeny resulted in greater detection of relationships between traits and microhabitat than regression analyses on unadjusted data. This suggests that relatively recent evolutionary divergences drove these patterns and that they were obscured if more distant evolutionary divergences were not accounted for (Table 2).

Do environmental variables at site scale predict trait sets for whole assemblages of ants?

The fourth corner analysis revealed a range of significant interactions between ant assemblage traits and the environment (Figs 3, 4). These relationships were not always the same as those detected at the species level because the fourth corner analysis considered the whole assemblage of ants. Weber’s length was positively correlated with bare ground and negatively correlated with shrub cover, suggesting that larger ants dominated more in more open plantings. It was also positively related to slope. Pilosity was positively related to bare ground, suggesting that hairier ants were more prevalent in more open habitats. Polymorphism was negatively related to bare ground and canopy cover, indicating that monomorphic ants were more prevalent where the ground layer was more complex and the canopy sparser. Ants with narrow heads were most abundant where shrub cover and CWD availability were highest.

Discussion

We used ant assemblages collected along an environmental gradient to determine if morphological variation among species predicts trophic position or preferred microhabitat, whether these relationships suggest recent trait divergence and if environmental variables at site scale predict trait sets for whole assemblages of ants.   Morphology did predict some of the ecological differentiation in both trophic level and microhabitat use. Although analyses accounting for phylogeny are often considered more conservative, the phylogenetically adjusted approach allowed us to detect patterns that were obscured in the standard regression approach. This suggests that phylogeny concealed, rather than confounded, some patterns.

At larger scales, the prevalence of traits in the assemblage was dependent on a range of habitat variables, but these were not always the same as those determining the traits of species at the local scale. This highlights not only the differences between species-based and assemblage-based assessments of traits, but also the potential for some trait-environment relationships to be scale dependent. Although the exact habitat elements measured changed with scale, the scale dependence we see here may suggest that the important biotic filters are different at different spatial scales. This could reflect the difference between scales of daily activity and the scale of habitat selection or dispersal. In addition, the inclusion of abundance in assemblage-level metrics means that species interactions contribute to trait-environment relationships. While it makes sense that the outcomes could be scale dependent, it also serves as a warning regarding how far one might be able to generalise predictions based on traits.

Does the strength of morphological associations suggest recent trait divergence?

Relationships between morphological traits and diet showed similar patterns, with or without adjustments for phylogeny. In contrast, trait-microhabitat relationships were more pronounced when phylogeny was accounted for. This suggests that recent and more distant evolutionary divergences were of similar importance in determining relationships between diet and morphology, but that recent divergences were of key importance for microhabitat-morphology relationships. Diet may be largely conserved phylogenetically amongst ants, e.g., all ectatommines are considered to be predators. Traits related to diet might therefore be more evolutionarily constrained than those related to microhabitat use.

Can we use morphological variation among species to predict trophic position?

Several traits were correlated with Carbon to Nitrogen ratio (C:N) and/or δ^{15}N of body tissue, both with and without phylogenetic adjustment. A lower C:N or higher δ^{15}N indicates a more predatory genus (DeNiro and Epstein 1981; Fagan et al. 2002; Davidson 2005). C:N predators were larger than predominantly omnivorous ant species. C:N predators included *Myrmecia, Rhytidoponera, Tetramorium* and *Amblyopone*, all of which are considered highly predatory and most of which also had high δ^{15}N values in a previous study (Gibb and Cunningham 2013). Most of these genera include relatively large species, in contrast with previous findings that predatory ants are smaller on average in the New World (Weiser and Kaspari 2006). While overall size was greater in more predatory species, analysis of δ^{15}N showed that variation in the size and physical proportions of workers within a colony (caste polymorphism) was lower. This might be expected if task specialisation was lower in species that are predominantly predatory (Oster and Wilson 1978).

Carbon to Nitrogen ratios increased with eye width, consistent with Weiser and Kaspari's (2006) finding that predatory genera have smaller eyes. The eyes of C:N predators were also positioned closer to the side of their heads, suggesting that acute forward vision was not critical for most predatory species in the study system (with *Myrmecia* as an obvious exception). Contradicting this finding, $\delta^{15}N$ predators (those with higher $\delta^{15}N$) had eyes positioned higher on their heads. It is unclear why these two stoichiometric measures gave opposing results, but the relationship between C:N and eye position ($R^2 = 0.36$, $p = 0.0004$) was much stronger than the marginally significant relationship between $\delta^{15}N$ and eye position ($R^2 = 0.14$, $p = 0.038$) and was consistent with predictions.

Predatory ant species had greater physical protection than predominantly omnivorous species, being both more sculptured (negative correlation with C:N) and more pilose (positive correlation with $\delta^{15}N$). Cross-species variation in sculpturing and pilosity in arthropods is poorly understood, but it is likely that these features provide protection from harsh microclimates and/or attack by other animals. Carbon to nitrogen ratios might be related to the ratio of protein (high nitrogen) and chitin (low nitrogen) in the exoskeleton or the cuticle. Greater 'sculpturing' is associated with more complex, thicker cuticles, which might be more protein-rich, and may provide better physical protection for predatory species. Pilosity may have a similar protective function, with hairs reported to increase tolerance to dehydration (Wittlinger et al. 2007).

Can we use morphological variation among species to predict preferred microhabitat?

Microhabitat variables measured at the level of the pitfall trap correlated with a range of morphological traits when we accounted for phylogeny. Narrow heads, small mandibles, dorsally positioned eyes and a lack of spines were associated with more open habitats. Smaller heads and mandibles may be associated with more streamlined genera with faster running speeds, such as *Iridomyrmex*, that dominate in open habitats (Gibb and Parr 2013) or reduced dietary specialisation in simple habitats. Previous studies show that larger ants (Gibb and Parr 2010; Arnan et al. 2013) and ants with relatively longer legs (Gibb and Parr 2010; Wiescher et al. 2012) dominate in more open environments. However these relationships were not significant at the microhabitat scale in this study.

Ant species with dorsal eyes used bare ground more than those with more laterally positioned eyes, indicating that a broad visual field is likely to be more important in open habitats (Weiser and Kaspari 2006; Gibb and Parr 2013), as may be a greater awareness of aerial predators. Spinosity, which was highest in association with high canopy cover (and low bare ground), might also be related to predation risk. However, little is known about how the assemblage of predators of ants differs among habitats differing in complexity.

Do environmental variables at site scale predict trait sets for whole assemblages of ants?

The fourth corner analyses revealed a range of associations between morphological traits and the environment at the level of assemblage. Assemblage-level patterns contrasted with the patterns observed at the level of species. For example, none of the characteristics associated with bare ground or canopy cover at the species level showed significant associations at the assemblage level. Differences did not result from the use of phylogenetic independent contrasts because relationships from standard regressions did not parallel those from the fourth corner analysis. Differences in the scale at which species respond to their habitats may have resulted in differences in trait-environment relationships between tests based on microhabitat and macrohabitat. Alternatively, the failure of the species-based regressions to account for the relative abundances of species and species and to therefore consider the interactions leading to the observed relative abundances of species may limit our ability to extrapolate from species- to assemblage-level traits.

At the site scale, ant species with larger body size (Weber's length) were more prevalent where there was more bare ground and less shrub cover. This contrasts with findings for North American ants, for which ants in environments with less groundcover had relatively longer legs but did not differ in size (Wiescher et al. 2012) but is in agreement with a range of studies showing that body size or the body size index (the product of femur length and pronotum width) is greater in open habitats (Sarty et al. 2006; Gibb and Parr 2010; Arnan et al. 2013). Species with broader heads, including *Myrmecia* spp., *Crematogaster* spp., *Notoncus* spp., *Amblyopone australis* and *Tetramorium* sp., were most common in sites with little shrub cover and woody debris.

Polymorphic species were more prevalent in sites with bare ground and greater canopy cover. This may reflect a high abundance of relatively large polymorphic Camponotine ants and medium-sized polymorphic *Melophorus* in later successional habitats with open ground and low shrub cover (Gibb and Cunningham 2013). Greater polymorphism in open (burned) habitats was also detected by Arnan et al. (2013), who attributed the relationship to greater variability in the response of individuals within a colony to temperature, which could increase foraging time and therefore enhance colony success (Cerdá et al. 1997). A high prevalence of pilose ants was also associated with bare ground, providing support to the hypothesis that hairs increase tolerance to dehydration (Wittlinger et al. 2007).

Conclusions

We have shown that we can use morphology to make predictions about species function, including trophic status and habitat use. These relationships were biologically plausible and not driven primarily by distant phylogenetic relationships, despite strong differentiation of subfamilies by morphology (Appendix II). This suggests that more recent evolutionary pressures may drive many trait-environment relationships observed here. Further, it reinforces that functional traits provide information on likely species biology over and above what can be predicted by phylogeny alone. We also extended our test to the level of the assemblage to examine how the environment regulates the prevalence of traits in an ecological community and found that the prevalence of many traits reflects the environment. We thus show that a trait-based approach to understanding community assembly is achievable when integrating stoichiometry, morphology and phylogeny and will help to build a more predictive framework for invertebrate ecology. However, we caution that a greater understanding of the scale-dependency of these relationships is needed.

Ultimately, the functional trait approach should be applicable to assemblages across biogeographic regions and even across multiple taxonomic groups, independent of the phylogenetic history of the biota. To establish the generality of the trait associations we measured here requires comparative studies considering phylogenetically distinct assemblages (e.g., Gibb and Parr 2013). Experimental tests of specific traits across species would also aid in verifying function. More broadly, another important early step is to extend this technique from ants to include other epigaeic invertebrates, which are of similar size and dwell in similar microhabitats and therefore face similar challenges (e.g., beetles, Barton et al. 2011; and spiders, Langlands et al. 2011). New modelling techniques such as the fourth corner analysis used here allow a more predictive approach, where relative abundances and covariances of species can be better accounted for, although it is so far unable to account for phylogeny. A predictive approach is particularly important in anticipating the biotic response to the broad impacts of anthropogenic drivers of global change, such as habitat disturbance and climate change (Andrew et al. 2013), both of which have significant impacts on the ground-layer and thereby influence assemblages of epigaeic species.

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Data accessibility

Data on which this paper is based will be archived in Figshare (www.figshare.com) following acceptance for publication.

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Figure captions

Figure 1: Significant phylogeny-adjusted relationships between morphological traits and measures of diet. Each point represents the mean value for a species, adjusted for phylogeny.

Figure 2: Significant phylogeny-adjusted relationships between morphological traits and measures of microhabitat use. Each point represents the mean value for a species, adjusted for phylogeny.

Figure 3: Standardised interaction coefficient estimates for interaction terms from the fourth corner analysis testing the relationship between morphological traits and the environment, accounting for species abundances. Coefficients shown in red (positive) or blue (negative) were significant in the best model. All trait variables except Weber's length, sculpturing, pilosity, polymorphism and the number of spines were residuals of regressions with Weber's length.

Figure 4: Contour plots of linear predictor values for each trait-environment interaction selected by SIC (score information criterion) in the fourth corner analysis. Darker (redder) areas correspond to larger predicted abundance across the trait-environment values. Circles represent the partial residuals, where larger circles correspond to larger observed abundance.

Table 1: Morphological traits, hypothesised functions, measures taken and summary of significant associations from this study.

Trait	**Hypothesised function**	**Measure**	**Regressions**		**4th corner**
			PIC adjusted	**Unadjusted**	
Weber's length	Indicative of worker body size (Weber 1938), which correlates with metabolic characteristics	Distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum	- C:N	- C:N	+ bare ground - shrub cover + slope
Femur length[a]	Indicative of foraging speed, which reflects the complexity of the habitat (Feener et al. 1988)	Length of the femur of the hind leg			
Head width[a]	Size of gaps through which worker can pass (Sarty et al. 2006); mandibular musculature (Kaspari 1993)	Measured across the eyes	- bare ground	- C:N	- shrub cover - CWD
Mandible length[a] *and width*[a]	length, width and gape of mandibles relate to diet (Fowler et al. 1991); clypeus width indicates sugar feeding (Eisner 1957)	The straight line distance from the insertion to the tip of the mandible	- bare ground	- C:N + δ^{15}N	
Eye width[a]	Eye size is indicative of food searching behaviour and activity times (Weiser and Kaspari 2006)	Measured across the maximum width of the eye	+ C:N	+ C:N	
Eye position[a]	Related to hunting method (Fowler et al. 1991) or the component of the habitat occupied (Gibb and Parr 2013)	Head width across the eyes minus head width between the eyes – higher eye position indicates more dorsal eyes	- canopy + C:N + δ^{15}N	+C:N	
Scape length[a]	Sensory abilities: longer scapes facilitate following of pheromone trails (Weiser and Kaspari 2006)	Length of the antennal scape			
Sculpturing	Thickened, structured cuticles may increase dehydration tolerance	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	- C:N	- C:N - canopy	
Spinosity	Spines may act as an anti-predation mechanism (Michaud and Grant 2003)	Count of spines on propodeum and petioles	- bare ground + canopy		
Pilosity	Hairs may increase tolerance to dehydration or may relate to mechanoreception (Wittlinger et al. 2007)	0 = no or very few hairs; 1 = a sparse but regular covering of hairs; 2 = a consistent, moderate covering of hair; 3 = very dense hair covering	+ δ^{15}N		+ bare ground
Polymorphism	Different worker castes perform different tasks within the colony, allowing greater specialisation (Wilson 1953)	1 = monomorphic; 2 = polymorphic; 3 = dimorphic	- δ^{15}N		+ bare ground + canopy

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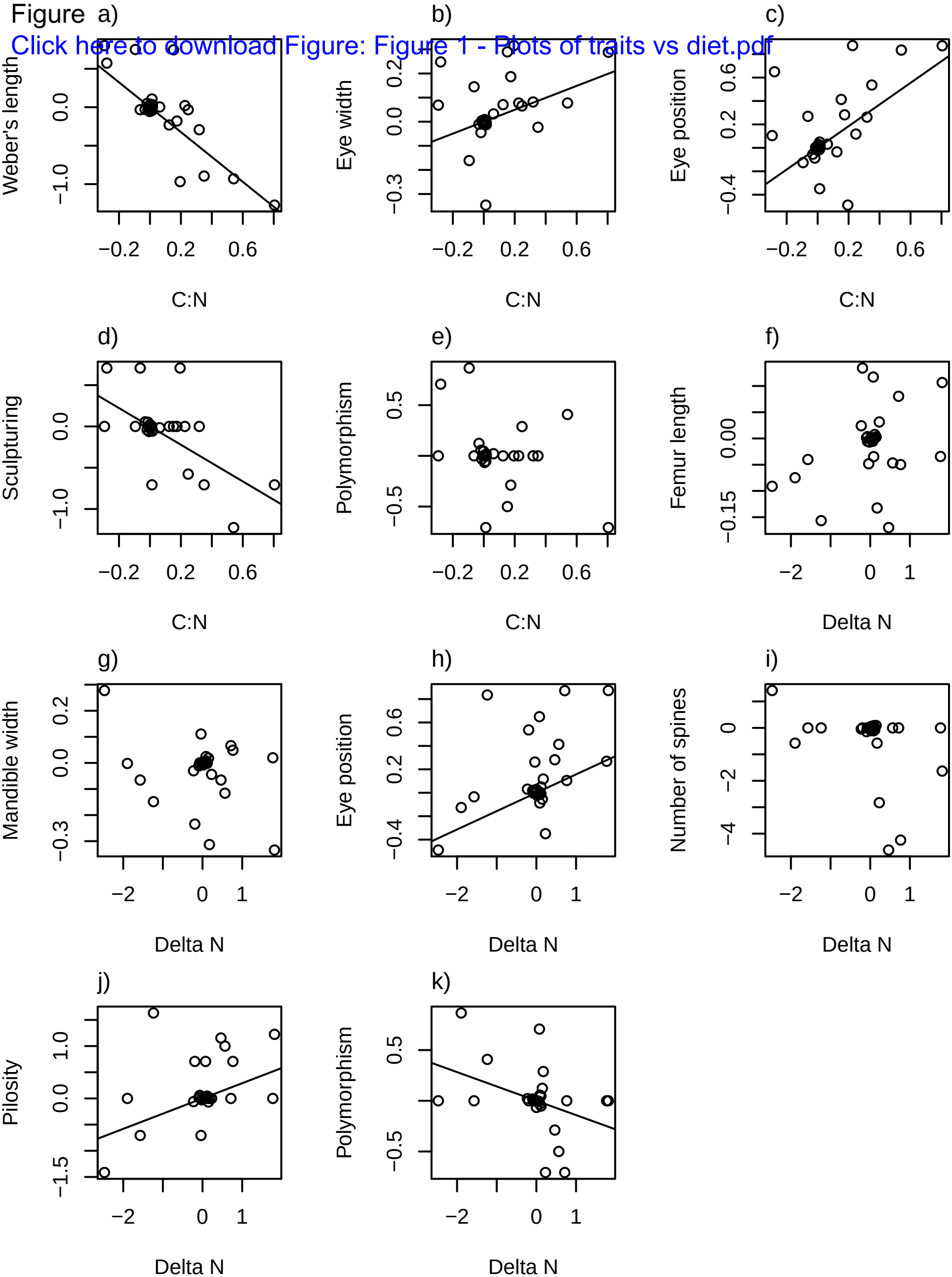
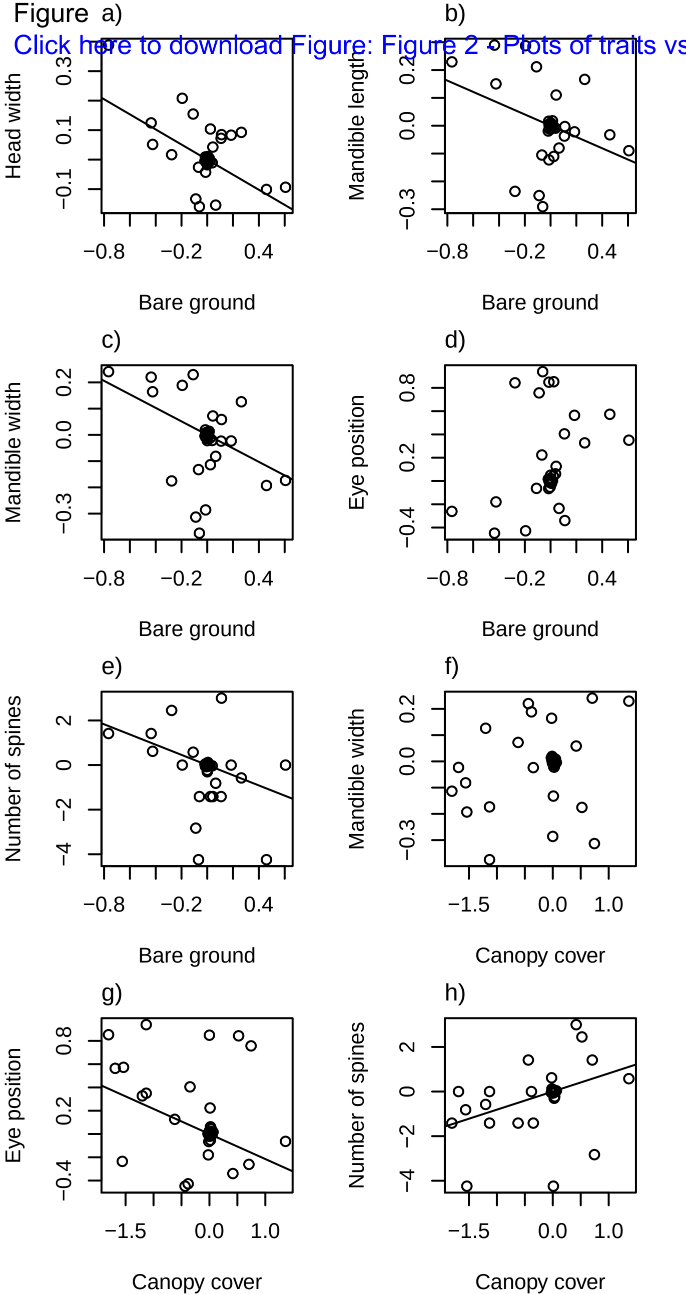
[a] As many size-related characteristics are correlated and we are interested in deviations from the expected value, these features were considered as residuals based on the regression with Weber's length.

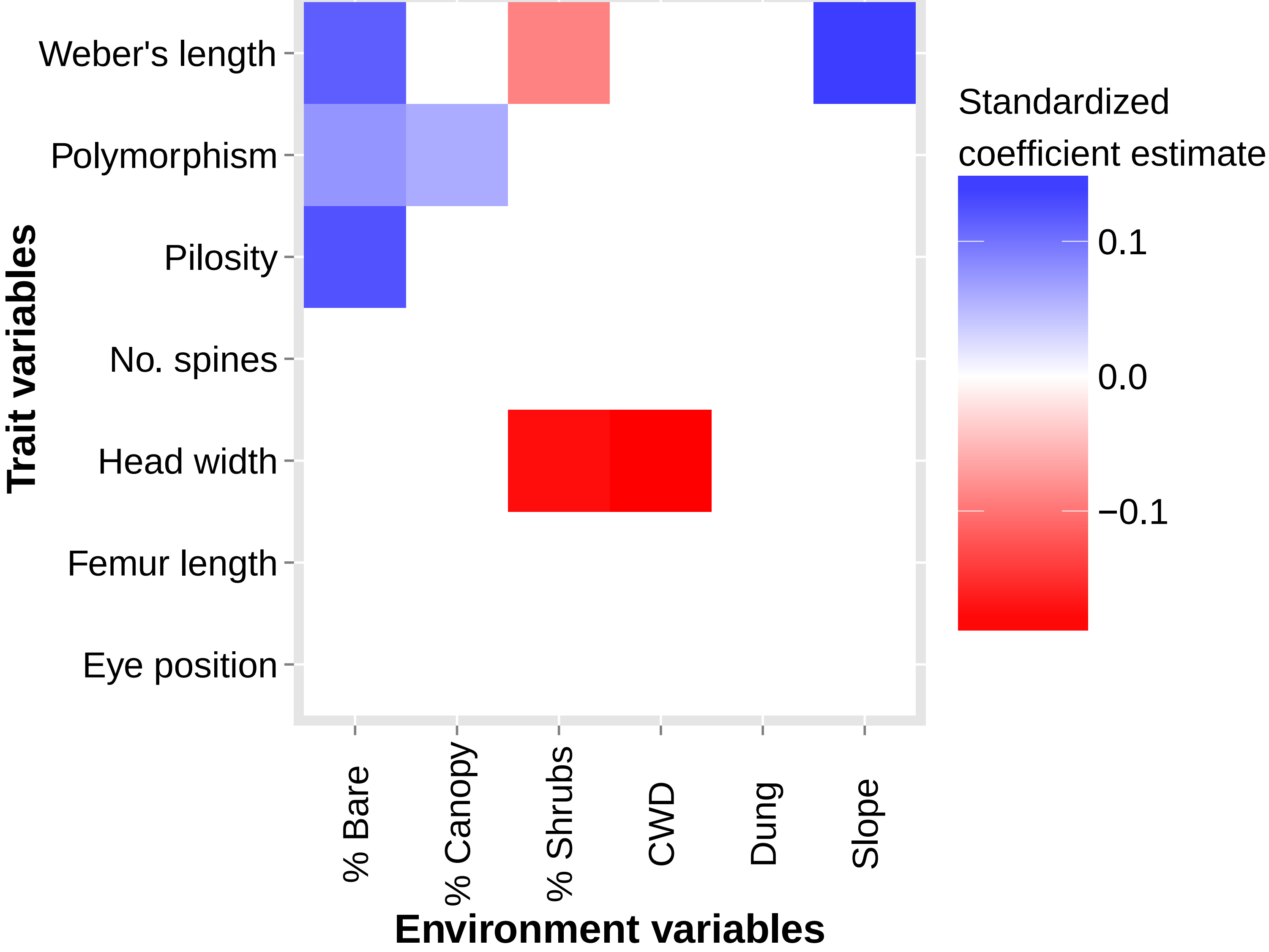
Table 2: R^2 and significance for regressions with adjustment for phylogeny using phylogenetic independent contrasts and linear regressions testing the relationship between the morphological trait predictor variables and the diet-based response variables C:N and δ^{15}N (n = 30) and microhabitat response variables percentage bare ground, canopy cover and leaf litter (n = 37). + 0.05<*p*<0.10, * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

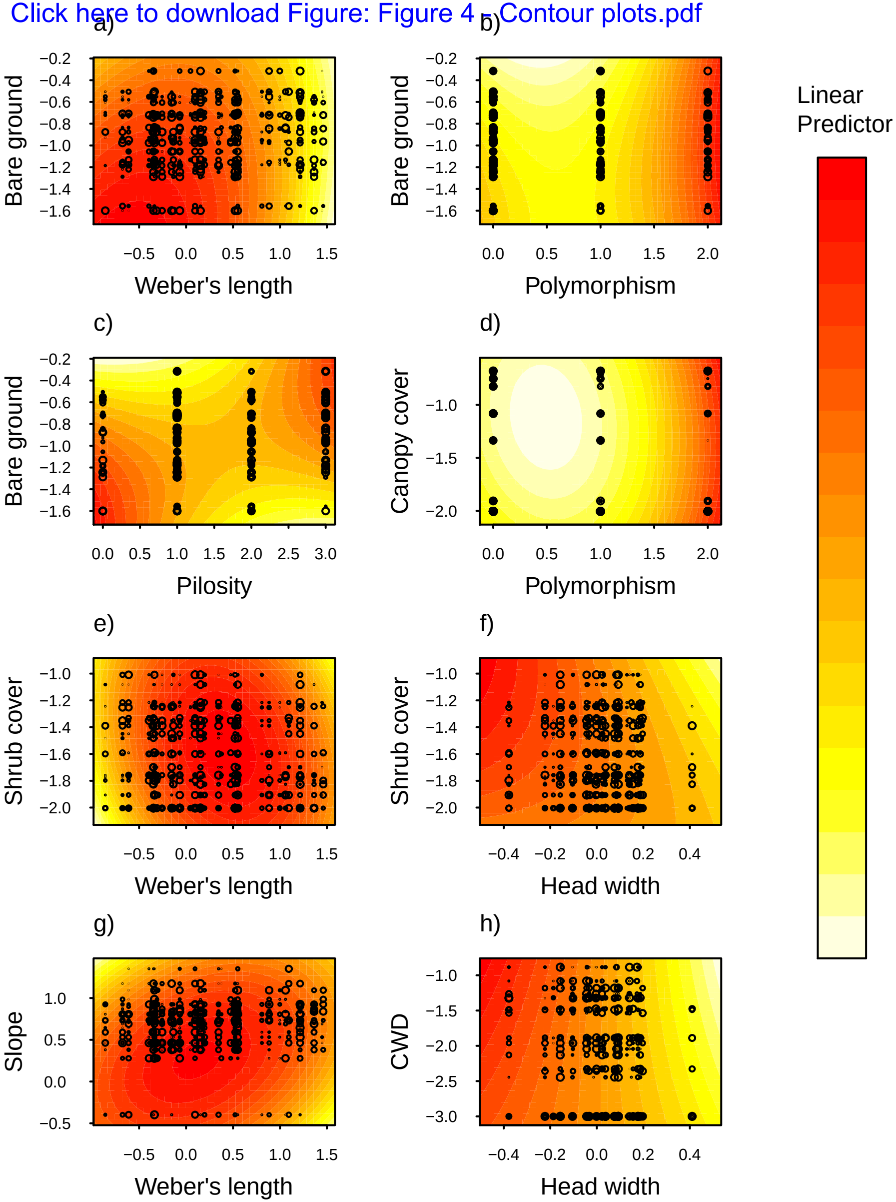
	C:N		**δ^{15}N**		**Bare ground**		**Canopy**		**Litter**	
	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted
Weber's length	0.63 ***	0.17 *	0.05	0.02	0.07	0.02	0.00	0.02	0.00	0.01
Femur length	0.02	0.01	0.12 +	0.00	0.00	0.05	0.05	0.00	0.05	0.01
Head width	0.06	0.23 **	0.00	0.11 +	0.32 ***	0.08 +	0.03	0.02	0.01	0.09 +
Mandible length	0.05	0.27 **	0.01	0.13 *	0.13 *	0.02	0.02	0.03	0.01	0.04
Mandible width	0.08	0.30 **	0.11 +	0.03	0.17 *	0.07	0.09 +	0.00	0.00	0.07
Eye width	0.17 *	0.15 *	0.00	0.03	0.01	0.02	0.07	0.07	0.01	0.01
Scape length	0.01	0.06	0.05	0.09	0.00	0.01	0.01	0.04	0.05	0.02
Eye position	0.36 ***	0.32 **	0.14 *	0.00	0.08 +	0.06	0.16 *	0.04	0.00	0.00
Spines	0.00	0.05	0.11 +	0.01	0.13 *	0.03	0.17 *	0.01	0.04	0.00
Pilosity	0.03	0.02	0.17 *	0.06	0.00	0.00	0.07	0.04	0.05	0.04
Sculpturing	0.40 ***	0.27 **	0.00	0.06	0.01	0.00	0.03	0.13 *	0.06	0.10 +
Polymorphism	0.11 +	0.08	0.15 *	0.02	0.02	0.00	0.01	0.04	0.00	0.03


a)
Weber's length
0.0
−1.0
−0.2
0.2
0.6
C:N
b)
Eye width
0.2
0.0
−0.3
−0.2
0.2
0.6
C:N
c)
Eye position
0.6
0.2
−0.4
−0.2
0.2
0.6
C:N
d)
Sculpturing
0.0
−1.0
−0.2
0.2
0.6
C:N
e)
Polymorphism
0.5
−0.5
−0.2
0.2
0.6
C:N
f)
Femur length
0.00
−0.15
−2
0
1
Delta N
g)
Mandible width
0.2
0.0
−0.3
−2
0
1
Delta N
h)
Eye position
0.6
0.2
−0.4
−2
0
1
Delta N
i)
Number of spines
0
−2
−4
−2
0
1
Delta N
j)
Pilosity
1.0
0.0
−1.5
−2
0
1
Delta N
k)
Polymorphism
0.5
−0.5
−2
0
1
Delta N

Figure


a)
Head width
−0.1
0.1
0.3
−0.8
−0.2
0.4
Bare ground
b)
Mandible length
−0.3
0.0
0.2
−0.8
−0.2
0.4
Bare ground
c)
Mandible width
−0.3
0.0
0.2
−0.8
−0.2
0.4
Bare ground
d)
Eye position
−0.4
0.2
0.8
−0.8
−0.2
0.4
Bare ground
e)
Number of spines
−4
−2
0
2
−0.8
−0.2
0.4
Bare ground
f)
Mandible width
−0.3
0.0
0.2
−1.5
0.0
1.0
Canopy cover
g)
Eye position
−0.4
0.2
0.8
−1.5
0.0
1.0
Canopy cover
h)
Number of spines
−4
−2
0
2
−1.5
0.0
1.0
Canopy cover


Weber's length
Polymorphism
Pilosity
No. spines
Head width
Femur length
Eye position
Trait variables
% Bare
% Canopy
% Shrubs
CWD
Dung
Slope
Environment variables
Standardized coefficient estimate
0.1
0.0
−0.1


a)
Bare ground
−0.2
−0.4
−0.6
−0.8
−1.0
−1.2
−1.4
−1.6
−0.5
0.0
0.5
1.0
1.5
Weber's length
b)
Bare ground
0.0
0.5
1.0
1.5
2.0
Polymorphism
c)
Bare ground
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Pilosity
d)
Canopy cover
−1.0
−1.5
−2.0
Polymorphism
e)
Shrub cover
−1.0
−1.2
−1.4
−1.6
−1.8
−2.0
Weber's length
f)
Shrub cover
−0.4
−0.2
0.0
0.2
0.4
Head width
g)
Slope
1.0
0.5
0.0
−0.5
Weber's length
h)
CWD
−1.0
−1.5
−2.0
−2.5
−3.0
Head width
Linear
Predictor