

Do functional traits improve prediction of predation rates for a disparate group of aphid predators?

J.R. Bell^{1,2,4*}, A. Mead², D.J. Skirvin², K.D. Sunderland²,
J.S. Fenlon³ and W.O.C. Symondson⁴

¹Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK:

²Warwick HRI, University of Warwick, Wellesbourne, Warwick,

CV35 9EF, UK: ³Department of Statistics, University of Warwick,

Coventry, CV4 7AL, UK: ⁴Cardiff School of Biosciences, Cardiff University,
Biomedical Sciences Building, Museum Avenue, Cardiff CF10 3US, UK

Abstract

Aphid predators are a systematically disparate group of arthropods united on the basis that they consume aphids as part of their diet. In Europe, this group includes Araneae, Opiliones, Heteroptera, chrysopids, Forficulina, syrphid larvae, carabids, staphylinids, cantharids and coccinellids. This functional group has no phylogenetic meaning but was created by ecologists as a way of understanding predation, particularly for conservation biological control. We investigated whether trait-based approaches could bring some cohesion and structure to this predator group. A taxonomic hierarchy-based null model was created from taxonomic distances in which a simple multiplicative relationship described the Linnaean hierarchies (species, genera, etc.) of fifty common aphid predators. Using the same fifty species, a functional groups model was developed using ten behavioural traits (e.g. polyphagy, dispersal, activity, etc.) to describe the way in which aphids were predated in the field. The interrelationships between species were then expressed as dissimilarities within each model and separately analysed using PROXSCAL, a multidimensional scaling (MDS) program. When ordinated using PROXSCAL and then statistically compared using Procrustes analysis, we found that only 17% of information was shared between the two configurations. Polyphagy across kingdoms (i.e. predatory behaviour across animal, plant and fungi kingdoms) and the ability to withstand starvation over days, weeks and months were particularly divisive within the functional groups model. Confirmatory MDS indicated poor prediction of aphid predation rates by the configurations derived from either model. The counterintuitive conclusion was that the inclusion of functional traits, pertinent to the way in which predators fed on aphids, did not lead to a large improvement in the prediction of predation rate when compared to the standard taxonomic approach.

Keywords: behavioural traits, confirmatory MDS, functional groups, Procrustes analysis, PROXSCAL, multidimensional scaling (MDS)

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*Author for correspondence
Fax: +44(0)1582 760981
E-mail: James.Bell@bbsrc.ac.uk

Introduction

European farming is facing a shift in emphasis away from a reliance on agrochemicals to more sustainable methods of 'natural' pest control, driven by consumer demand and national government and European Union policy (Shepherd *et al.*, 2005; Maxey, 2006). An adjustment in farming systems, such as a move to organic approaches, is one way of achieving this goal, but relatively little is known about the effect of organic farming on ecosystem services as the results are often contradictory (Roschewitz *et al.*, 2005; Bianchi *et al.*, 2006). Perhaps this is because organic farming, like other cultural methods, has a broad multi-term treatment effect that is not targeted at a particular ecosystem function. For this and other cultural farming approaches, the outcomes are likely to be sub-optimal for the control of specific pests and diseases. Conversely, natural pest control is far more achievable in glasshouses using biocontrol agents to demonstrate a set of simple functional interactions. Commercially available stock are widely used and successful in controlling a range of pests (e.g. *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) for the control of whiteflies; phytoseiid predators to control two spotted spider mites). Increasingly common are more complex field-based scenarios that use, for example, wildflower strips as a biodiverse source of predators, parasitoids and pollinators to target at a particular ecosystem function (e.g. Ambrosino *et al.*, 2006; Vattala *et al.*, 2006). These predators, parasitoids and pollinators are perceived to have an important role that can be managed through direct (e.g. inundation, push-pull) or indirect (e.g. habitat manipulation, provision of an alternative food source, etc.) manipulation of their populations (Symondson *et al.*, 2002a). However, these and other examples are either drawn from relatively cohesive groups of natural enemies that have narrow definable functions (e.g. parasitoids, stenophagous predators) or from artificial ecosystems (such as glasshouses) with relatively simple food webs.

The real challenge for functional group manipulations are with organisms that have multiple or poorly defined functions. For example, ground-active beetle and spider predators have been shown to have a positively synergistic effect on aphid mortality rates when they were combined with climbing foliar foragers such as ladybirds, rove beetles or lacewing larvae (Losey & Denno, 1998; Dinter, 2002). Such synergisms occurred because the ground-active predators did not have access to the prey unless the aphids were caused to fall to the ground in the presence of a canopy foraging predator that had a multiple function as both an aphid predator and an aphid predation facilitator. Positive synergisms support the concept of predators belonging to separate, non-taxonomic, ecologically-based functional groups, reflecting an ecosystem function which is itself shaped by one or many behavioural trait differences (Ladislav, 1997; Foster & Brooks, 2005).

Even multi-function experiments simplify the rather complex set of predator-prey, predator-predator and predator-scavenger interactions that occur in the field (e.g. Foltan *et al.*, 2005; Harwood & Obrycki, 2005). Aphid predators, particularly ground active species, are rarely stenophagous but instead are generalists with no specialised aphid-specific prey detection adaptations (Symondson *et al.*, 2002a). In the case of *Pterostichus melanarius* (Illiger) (Coleoptera, Carabidae), a beetle that is common in British farmland and has consequently been well studied,

individuals are known to predate up to 26 different orders across three phyla (e.g. Sunderland, 1975; Pollet & Desender, 1985; Sunderland, 2002). *P. melanarius* is also a major predator of slugs and, yet, still has impressive aphid predation rates (Sunderland *et al.*, 1975; Symondson *et al.*, 2002b; Foltan *et al.*, 2005). How can the ecosystem services provided by such a dynamic organism be defined and, if defined, how does one manipulate its numbers to maximise beneficial effects? Such problems are not trivial, requiring multivariate statistical analysis methods to make tractable complex interactions (Blondel, 2003) and large-scale experiments, combined with new molecular methods to demonstrate multiple trophic links (Harper *et al.*, 2005).

Here, we consider the trait-based ecological functional profiles of 50 common predators found in the cereal ecosystem in northern Europe, derived from an analysis of over 250 published sources of data. The ecosystem service and thus the functional significance of this group of species is that they have all been demonstrated to be effective aphid predators. The attraction of pursuing the functional group approach is that aphids do not perceive the combined risk of multiple predators but instead can only respond to a predator with which it is in close contact, such as a ladybird (Dill *et al.*, 1990). If two or more functional groups converged on an aphid colony (e.g. ladybird and spider), the combined effect would be predicted to be better than if the same number of individuals from one functional group were present.

Our objectives were twofold: to investigate the methods used to discriminate functional groupings and assess their independence from taxonomic groupings, a need which has been recognised since the 1970s (Cummins, 1974; Blondel, 2003; Lindborg & Eriksson, 2005) but largely overlooked (e.g. Faber, 1991; Cole *et al.*, 2002; Dumay *et al.*, 2004; Lassau *et al.*, 2005); and to analyse whether functional groups provide improved predictions of aphid predation rates compared with simple taxonomic groupings.

Methods

Species selected for study

A total of 50 arthropod species were selected because these had known *a priori* rates of aphid predation (numbers consumed individual⁻¹ day⁻¹) and were considered abundant in cereal fields across northwest Europe from May to July, when aphids can have an economic impact on quality and yield of winter wheat. A full list, with levels of Linnaean classification, can be found in appendix 1a.

Statistical approach

We used multidimensional scaling (MDS) to construct configurations in a relatively low number of dimensions, such that the fitted distances between aphid predator species closely match the observed dissimilarities between all species. This technique is widely used to summarise and then simplify complex multivariate data. MDS executes this procedure by dimension reduction, presenting the interrelationships between entities in a low-dimensional Euclidean space (Borg & Groenen, 2005). Throughout this paper, we use the notation developed by Borg & Groenen (2005), a publication which also provides a comprehensive description of the PROXSCAL algorithm and its properties.

As input, MDS requires one or more dissimilarity matrices between entities from which low-dimensional configurations can be constructed. Here, we describe how such dissimilarities were generated for both the taxonomic (null) and ecologically-based functional (alternative) models.

Taxonomic dissimilarity matrix

At best, knowledge of the phylogenetic relationships between aphid predators can be described as poor; not only are lower order relationships little understood, but higher order systematics within the major clades of the Arthropoda remain one of the most contentious issues (Giribet *et al.*, 2001; Hwang *et al.*, 2001). In short, there is no consensus phylogeny from which to derive taxonomic distances; thus we avoid taking any phylogenetic viewpoint or hypothesis. Instead, we developed a method which circumvents phylogenetics and avoids any expression of evolutionary pre-conception.

Simple approximate taxonomic distances were generated from known taxonomic hierarchies, giving a measure of dissimilarity suitable for constructing a 'null' taxonomic model for n species in n -dimensional space. We started with distances that separated taxonomic hierarchies between species of the same genera with a value of unity (i.e. 1.0). At each higher level in the taxonomic hierarchy (i.e. family, suborder, order, subclass, class and subphylum), the distance between species was increased by multiplying by a factor of $\lambda = 1.5$ (e.g. the distance between two species of the same family but different genera was 1.5, and so on). This multiplicative factor of $\lambda = 1.5$ was derived by constructing MDS configurations for a range of λ values. With $\lambda = 2$, the configuration collapsed to a simple dichotomy between two subphylum; whilst, with $\lambda = 1.1$, the configuration showed little discrimination between groups at any level. Five of the 50 species in the dataset had both adult and larval lifestages (four Coleoptera, Coccinellidae: *Adalia bipunctata* (L.), *Propylea quatuordecimpunctata* (L.), *Coccinella undecimpunctata* L., *C. septempunctata* and one Coleoptera, Carabidae: *Agonum dorsale* (Pontoppidan)). These within-species comparisons were given a distance of 0, given that they are taxonomically identical. *Tachyporus* (Coleoptera, Staphylinidae) larvae have yet to be differentiated to allow species level identifications. Consequently, on the three occasions when adult lifestages (i.e. *Tachyporus hypnorum* F., *T. obtusus* (L.), *T. chrysolimelinus* (L.)) were compared pairwise with the *Tachyporus* larvae sp., each scored 0. When all distances were computed ($n = 1225$), a lower triangular dissimilarity matrix (X_p) was formed summarising these derived taxonomic relationships.

Functional groups dissimilarity matrix

Ten functional traits were used to describe how 50 aphid predator species were each adapted to feeding on aphids in the field (table 1). As yet, conventions on coding traits for multivariate analysis have not been established, although it is accepted that these traits should not be couched in terms of their taxonomic classification (e.g. winged). Instead, traits should be free of any phylogenetic assumptions and not nested in predefined morphological terms (e.g. aerially active is acceptable but winged is not because it excludes spider ballooning as a mode of dispersal, an inherent trait in small spiders that predate upon aphids). In this study, we selected ten non-nested independent traits which described

the functional relationships of aphid predators within the context of a winter wheat field. These traits did not include any aphid consumption rate data that would deem later analysis circular, but instead related purely to behavioural information that described attributes of their feeding ecology. These included: phenology, diel activity, vertical distribution, mean abundance, higher and fine scale order trophic ranges (numbers of kingdoms and orders predated respectively), starvation capability, foraging mode, walking and flight capability (table 1). Data were sourced from 236 papers and other media, representing 1138 data entries. Values were scaled and normalised within each trait, yielding values between 0 and 1 for each of the ten equally weighted traits. Based on these ten traits, Euclidean distances were then calculated between each pair of species. Distances formed the dissimilarity matrix (X_{fg}), which formalised the alternative functional relationships model between taxa.

Formulating multidimensional scaling models

We used the Proximity Scaling (PROXSCAL) algorithm as a dimension reducing technique, a variant of multidimensional scaling (MDS), and implemented in SPSS Categories 14.0 (SPSS Inc. Chicago v.14). Specifically, PROXSCAL generates proximity data from a least squares representation of the objects in a low-dimensional space. Uniquely, PROXSCAL minimises normalised raw stress (NRS), a type of goodness of fit statistic, through a process called iterative majorization. NRS is an indication of the fit between the dissimilarity between n objects observed in the (transformed) raw data and the Euclidean distances between n objects observed in the MDS model in p dimensional space. In short, NRS alludes to a loss function. This method has the advantage that ever lower values of NRS are found until no improvement is possible, even by the smallest steps. When a local minimum is reached, the indication is that small changes of the configuration all lead to worse NRS values. At this point, the goodness of fit (i.e. NRS) is optimal, and thus the best model has been found. We also found that PROXSCAL shows particular merit over other algorithms (e.g. ALSICAL and Kruskal's) in recovering proximities when there are a large number of incrementing higher order ties in the dissimilarity matrix (James Bell, unpublished data).

For both X_p and X_{fg} , the best solution to representing the observed dissimilarities as distances in a reduced number of dimensions was obtained using the ordinal model with a primary treatment for ties. The best description (global minimum measured by NRS) was found using a simplex start with dimensional constraints imposed slowly by first finding the maximum dimensional solution (in 49 dimensions) and gradually reducing the number of dimension to identify the most parsimonious, yet adequate, solution (i.e. in three dimensions) within a maximum of 1000 iterations. Using the default convergence criteria suggested by SPSS resulted in the identification of potential solutions in higher numbers of dimensions, as indicated by local minima and a lack of monotonicity in the relationship between NRS and the number of dimensions. Increasing the precision of the stress convergence criteria resulted in a smoother relationship and much greater reductions in NRS as the number of dimensions was reduced. Dimensions were specified as optimal→parsimonious with stress convergence criteria set at 0.0000001 for X_p and 0.000001 for X_{fg} . For both models, the

Table 1. Trait coding for the functional groups approach. It should be noted, as per the statistical methods, that, following coding, all traits were normalised.

Trait	Data	Coding	Reasoning
Phenology	May June July	May = 4; June = 2; July = 1 May & June = 6 May & July = 5 June & July = 3 May, June & July = 7	The best strategy is to arrive in May when the aphid population has not started its exponential growth. The best strategy of all is to arrive in May and stay the duration until July at the point of crop senescence when the aphids are leaving/dying. Less important is arriving in June or, worse still, in July when the aphid population could have already approached the economic damage threshold.
Diel activity	nocturnal diurnal both	nocturnal = -1 both = 0 diurnal = 1	Both diurnal and nocturnal predation are of equal weight compared to a non-circadian strategy in which predation could happen at anytime.
Vertical distribution	ground canopy both	ground = 1 canopy = 3 both = 4	If predators occupy the canopy, where the aphids are feeding, then this strategy is three times as important as waiting for aphids to drop off. Falling aphids are only available for a short time on the ground before they ascend back into the canopy, whereas in the canopy they are continuously exposed to foraging predators.
Number of kingdoms	invertebrates plants fungi	a count of kingdoms consumed where one kingdom = 1; two kingdoms = 3; three kingdoms = 4	All aphid predators must consume aphids, thus scoring 1. If, however, they are able to broaden their niche and include either fungi or plants, then this may help maintain their fitness in times of food scarcity. The broadest width is when all kingdoms are consumed, scoring 4.
Number of orders	from 1 order (i.e. Aphidae) up to 28 orders recognised	square-root of the total count of all orders consumed per predator species	For reasons that became clear during data acquisition, there were both taxonomic and functional orders. Functional orders were either a type of feeding that did not mention species (e.g. granivory) or a type of predation that was generalised (other invertebrates). Taxonomic orders: aphid; mites and ticks; spiders; centipedes; beetles; springtails; earwigs; millipedes; flies; mayflies; slugs, snails; true bugs (other); ants, bees, wasps; woodlice; butterflies and moths; lacewings; earthworms; harvestmen; grasshoppers; crickets; thrips. Functional orders: other invertebrates (not given above); egg eating; eating larvae; pollen; vegetable tissue; seed eating; sap; fungi. Each one of these orders scored 1 if present in the literature.
Foraging mode	active hunter sit and wait both	active hunter = 2; sit and wait = 1; both = 3	Sit and wait is less favoured than actively searching for prey due to prey heterogeneities, but best of all is doing both.
Starvation capability	high (months) medium (weeks) low (days)	high = 3 medium = 2 low = 1	The ability to withstand starvation is viewed as advantageous because aphid populations and prey can be unpredictable. Tenacity to maintain a population in the field is regulated by this ability and scores highest for months and lowest days.
Aerial activity	static weak dimorphic strong	static = 0; weak (generally considered within field) = 1 species with wing dimorphism = 1.5; strong (generally considered between field) = 2	Some aphid predators are not aerially active (e.g. larvae or harvestmen) which is inferior to either weak or strong aerial activity that can potentially track prey over longer distances. Two carabid species are wing dimorphic (<i>N. biguttatus</i> and <i>B. lampros</i>), which scored 1.5.
Walking activity	weak strong	weak (generally considered within field) = 1; strong (generally considered between field) = 2	Roaming tendencies are positive traits and infer that the ability to disperse by walking is advantageous and better than weak dispersal or sedentary behaviour.
Mean density	density of individuals recorded within the field	a mean count of the density of individuals per m ² that were then square-rooted	Density is positive and considered monotonic in relation to aphid predation.

proximities associated with the fitted configurations are available (X_{fg} : appendix 1b; X_p : appendix 1c).

For all proposed MDS solutions, we ensured a global minimum (that the fitted distances matched the observed proximities as closely as was possible) by specifying the best model coordinates as the initial configuration, and re-running the analysis. Once the best fitting three-dimensional configurations for X_p and X_{fg} had been obtained, groupings of species were identified. We followed the approach of Foster & Brooks (2005) using ANOSIM to test for the significance of observed clusters defined from the fitted proximities generated from the MDS configurations. We first split the species into groups using K-means clustering, a user-independent method of grouping, applied to the distance matrices (X_p ; X_{fg}) generated from the fitted coordinates $X_{fg,xyz}$ $X_{p,xyz}$, and specifying a sequence of different numbers of groups. The ANOSIM algorithm was then used to test for higher order clustering by comparing results with different specified numbers of groups at a 5% significance level. Simulations were achieved through comparison of the observed test statistics obtained from 10,000 Monte Carlo randomizations (analysis performed using Genstat 8th Edition, VSN International).

Comparing multidimensional scaling models

Once both models were established for X_p and X_{fg} , the central tenet was to test whether the taxonomic and functional datasets produced the same configurations. A suitable test of similarity is through the application of Procrustes analyses to compare fitted configurations; $X_{p,xyz}$, the taxonomic model, represented the 'fixed' coordinates onto which the functional model coordinates $X_{fg,xyz}$ were 'fitted'. Due to the use in MDS of principal axes, which automatically centre and scale the configurations, only reflections and isotropic scaling needed to be prescribed. The goodness of fit between the two configurations was given by expressing the fitted sum of squares (fixed sum of squares-residual sum of squares) as a percentage of the fixed sum of squares. In this application, this measure of goodness of fit is independent of the choice of fixed configuration, and can also be obtained from an analysis of the normalised configurations as $(1 - m^2_{xyz})$, where m^2_{xyz} is the residual sum of squares from this normalised analysis (John Gower and Wojtek Krzanowski, personal communications). Thus, $(1 - m^2_{xyz}) \times 100$ is analogous to percentage R^2 , a rarely used but obvious measure of goodness of fit, and much more intuitive than m^2 .

Decomposing functional groups models

Jack-knifing is not often applied within a multidimensional scaling analysis, but the process does provide an approach to identifying the traits that are important in the overall model (Groenen, personal communication). For the trait data, single traits were individually removed from the dataset, new distance measures calculated and the revised distance matrices reanalysed using MDS to generate new coordinate sets $x_{fg(j1,j2, \dots, j10)}$. Each set of jack-knifed coordinates, $x_{fg(j1,j2, \dots, j10)}$, were then compared with the full dataset coordinates, x_{fg} , using Procrustes analysis. Goodness-of-fit statistics were then ranked in order to assess the contribution of each traits to the overall configuration.

Comparing multidimensional scaling models as predictors of aphid predation rate

Through a process of calculating canonical correlations with the obtained eigenvectors, confirmatory MDS was used to assess the relationship between either the functional or taxonomic solutions, and a measure of aphid predation rate. PROXSCAL is unique in allowing the MDS solutions to be constrained by one or more external independent variables in this way, finding the linear combinations which relate most closely to the MDS dimensions. This is an explicit test of the n -dimensional hypervolume in functional space (Rosenfeld, 2002), which tests the relevance of the groups to a particular trophic process. Simply, we might expect that aphid predation would provide a more meaningful configuration if the classification of aphid predators by functional traits had some internal structure relevant to the consumption of aphids. Thus, including aphid predation into the model introduces a gradient onto which the existing functional or taxonomic models must be constrained; the amount of constraining is then a measure of that internal structure. The optimal solution, if aphid predation has a meaningful relationship with either model, is if the normalised raw stress, an indicator of the lack of confirmation fit, is equal to zero (i.e. that the model is not being constrained at all). The closer to zero NRS becomes, the stronger the implication that a model's inherent latent structure is pertinent to the predation of aphids. Full treatment of this conceptual modelling can be found in De Leeuw & Heiser (1980) and Heiser & Meulman (1983).

Both X_p and X_{fg} were independently constrained by the external variable 'mean rates of aphid predation per species', denoted as ' $C_{raw\ ACR}$ ' (raw aphid consumption rates), using the $mds(X_p)$ and $mds(X_{fg})$ model criteria. This external variable was determined from 37 references in which 276 rates were described and from which means were then calculated (appendix 1d). These mean rates detail the numbers of individual aphids consumed individual⁻¹ day⁻¹ to species level (appendix 1e). All aphid stages and species were considered, the only pre-requisite being that each of these experiments expressed aphid consumption that either was, or could be, translated to 'per individual per day'. The 'mean rates of aphid predation per species' implicitly contains some taxonomic information, at least at the generic level (i.e. within genera all species tend to have similar body sizes, e.g. *Pterostichus* beetles (large); *Coccinella* ladybird beetles (medium); *Erigone* spiders (small)). To understand the significance of this, we divided the 'mean rates of aphid predation per species' variable by the mass of each predator to remove the effect of taxonomy (appendix 1e). Thus, we tested associations with two constraining variables, ' $C_{raw\ ACR}$ ' and ' $C_{mass\ ACR}$ ' (individual aphid consumption rates divided by the mass of each predator). $C_{mass\ ACR}$ was included in a confirmatory MDS analysis as described above for $C_{raw\ ACR}$. Both the taxonomic model and ecologically-based functional model constrained MDS solutions were compared with the MDS unconstrained solutions for the equivalent models (i.e. denoted as $U_{taxonomy}$ and $U_{functional}$) using the $1 - m^2_{xyz}$ statistic.

Assessing the contribution of individual axes as predictors of aphid predation rate

In addition to confirmatory MDS, we calculated Spearman rank correlation coefficients between the measures of

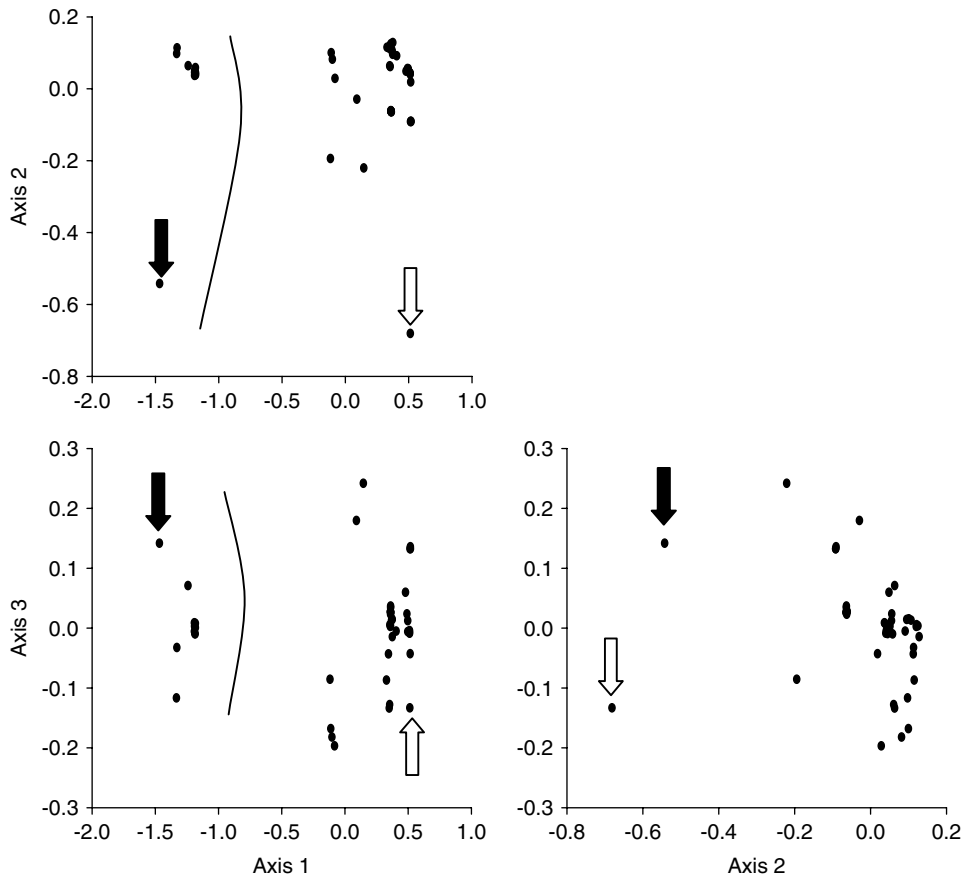


Fig. 1. Two-dimensional scatterplots showing the three-dimensional unconstrained PROXSCAL analysis solution for the taxonomy dissimilarity matrix (X_p), for which the normalised raw stress obtained is 0.00000130. On both axes 1 vs. 3 and 1 vs. 2, annotated lines clearly indicate the separation of spiders and harvestmen (negative axis 1 scores) from the Hexapoda, the class which include all insects (positive axis 1 scores). Within these plots, the black arrows indicate the harvestman, *Phalangium opilio* (Opiliones), as an outlier to all spiders (Araneae). *Forficula auricularia*, an earwig (Dermaptera), occupies a similar position (white arrow) with the Hexapoda and is clearly differentiated from the hexapods in axes 1 vs. 2. *F. auricularia* is the only hexapod species within this analysis drawn from the sub-class Pterygota; all others having been placed within the Endopterygota. *F. auricularia* and *P. opilio* become very prominent within axes 2 vs. 3, where spiders and insects form one large loose cluster in opposition to these two outliers. These four significant higher-order groupings were supported by the ANOSIM test and were 'all spiders', a harvestman (*Phalangium opilio* Palpatores: Phalangidae), all hexapods and an earwig (*Forficula auricularia* Forficulina:Forficulidae) (ANOSIM $R=0.9992$, $P < 0.0002$), demonstrating that taxonomic hierarchies can accurately be recovered using distances constructed from a multiplicative model between Linnaean hierarchies.

aphid predation rate and the individual axes scores from the unconstrained MDS solutions for both the taxonomic and functional unconstrained MDS solutions. Separately, we assessed the relationship of each of the three axes with each of $C_{raw\ ACR}$ or $C_{mass\ ACR}$. This provided a simple breakdown of the contribution of each axis to predictions of aphid predation rate.

Results

Our results strongly suggested that little information was shared between the ecologically-based functional model and taxonomic model unconstrained configurations ($X_{p\ xyz}$ vs. $X_{fg\ xyz}$, $r^2=17.04\%$) as assessed by the Procrustes analysis. Functional traits produced a different paradigm of aphid predators to that which was expressed by the taxonomic relationships. Detailed inspection of the Procrustes analysis

indicated that the arachnids had relatively large Procrustes residuals (mean residual distance between points = 1.180 ± 0.050 (S.E.)), demonstrating that this group were more dissimilar in their positions in the two configuration than other species groups (mean residual distance between points = 0.4011 ± 0.025 (S.E.)). These large Procrustes residuals were an artefact of the taxonomic model dissimilarities which emphasised large divisions between insects (hexapods) and spiders and harvestmen (arachnids) (fig. 1). Conversely, arachnids and hexapods were more similar under the functional groups model. The division in the functional groups model provided prescient importance to predator life stages (fig. 2), indicating that the selected traits include detectable, but implicit, information on the different behavioural traits of larval and adult aphid predators.

The contributions of each of the different functional traits on the MDS-derived configurations was revealed by

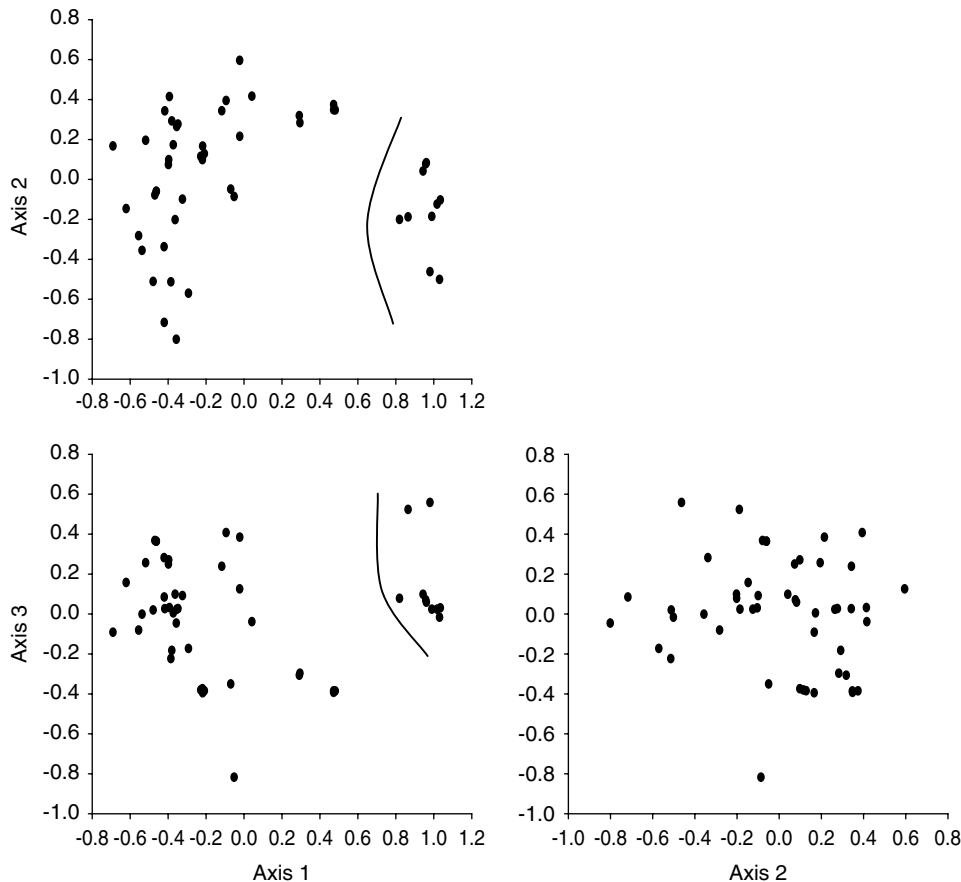


Fig. 2. Two-dimensional scatterplots showing the three-dimensional unconstrained PROXSCAL analysis solution for the functional dissimilarity matrix (X_{fg}), for which the normalised raw stress obtained is 0.00684. Compared to the taxonomy scatterplots, *Phalangium opilio* and *Forficula auricularia* have been absorbed by the main cluster and are no longer outliers. Instead, the two major clustering divisions are not along taxonomic lines, but between life stages. The annotated lines on both axes 1 vs. 2 and 1 vs. 3 indicate the clustering of the larval stages (high axis 1 scores), even though life stage was not explicitly stated as a trait. This division appears as a result of their ecology since many authors agree that the behaviour of larvae is fundamentally different to that of the respective adult stage (low axis 1 scores). ANOSIM supports three higher-order clusters, which include all arachnids + *Nabis ferus* (Heteroptera: Nabidae) + *Tachinus signatus* (Coleoptera: Staphylinidae), all larvae and, lastly, all beetles + *Anthocoris nemorum* (Heteroptera: Cimicidae) + *Forficula auricularia* (Forficulina: Forficulidae) (ANOSIM $R = 0.7707$, $P = < 0.0001$).

the jack-knife analysis of the dataset, comparing pairs of configurations using Procrustes analysis. These analyses revealed that the ecologically-based functional traits model was dominated by traits related to food (number of kingdoms consumed and the ability to withstand starvation), dispersal (strength of movement on the ground and in the air) and diel activity (nocturnal, diurnal or both) (fig. 3). Little importance was attached to field densities, phenology, the way in which species forage and the number of orders and individual species that each predator species consumes.

Confirmatory MDS was used to assess whether the mean rates of aphid predation could be predicted by either the taxonomic or functional trait models. In all constrained MDS solutions, the normalised raw stress increased compared with the equivalent unconstrained MDS solutions ($x_p = 0.00000130 \rightarrow 0.00000226 - 0.00000363$; $x_{fg} = 0.00684 \rightarrow 0.0186 - 0.0231$). Aphid predation, the external variable, forced a poorer fit for both the taxonomic and functional trait models. However, the proportional increase in NRS, expressed as the

percentage change in these stress values, was a much greater range for the taxonomic model ($x_p = 36 - 57\%$) than for the functional groups model ($x_{fg} = 30 - 37\%$), implying that there was more of a latent structure to x_{fg} models generally. Furthermore, observing the signs of the correlations with the MDS axes from both the taxonomic and functional trait models, it was clear that the transformed mean rates of aphid predation per species and the axes were in the same direction for the taxonomic model (correlation with axis 1 = -0.473 and with axis 2 = -0.466), suggesting a strong additive combination. However, these correlations were of different signs for the first two axes of the ecologically-based functional traits model (correlation with axis 1 = 0.495 and with axis 2 = -0.171).

Importantly, within-model Procrustes analyses revealed that when mean rate of aphid predation is compared between its raw ($C_{raw\ ACR}$) and mass adjusted ($C_{mass\ ACR}$) form, the unadjusted and adjusted models within both taxonomic ($r^2 = 89.35\%$) and functional trait models ($r^2 = 84.88\%$) were much the same: adjusting predation rates for species mass does not improve confirmatory MDS

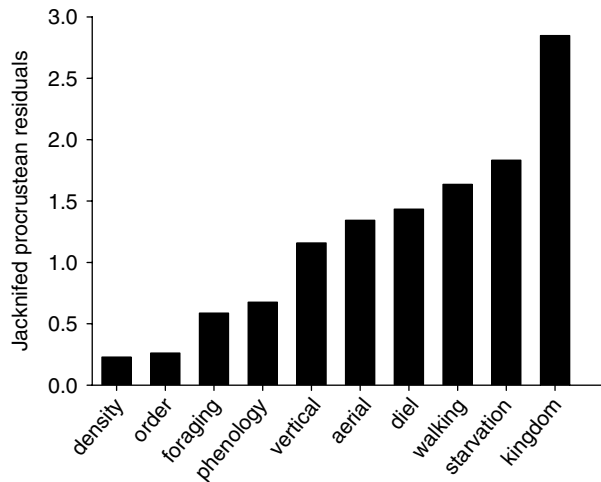


Fig. 3. Bar chart showing the Procrustes analysis goodness-of-fit statistics comparing MDS solutions of jack-knifed functional trait distance matrices against the MDS solution for the full functional trait distance matrix. Each value relates to the comparison with the identified trait removed from the functional traits dataset. The lower the Procrustes statistic, the less the trait contributes to the full model; the jackknife and full model configurations are then considered more similar. The ability of a predator to be widely polyphagous, consuming prey from plants, animals or fungi, shows the kingdom trait to be the most divisive within the model. This and other important traits can be related to the divisions observed in the functional groups dissimilarity matrix. Commonly, polyphagy across kingdoms is a behaviour bestowed upon adults, although there are degrees and anomalies (e.g. spiders). Note that the number of orders consumed is of little importance since it was often true that both adults and larvae consumed a wide array of orders. Other traits, with higher residual values, indicate that adults generally also are better able to tolerate starvation, show an ability to disperse widely and have diel patterns, which are fuzzy, not fixed. Conversely, traits with low residual values, such as density, affect adults and larvae in the same way, in that within both there are examples of high and low levels of density.

predictions, as indicated by the low Procrustes residual values (11–16% of the fixed sum of squares).

Spearman rank correlations between the taxonomic model MDS axes scores and aphid predation rates revealed that none of the three X_p axes correlated strongly with either $C_{raw\ ACR}$ (r_s with axis 1=0.127 ($P=0.378$); r_s with axis 2=−0.071 ($P=0.624$); r_s with axis 3=0.009 ($P=0.952$)) or $C_{mass\ ACR}$ (r_s with axis 1=0.214 ($P=0.136$); r_s with axis 2=−0.004 ($P=0.977$); r_s with axis 3=0.030 ($P=0.834$)). However, for the functional trait model (X_{fg}) stronger correlations existed with axes 2 and 3, suggesting that this classification has greater predictive power (for $C_{raw\ ACR}$, r_s with axis 1=0.126 ($P=0.383$); r_s with axis 2=−0.399 ($P=0.004$); r_s with axis 3=0.317 ($P=0.025$); for $C_{mass\ ACR}$, r_s with axis 1=0.090 ($P=0.536$); r_s with axis 2=0.116 ($P=0.424$); r_s with axis 3=0.317 ($P=0.025$)).

Discussion

Discrimination of functional groupings and their independence from taxonomic groupings

We have rigorously investigated the validity of aphid predator functional groups and found that there are at least

two groups. Traditionally, arachnids are the morphological outliers to the insects, but this distinction disappears when functional traits are imposed. Using functional traits, the major division between aphid predators is based on life stage, expressed as a result of the differences that were broadly synonymous with a dichotomy between stenophagy and polyphagy and behaviours therein (see fig. 3). This seems a more logical classification than that of taxonomy because stenophagous aphid predators, such as hoverfly or ladybird larvae, are highly dependent on, and positively search for, patches of aphids (Hemptinne *et al.*, 1993). Observed in the functional traits model and evident in nature, these stenophagous aphid predators are neither mobile nor able to withstand starvation for any period (Hemptinne *et al.*, 1993) – traits which appear to be discriminating factors. In contrast, polyphagous predators, particularly adult beetles, are very different in behaviour, actively hunting for prey in an attempt to redress nutritional imbalances (Symondson *et al.*, 2002a; Mayntz *et al.*, 2005). As might be expected, encounter rates between aphids and polyphagous predators are markedly different than those with stenophagous aphid predators that are cued into their prey.

A new approach was developed during this study, yielding a test between the MDS configurations generated for the null (i.e. taxonomic) and alternative (i.e. ecologically-based functional traits) models using Procrustes analysis. The need to discriminate functional groupings and assess their independence from taxonomic groupings is a recalcitrant problem (Cummins, 1974) and largely overlooked. Here, we have demonstrated that our simple method allows us to investigate whether the functional traits model can provide a different, and more appropriate, paradigm to that provided by classical taxonomy. Whilst not an absolute method that encapsulates shared and unique morphologies, the generalised hierarchical approach to specifying taxonomic similarities was able to recover realistic taxonomic distances between taxa (fig. 1) and provide a promising blueprint for deriving similar null taxonomic models in the future. However, this should not be identified as a suitable generic method for generating phylogenetic hypotheses, as that would require morphological data rather than a simple hierarchy-based measure of the dissimilarity between species.

Does implicit ecological information improve model prediction?

Neither life stage, determined from a study of functional traits, nor morphology, which is implicit in taxonomic description, were natural predictors of laboratory rates of aphid predation. Confirmatory MDS showed that both provided a relatively poor prediction of both raw and biomass-adjusted mean rates of aphid predation. In either of the confirmatory MDS models, the ideal solution would have been to find that normalised raw stress was zero. This would have inferred that there was an inherent latent structure that was informative and meaningful to a particular model. Instead, all models increased in stress equal to or greater than >30%, although the functional groups model was subject to less change overall. When single axes were compared rather than complete models, the implication drawn from the Spearman rank correlations between individual axes and aphid predation rates, was that the

ecologically-based functional traits model had more predictive power than the taxonomic model. Yet these improvements were small and not especially outstanding in their significance.

Whilst it is disappointing that the whole confirmatory MDS model did not complement the rank correlations, it is also not surprising given that the vast majority of species included were polyphagous, with high levels of natural variation both within and between species. Unlike most larvae, polyphagous predators cannot exist solely on aphids because this taxon contains digestive inhibitors and metabolic toxins, inducing oxidative stress in the predator's gut (Toft, 2005). It is now hypothesised by many that a range of foods must be available to sustain predators that are exposed to aphid prey (Settle *et al.*, 1996; Harwood *et al.*, 2004). Therefore, a search for a linear combination of functional traits, as tested in the confirmatory MDS model, might be less tenable than a coarse ranking because predation by polyphagous predators is inherently 'noisy'.

One of the interesting facets which has significant implications for the prediction of aphid predation rate from the functional traits model, is that not all larval stages are stenophagous aphid predators. This group also contains polyphagous beetle larvae, which clearly have similar ecologies to stenophagous aphid predators, hence their close proximity in the functional trait model. But despite their closeness, polyphagous beetle larvae implicitly have a much broader diet (e.g. the carabid larvae, *A. dorsale*, consumes a wide variety of foods including aphids, mites, spiders, flies, ants and thrips (Pearson, 1980; Griffiths, 1983)) compared to stenophagous aphid predators. Surprisingly, the degree of polyphagy does not appear to adversely affect aphid predation rates for predatory larvae; for both *A. dorsale* larvae and the rove beetle (*Tachyporus* sp.) larvae, the mean rates of aphid predation, even when adjusted for mass, are noticeably higher than those for stenophagous larvae (appendix 1e). This is likely to be attributable to the fact that the larvae of these beetles have relatively low mass but (in the laboratory at least) a high voracity for aphids.

Clearly, aphid predation rates by predators in the field provide the best test of the two hypothesised models of aphid predators. However, we found such data wanting after completing a trawl of the available sources (appendix 1f). The rates of aphid predation for many species are not available because they are expressed merely as a positive/negative dichotomy, which cannot be transformed to numbers of individuals consumed. Further, in contrast to laboratory observations, there are a number of difficulties in interpreting these data, such as differences in aphid decay rates in the guts of predators, the specificity and sensitivity of the techniques used, levels of satiation, degree of scavenging and secondary predation (Symondson, 2002). A further confounding factor is field temperature, which has a positive effect on the rates of digestion which also reduces detection periods (Hoogendoorn & Heimpel, 2001).

Whilst our research group and its associates are continually developing new molecular techniques to quantify rates of predation (Agustí *et al.*, 2003; Foltan *et al.*, 2005; Harper *et al.*, 2005; Read *et al.*, 2006), quantitative methods which equate to numbers of aphids eaten currently seem impractical and are further complicated because first or second instar aphids will have less DNA than fully grown adults. Despite these known difficulties, such tools are now being developed using PCR-based techniques (e.g. Deagle & Tollit,

2007). Their application to invertebrate trophic ecology, particularly regarding the calculation of prey biomass consumed by individual predators, must now be considered a possibility.

The need for robust models that could improve the effectiveness of conservation biological control

Within entomology, functional trait studies are very much at an embryonic stage, except perhaps in stream ecology which has well-defined functional types (Cummins, 1974). For terrestrial ecosystems, the problem has been that unless a simplification of the functional role can be established easily, insects and spiders often perform multiple roles (Cole *et al.*, 2002) and functional traits become somewhat fuzzy under the influence of multi-trophism (Finke & Denno, 2005). By contrast, botany rarely faces this problem and has, consequently, always been strides ahead, such that functional trait studies are routine. Grime (2006) has argued that the functional trait approach should always be used and that taxonomic methods should be confined to history, though not all datasets support this view (Lindborg & Eriksson, 2005). The conclusion from our study is that a functional groups approach in entomology may not deliver what logic would predict. This is because we cannot as yet scale traits to capture the fuzzy nature of predator behaviour, which appear to need some sort of moving average or variance model. If achievable, it would be worthwhile re-visiting aphid predator functional groups because, by doing so, groups of species could be more precisely aligned to particular ecosystem services, revealing the structure and functionality of the food webs surrounding aphids in agroecosystems.

Meanwhile, in lieu of such an approach, it may be worthwhile comparing aphid predation rates between treatments in which functional groups are combined in different ways. For example, at the highest functional level, more interference and less synergy would be expected if two species in their larval stages were compared with a mixed population of larvae and adult aphid predators. This would be a very simple experiment to do with ladybirds, building to more complex designs that included ground beetle or hoverfly larvae, as appropriate.

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Supplementary Material

The following online appendices can be viewed at journals.cambridge.org/ber

Appendix 1a–f: Excel spreadsheet of classification of 50 aphid predators used (appendix 1a), proximity matrices (appendices 1b,c), aphid predation database (appendix 1d) aphid predation rates as an external variable (appendix 1e) and mini review of molecular methods (appendix 1f).

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