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Behavioural hypervolumes of spider communities predict community performance and disbandment

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Trait-based ecology argues that an understanding of the traits of interactors can enhance the predictability of ecological outcomes. We examine here whether the multidimensional behavioural-trait diversity of communities influences community performance and stability *in situ*. We created experimental communities of web-building spiders, each with an identical species composition. Communities contained one individual of each of five different species. Prior to establishing these communities in the field, we examined three behavioural traits for each individual spider. These behavioural measures allowed us to estimate community-wide behavioural diversity, as inferred by the multidimensional behavioural volume occupied by the entire community. Communities that occupied a larger region of behavioural-trait space (i.e. where spiders differed more from each other behaviourally) gained more mass and were less likely to disband. Thus, there is a community-wide benefit to multidimensional behavioural diversity in this system that might translate to other multispecies assemblages.

1. Introduction

Individual variation in behavioural traits is ecologically notable because of its potential to change the outcome of a variety of processes, including population dynamics [1,2], range expansion/recession [3,4], trophic cascades [5,6], community assembly [7,8], extinction risk [9] (but see [10]) and species interaction networks [11]. In behavioural ecology, the majority of research on individual variation in behaviour has focused on single-species studies or two-species interactions [12–14]. For instance, individual differences in behaviour are known to shape foraging efficiency [15,16], diet breadth [17], susceptibility to predation [18,19] and propensity to be parasitized [20,21]. However, empirical information on how the impacts of such behavioural differences scale to influence species-rich ecological modules is still scant [22,23].

Here, we explore whether and how the multidimensional behavioural diversity exhibited by whole communities influences the success of each constituent species of the community, the success of the community as a whole and community persistence in the wild. Inspired by niche hypervolumes of general ecology [24,25] and recent advances in trait-based plant community ecology [26], we quantify behavioural-trait diversity as a multidimensional behavioural hypervolume. We define a *behavioural hypervolume* as the *n*-dimensional volume occupied by an individual, population or community in behavioural-trait space. To the extent to which behavioural differences map to niche differences, and there is some evidence that it should and does (e.g. [17,27–29]), we predict that

communities that occupy a larger behavioural hypervolume will outperform behaviourally homogeneous communities. This prediction is analogous to classical studies linking species richness and reduced species similarity with improved system-level performance [30,31]. The benefits of large behavioural hypervolumes may result from adaptive division of labour [32], reduced competition among community constituents [33] or other more subtle mechanisms of trait complementarity [34]. Positive effects of within-group behavioural diversity have been documented for a variety of animal societies of a single species (e.g. as a consequence of adaptive social niche specialization [35–37]). We predict that a similar positive relationship between behavioural-trait diversity and collective outcomes will scale up to the community level when examining mixed species assemblages [38–40].

The facultatively social spider *Anelosimus studiosus* (Araneae, Theridiidae) constructs three-dimensional webs that serve as habitat for more than 50 other species of spiders [41,42]. These foreign spiders typically contribute a modest amount to the architecture of a shared chimaeric web, but *A. studiosus* is the nuclear species of the association [43]. If the resident *A. studiosus* perish or disperse, then the community quickly disbands and vanishes [41]. Generally, more species-rich communities exhibit higher rates of extinction and disbandment in this system [41,42]. Yet, whether or how behavioural-trait variability *per se* contributes to the extinction and disbandment of a community is unknown. Here we evaluate the degree to which the behavioural hypervolumes occupied by communities of spiders influence individual- and community-level performance metrics. In particular, we test the hypotheses that: (i) communities that occupy a larger behavioural hypervolume will be less likely to disband; (ii) the size of the behavioural hypervolume occupied by a community will be positively associated with the average mass gained by all community constituents; and (iii) if communities that occupy a larger behavioural hypervolume are more successful, and thus are more profitable to join, then behaviourally diverse communities will attract a larger number of spider immigrants into the chimaeric web.

2. Material and methods

(a) Collection and behavioural assays

Adult females of five different species of web-building spiders were collected along a riparian habitat in eastern Tennessee in May 2015 (Melton Hill, 35°59′29.76″ N, 84°11′44.55″ W). The five focal species were *Leucauge venusta*, *Barronopsis texana*, *Theridion murarium*, *Theridion flavonotatum* and *A. studiosus*. These species were selected because they represent some of the most common species in these communities [42,44]. We ran 52 individuals of each species through three behavioural assays to assess individual differences in boldness, foraging aggressiveness and activity level. Boldness was assessed using individuals' latency to resume movement following an aversive stimulus (detailed in [45,46]). Foraging aggressiveness was determined using individuals' latency to attack prey (termite workers) placed into the spider's web (detailed in [47,48]). Activity level was the distance (no. of gridlines) traversed by spiders in a novel open field environment over 10 min (detailed in [13,49]). Some animal personality researchers have used this assay as a metric of exploratory behaviour. To measure behavioural repeatability, 12 individuals from each species were run through all three assays once daily for 10 consecutive days. The remaining

40 individuals per species were randomly assigned to 40 experimental communities created using one individual of each of the five species. This produced 40 replicate communities that were identical in species composition, but varied in community behavioural hypervolume.

(b) Community creation and establishment

Communities were initiated by placing one *A. studiosus* individual in a 1.5 l container with a tangled ball of poultry wiring to facilitate web construction. Each individual *A. studiosus* was first given one week to construct a web before adding any other spiders. We then added one spider into the community each day for 4 consecutive days. To limit predation, all spiders were fed to satiation 24 h prior to being added to the community. Spiders were added in the following sequence, with one spider added every 24 h: *T. murarium*, *T. flavonotatum*, *L. venusta* and *B. texana*. All individuals were uniquely marked using fast-drying modelling paint atop their cephalothorax and weighed using an analytical balance. After all five individuals were added we allowed the community a 48 h settling period before deploying it in the field. To deploy communities at naturally appropriate locations, we first identified pre-existing *A. studiosus* webs, removed them using pruning snips and fastened an experimental community to the same location using topiary guide wires. Fourteen of the 40 experimental communities were either destroyed by predatory ants or were somehow dislodged and fell into the river within 48 h of being deployed. The remaining 26 communities were used for our analyses here.

To determine community success we collected all the experimental communities after 20 days. Instances where the resident *A. studiosus* dispersed always resulted in community disbandment, where all of the other species of spiders dispersed into adjacent foliage and constructed independent webs. The precise moment at which these disbandment events occurred is unknown; however, we did not observe community disbandment events during the first 8 days of the experiment. When possible, we collected all the original tagged spiders whether or not the community had disbanded. We then measured the mass of each spider to determine its change in body mass, which was our estimate of individual performance. In the 15 communities that disbanded, the resident *A. studiosus* died in two instances (carcass recovered) and dispersed to adjacent foliage in the 13 other cases. When the community remained intact, we counted the number of individuals of non-focal spiders that had recruited to the community during the 20 days of our experiment. These new spiders were primarily small subadult theridiids of genus *Theridion*.

(c) Statistical approach

Repeatabilities and 95% CI for each behavioural trait were estimated using the rptR package in R [50]. For Gaussian error distributions, rptR uses GLMMs and restricted maximum likelihood to calculate repeatability values, bootstrapping to estimate the 95% confidence intervals (number of simulations = 1000), and permutation tests to assess significance (number of permutations = 1000). We designated individual ID as a random effect in these models. Behavioural data were log-transformed to achieve a normal distribution for most species. However, we found that the latency to attack for *L. venusta* was highly bimodal; thus we estimated the repeatability values using both the log-transformed latencies and a Gaussian error distribution as well as binomial transformed responses and a binomial error distribution. Using a binomial error distribution yielded a slightly lower repeatability (0.34 versus 0.40), but the estimate was still significant ($p = 0.001$, 95% CI 0.033–0.556). For ease of comparison, we present the results of the log-transformed data (electronic supplementary material, S1). We tested for behavioural syndromes via pair-wise Spearman correlations of subjects' average behavioural response across trials.

Table 1. Results of our principal component analysis. Factors included were spiders' activity level, foraging aggressiveness (latency to attack prey) and boldness.

eigenvalues			loadings		
	eigenvalue	% var explained	activity	foraging	boldness
PC1	1.32	44.08	−0.70	0.75	0.52
PC2	0.93	30.89	0.44	−0.17	0.84
PC3	0.75	25.03	0.56	0.64	−0.17

To quantify the behavioural diversity of the experimental communities, we computed behavioural hypervolumes. To allow for comparison across behaviours, we first standardized each behavioural trait by subtracting from it the mean value of all observations and dividing the difference by the standard deviation. In this analysis, each individual becomes a single point in a three-dimensional behavioural space, and the behavioural hypervolume of the community was estimated as the volume captured within the minimum convex polyhedron created by these five points. Volumes were computed using the *convhulln* function in MATLAB. To circumvent the potential sensitivity to sampling effort of the behavioural hypervolume, which relies on extreme values, we compared communities with an identical number of constituents ($n = 5$).

We assessed the predictive value of community hypervolume against a variety of rival measures using a series of univariate models. Each rival model contained only one predictor variable and one response variable. This procedure allowed us to pit the predictive value of behavioural hypervolumes against simpler extrema statistics, like the range of each behavioural measure, without issues of multicollinearity. Models were compared using the Akaike information criterion (AIC) and Akaike weights; lower AICs and higher Akaike weights convey superior (more informative) models [51,52]. Predictor variables included the highest and lowest values, and the ranges of activity level, foraging aggressiveness or boldness exhibited by any community constituent. We also examined the ranges of principal component axes 1 and 2 (details of our PCA analysis are provided in table 1). Finally, we tested volume-based measures including the product of the ranges of principal component axes 1 and 2, the community volume assuming a right rectangular prism shape (the product of the three ranges) and the actual community volume of the irregular convex polyhedron occupied by the community in behavioural-trait space (i.e. its behavioural hypervolume). Response variables included average mass gained by all community constituents recovered, colony disbandment (modelled with a binomial error distribution) and the recruitment of additional spiders into the community. Model comparisons were run using JMP 12.0.

To evaluate the degree to which individual variation in body size (mass) is associated or conflated with variation in behaviour, we tested for associations between mass and each of the three behavioural metrics for each of the five focal species using general linear models. An independent analysis was conducted for each combination of species and behavioural trait. To examine whether spiders' starting mass might impact their change in mass within each community, we used a general linear model with percentage change in body mass as our response variable and individuals' starting mass as our predictor variable.

3. Results

Our measures of activity level, foraging aggressiveness and boldness were repeatable for all traits and species (electronic

supplementary material, S1 and table S1): *A. studiosus* (all $r > 0.28$), *B. texana* (all $r > 0.36$), *T. flavonotatum* (all $r > 0.35$), *L. venusta* (all $r > 0.22$) and *T. murarium* (all $r > 0.55$). Using all 52 animals per species, we detected some significant correlations in behaviour for three species: *A. studiosus*, *B. texana* and *T. flavonotatum*. We found positive correlations between activity level and foraging aggressiveness for all three of these species (electronic supplementary material, S1 and table S2) and a positive correlation between foraging aggressiveness and boldness in *T. flavonotatum* (electronic supplementary material, S1 and table S2). These syndromes yield a diamond-shaped behavioural hypervolume for all three species (figure 1).

The species' behavioural hypervolumes varied across species (figure 1), with *B. texana* occupying the largest region in behavioural space and *L. venusta* the smallest: *B. texana* (13.05), *T. flavonotatum* (11.13), *A. studiosus* (4.89), *T. murarium* (3.83) and *L. venusta* (0.56). *Post hoc* inspection of our data indicated that the behavioural hypervolumes of some species (e.g. *B. texana*, *T. murarium*) might have been driven by one or a few individuals possessing extreme phenotypes. When removing the most extreme 5% of individuals (as done when creating two-dimensional 95% minimum convex polygons [53]), the resulting species behavioural hypervolumes had a similar rank-order as the full volumes: *T. flavonotatum* (8.38), *B. texana* (2.59), *A. studiosus* (2.21), *T. murarium* (2.05) and *L. venusta* (0.40).

Example communities exhibiting a wide range of hypervolumes are depicted in figure 2. Communities varied a great deal in their behavioural hypervolumes. Some communities were composed of constituents of very similar multi-dimensional behavioural tendencies ($BHV_{community} = 0.02$) while other communities were composed of individuals that exhibited very different multidimensional behavioural tendencies ($BHV_{community} = 5.79$). The most behaviourally diverse communities exhibited behavioural hypervolumes that exceeded those exhibited by whole species (e.g. *A. studiosus*, *T. murarium*, *L. venusta*). This variability among communities raises the question of whether this variation has any functional consequences for community behaviour or performance.

The behavioural hypervolume occupied by a community was the best predictor of community disbandment (Akaike weight = 0.69; figure 3) and the average mass gain of all community constituents (Akaike weight = 0.29; figure 4). Both of these models had Akaike weights at least twice that of the second best model (electronic supplementary material, S2). *Post hoc* inspection of the regression of average mass gain on community hypervolume indicated a possible curvilinear relationship. However, *post hoc* comparisons of linear versus various nonlinear fits confirmed a better fit for the positive linear model (all $\Delta AICc > 2.2$). To assess whether the
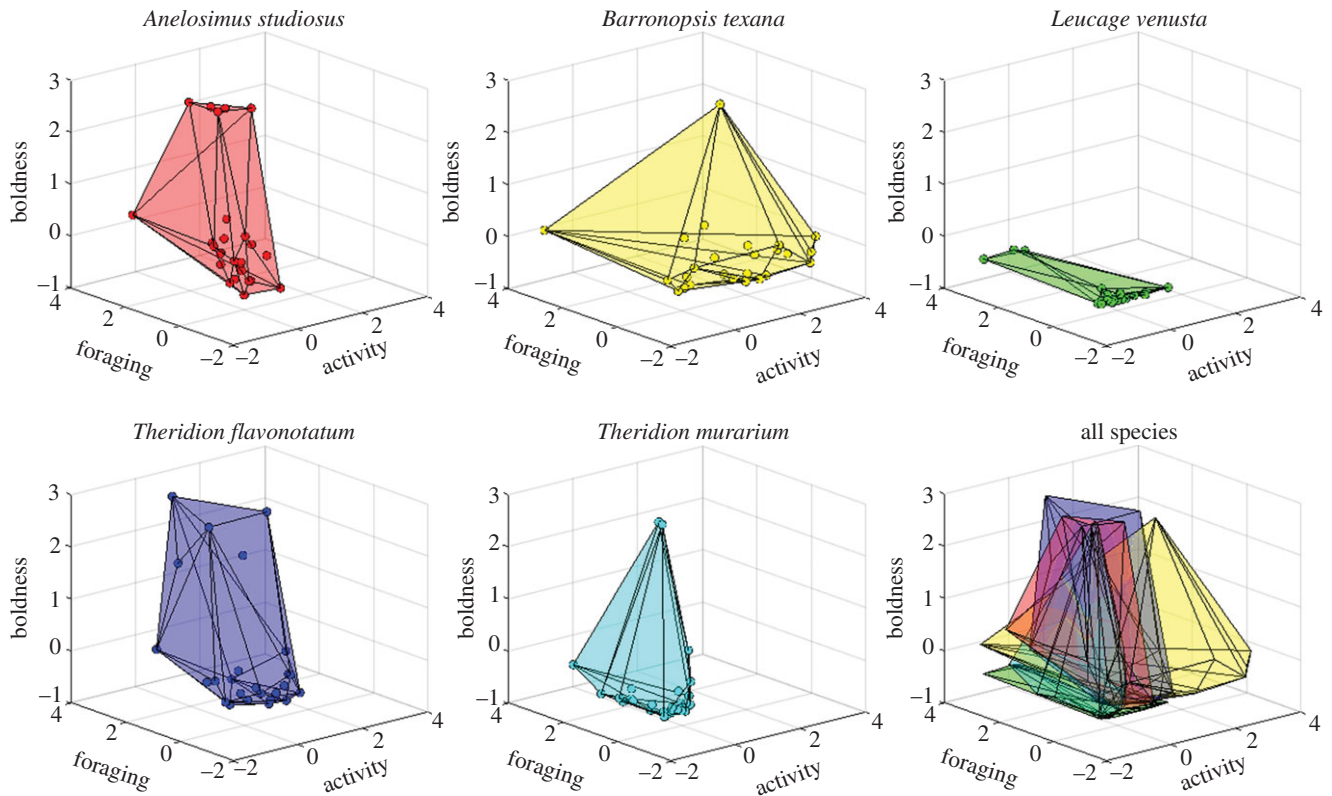
Figure 1. Behavioural hypervolumes of five species of web-building spiders. Points depict the activity level, foraging aggressiveness (latency to attack prey) and boldness of individual spiders. Polyhedrons are the behavioural hypervolume occupied by each species.

relationship between mass gain and behavioural hyper-volume was driven by communities that disbanded, we repeated the analysis with only the communities that remained together for the duration of the study ($n = 12$). Here again we detected a positive association between a community's behavioural hypervolume and the average mass gain of its constituents (L-R $\chi^2 = 9.51$, $p = 0.002$). Notably, many communities with relatively small behavioural hyper-volumes (less than 0.70) lost weight during the course of our study (figure 4).

Given that community-wide behavioural diversity had such large effects on the average mass gain of the community constituents, we conducted a *post hoc* analysis to determine whether individuals with behavioural tendencies unlike those of the rest of their community enjoyed superior per-formance, as one would predict if greater behavioural overlap caused greater competition. To conduct this analysis, we found the centre of gravity of the behavioural polyhedral of each community using the *centroid* function in MATLAB and calculated the Euclidean distance of each individual in the community from this centroid. This measure provided an estimate of each individual's behavioural dissimila-rity from the rest of its community. We failed to detect an association between individuals' mass gain and their behavioural dissimilarity from their community (electronic supplementary material, S3).

Community hypervolume was also the best predictor for the mass gained by *T. flavonotatum* (Akaike weight = 0.20) and *A. studiosus* (Akaike weight = 0.23) (figure 5; electronic supplementary material, S2). Situations where these two species lost weight nearly always involved communities with small behavioural hypervolumes (less than 1.1) (figure 5). Community behavioural hypervolume was poorer than other

measures at predicting the mass gain of the other species (depicted in the electronic supplementary material, S4) or the recruitment of additional spiders into the community.

Individual variation in body size was not significantly associated with individual variation in behaviour regardless of the species or behavioural trait considered (all $p > 0.10$; electronic supplementary material, S5). Thus, while individual variation in body size may interact with variation in behaviour in interesting ways, the behavioural results noted above cannot merely be attributed to variation in individual body size alone. With the exception of *L. venusta* ($F_{1,19} = 7.23$, $R^2 = 0.27$, $p = 0.014$), individual variation in starting mass was unrelated to spiders' percentage change in body mass over the course of our experiment (all $p > 0.43$). For *L. venusta*, individual spiders that were larger at the start of the experiment gained proportionally more mass by the end of our study.

4. Discussion

The multidimensional behavioural diversity of communities of web-building spiders was strongly associated with com-munity-wide outcomes such as likelihood of disbandment and collective mass gain. Interestingly, disbandment was also linked with community performance: communities tended to remain intact and gain more mass when they were more behaviourally diverse. Whether dispersing indi-viduals were able to detect the behavioural hypervolume of their community directly or indirectly (e.g. via low mass gains, poor prey capture efficiency, etc.) is uncertain. How-ever, we observed that greater behavioural diversity was positively associated with community-wide mass gain even
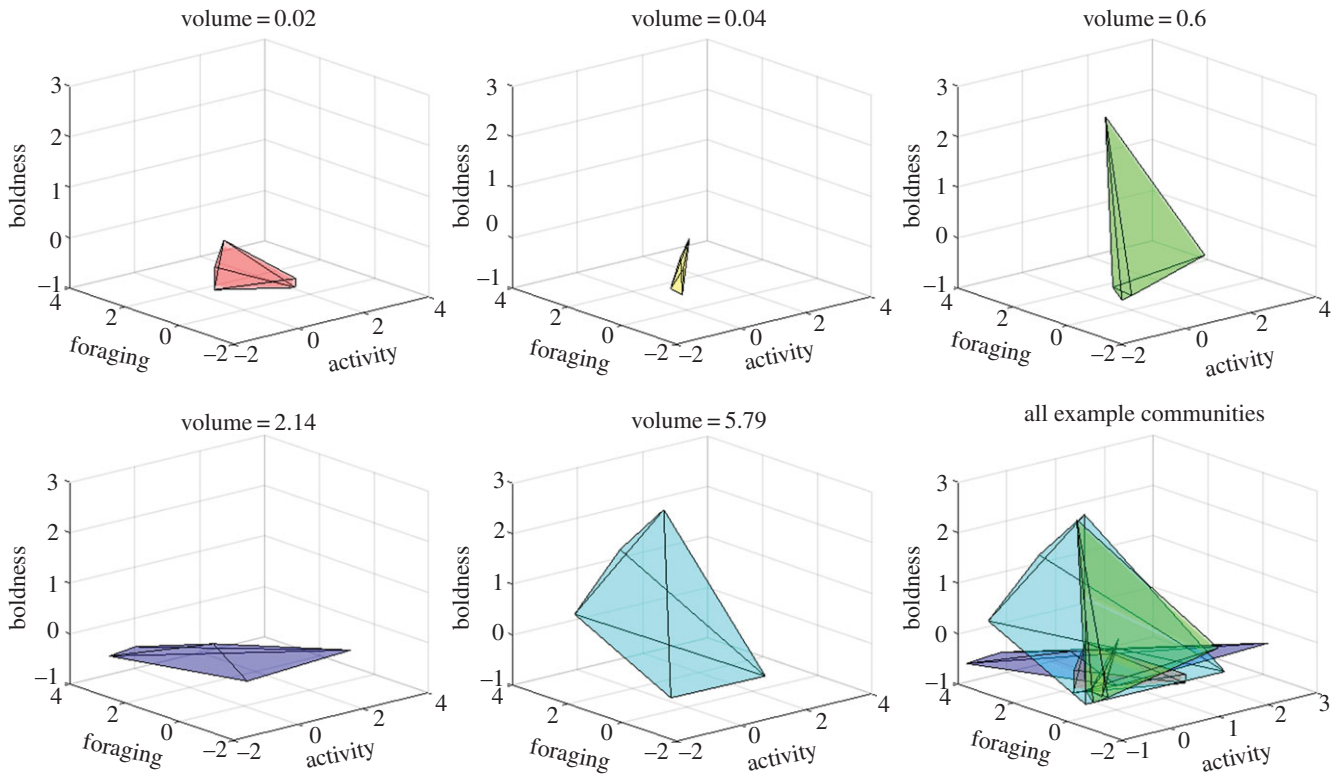
Figure 2. Behavioural hypervolumes of five example communities. The points of these polygons depict the activity level, foraging aggressiveness (latency to attack prey) and boldness of individual spiders. Communities were composed of five individual spiders, one from each of the following species: *A. studiosus*, *B. texana*, *L. venusta*, *T. murarium* and *T. flavonotatum*. Polyhedrons are the behavioural hypervolume occupied by each community.
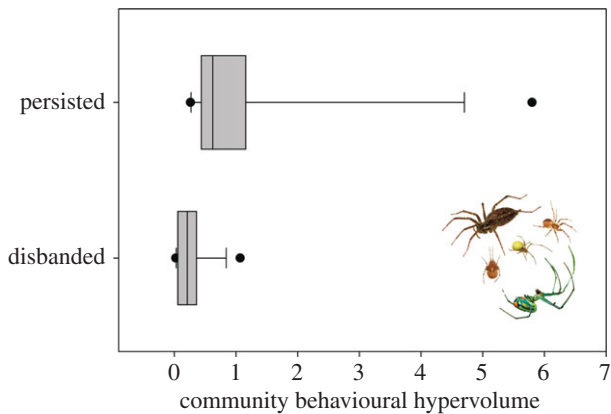

Figure 3. The behavioural hypervolume occupied by communities that persisted or disbanded over the course of our field study. The centre line designates the median, grey boxes give the interquartile range and vertical lines are the 90th and 10th percentiles. Note that community disbandment (*x*-axis) was the dependent variable for this analysis. Species positions and physical descriptions are as follows: *B. texana* (top left, large brown spider), *A. studiosus* (top right, small rust-coloured spider), *T. flavonotatum* (centre, yellow spider), *T. murarium* (bottom left, small brown spider), *L. venusta* (bottom right, large green spider).

when we restricted our analysis to only those communities that remained together for the duration of the study. This result conveys that more behaviourally diverse groups of heterospecific spiders outperform groups composed of behaviourally similar individuals independent of community disbandment. We discuss possible mechanisms for these findings below. Although positive effects of within-group behavioural variability have been noted for a variety of single-species social groups [35,36], our work represents a case where community-wide behavioural diversity has a
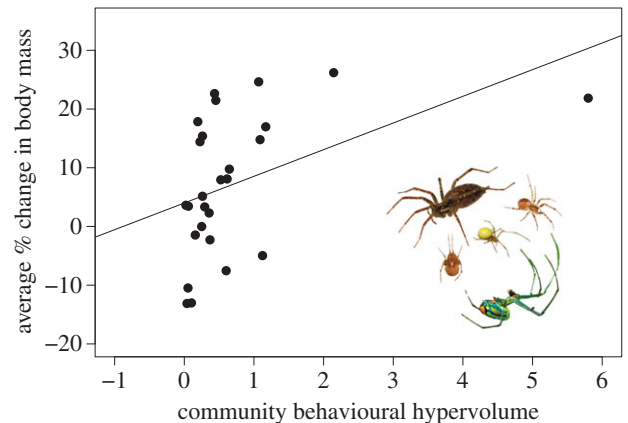

Figure 4. Average mass gain of community constituents in relations to community behavioural hypervolumes. Species positions and physical descriptions are as in figure 3.

positive impact on the stability and success of entire communities. Thus, we propose that positive effects of behavioural diversity could be a general phenomenon that occurs across multiple scales of biological organization.

The performance of *A. studiosus* and *T. flavonotatum*, both small-bodied theridiids, appears to be particularly susceptible to community-wide behavioural diversity. Both species gained more mass when occupying more behaviourally diverse communities. A positive relationship between behavioural diversity and enhanced performance has been detected previously in multi-female colonies of *A. studiosus*. Conspecific groups of behaviourally diverse *A. studiosus* outperform homogeneous groups [54], and dyadic interactions between *A. studiosus* and other species of spider (*Larinioides* and *Theridion*) often switch from parasitic to mutualistic when
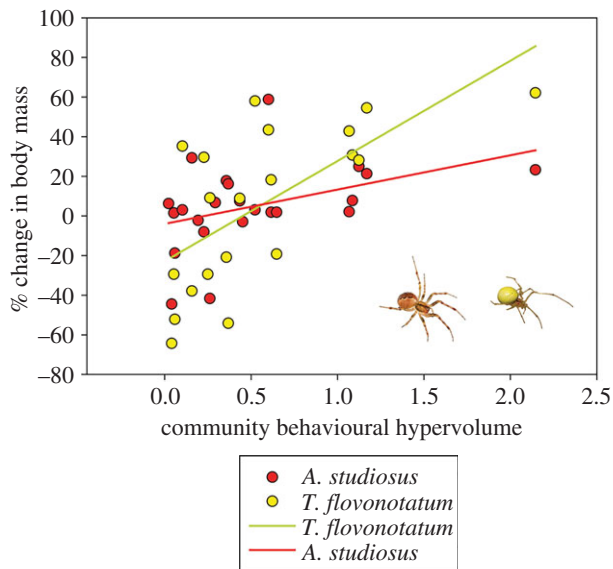
Figure 5. Percentage mass gain of *A. studiosus* (red dots, rust-coloured abdomen) and *T. flavonotatum* (yellow dots, yellow abdomen) in relation to community behavioural hypervolume.

interactors exhibit unlike personality types [34]. Whether this stems from trait-mediated reductions in competition, enhanced division of labour or some other element of trait complementarity remains elusive. Single-species studies on *A. studiosus* groups suggest that the first two factors play at least some role in the enhanced performance of behaviourally diverse societies [55]. Given that *A. studiosus* is also the foundation species for this community, it is plausible that the positive effect of community-wide behavioural diversity on community performance stems from the fact that these are the same conditions where *A. studiosus* (the host species) does best. This hypothesis is consistent with prior studies which showed that community persistence is linked with the performance of *A. studiosus* [41]. We also cannot fully eliminate the hypothesis that species differences in body size could be responsible for the enhanced benefits of large behavioural hypervolumes for small-bodied species. We at present simply do not have enough species to critically evaluate this hypothesis. However, the hypothesis does not

seem particularly viable merely because *T. murarium*, which is another small-bodied theridiid, failed to exhibit a similar pattern.

Finally, our results convey that a deep understanding of the relationship between behavioural variation and the ecology of *A. studiosus*'s chimaeric webs calls for a multispecies and multidimensional perspective [56]. At present, it appears that the individual behavioural types of multiple interactors (conspecifics and heterospecifics) might work together in a multidimensional manner to shape the rise, disbandment and persistence of both colonies and whole communities in this system. Our inability to detect a direct relationship between the mass gain of each individual and its behavioural dissimilarity from its community suggests that synergistic, rather than additive, effects underlie the relationship between community mass gain and its behavioural hypervolume. We further note that more common multivariate statistical methods (PCAs) were consistently outperformed by behavioural hypervolume metrics when predicting community outcomes (electronic supplementary material, S2). This finding suggests that the most phenotypically extreme species or extreme individuals within communities may play a disproportionately large role in determining collective outcomes [57,58]. Therefore, it appears that behavioural hypervolumes could be a useful tool for deconstructing and assessing multi-tiered and species-rich systems, like most biological communities, of which the silken reefs of *A. studiosus* represent but one example.

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