Trait overdispersion and the role of sociality in the assembly of social spider communities across the Americas

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Among the factors that may lead to differences in resource use among closely related species, body size and morphology have been traditionally considered to play a role in community assembly. Here we argue that for animals that live and forage in groups, level of sociality, reflecting differences in group size and cooperative tendencies, can be an additional and powerful dimension separating species in niche space. We compare 50+ communities of the social spider genus *Anelosimus* across the Americas against a null model that accounts for known effects of biotic and abiotic factors on the distribution of social systems in the genus. We show that these communities are more overdispersed than expected by chance in either or both body size and level of sociality, traits we have previously shown to be associated with differences in resource utilization (prey size, microhabitat, and phenology). We further show that the contribution of sociality to differences in the size of the prey captured is two to three times greater than that of body size, suggesting that changes in group size and cooperative tendencies may be more effective than changes in body size at separating species in niche space.

trait overdispersion | limiting similarity | habitat filtering | *Anelosimus* | functional diversity

An important goal of community ecology is to understand the mechanisms involved in the assembly of species into local communities and the pattern of similarities or differences among them. A local community is typically a subset of a larger pool of species whose co-occurrence may be mediated by a set of physical and behavioral characteristics (1, 2). Recent theory and empirical work explain the assembly of species into local communities as an interactive process where abiotic and biotic processes act on both species ecological similarities and differences at various spatial and temporal scales (3–6). For instance, environmental filtering is a process by which abiotic factors prevent some species from establishing locally (3, 7, 8). At the same time, through the principle of limiting similarity, biotic processes may drive closely related species to differentiate in key phenotypic traits to reduce resource use overlap (3, 9, 10). Because morphology typically predicts a species' use of resources (11), morphological measurements have been typically used to test trait-based patterns of community assembly in plants and animals. How species may diverge (or converge) in traits other than the traditional morphological ones is, however, far less understood in the context of community assembly.

Traits that lead individuals to form groups and cooperate may be particularly important in influencing a species' use of resources. Group foraging, in particular, may alter body size–prey size relationships by allowing animals to access prey that are too large, too fast, or too dangerous to be captured by solitary individuals of similar characteristics (12–15). By allowing access to food resources virtually unattainable by solitary individuals, group foraging may thus effectively move a lineage into a niche potentially orders of magnitude away from that utilized by solitary close relatives. Social groups may also differ in microhabitat requirements relative to solitary species of similar body size (16).

Sociality thus has the potential to be an immediate and powerful way to create large differences in resource and habitat use among closely related species. Studies addressing how such social traits scale up to influence niche use among co-occurring species (15–18), and their potential role in community assembly, however, remain rare.

Spiders that live and forage in groups provide an ideal opportunity to explore the potential role of sociality in niche differentiation and community assembly. Several spider genera contain species with a range of social systems (19). In solitary and subsocial species, colonies contain a single mother and her offspring, but in the former offspring disperse soon after hatching, whereas in the latter offspring remain together for several instars before dispersing to initiate their own nests. In both cases, colonies contain at the most a few dozen individuals. In social species, in contrast, colonies contain multiple adult females and their offspring. As offspring tend to mature and reproduce within the natal nest, colonies may grow over multiple generations to contain hundreds, thousands, or tens of thousands of individuals. Finally, some species may exhibit intermediate characteristics between social and subsocial, as colonies generally exhibit less developed cooperative behaviors and may partially disperse every generation or do so at smaller sizes (19, 20). Communities of the spider genus *Anelosimus* throughout the Americas are particularly well suited to explore the relative roles of morphology and behavior in niche differentiation, as they contain representatives of

Significance

Ecological theory predicts that communities should contain species that exhibit little overlap in their use of resources, typically assuming differences in body size or morphology. Here we show that level of sociality—whether individuals live solitarily or in groups—can be a powerful dimension separating species in niche space. In 50+ communities of the spider genus *Anelosimus* across the Americas, we show that co-occurring species are more likely to differ in their level of sociality than expected by chance. We also show that differences in level of sociality lead to greater differences in resource use (size of the prey captured) than differences in body size, highlighting the importance of sociality in the assemblage of natural communities.

all these social systems while also exhibiting a range of body sizes (21–23) (*SI Appendix*, Table S1-1). Furthermore, the social species, all of which occur in the American continent, are for the most part independently derived (22), thus providing multiple phylogenetically independent data points for comparative analyses.

Our earlier studies suggest that both level of sociality (15, 16, 24) and body size (25) are associated with differential resource and microhabitat use among co-ocurring *Anelosimus* species. At a site in southern Brazil we found that the four co-occurring *Anelosimus* species, each representing a different level of sociality (15, 16), differed in the size of the prey they captured (15) and the substrate and microhabitat their nests occupied (16). These differences were associated with the size and age structure of their colonies (15, 16) and the extent of cooperation among colony members (24), all components of a species "level of sociality" (26). Extreme body size differences, on the other hand, characterize *Anelosimus* communities at lowland tropical rainforests where only social species occur (23, 25). These differences were also associated with differential resource and microhabitat use, with the smallest species being a canopy specialist (27), an intermediate species occurring exclusively in the forest interior, and the largest species occurring primarily at the forest edge (25). We further found that the intermediate species had its prey size niche included within that of the largest one but was more efficient capturing insects in its preferred size range (25).

Having shown that differences in sociality and/or body size are associated with differential resource and microhabitat use in these two spider communities, we now ask whether the distribution of the two traits across *Anelosimus* communities in the Americas is more overdispersed than expected by chance as would be predicted by the theory of limiting similarity (7, 9, 10). For this we assembled data on the composition of 53 communities across the Americas containing at least two *Anelosimus* species and compared the observed average dispersion of sociality and body size across the observed communities with that expected under the hypothesis that the communities would form irrespective of the value of the two traits. In doing so, we considered the effect of differentially weighting sociality and body size as factors in resource use separation, a correction rarely implemented in similar studies (28, 29). For the latter, we used our own published or unpublished data on the distribution of prey sizes captured by *Anelosimus* species of a range of body sizes and all levels of sociality.

For our null model, we applied an environmental filter limiting the distribution of the social systems to particular environments. This filter is based on the observation that not all *Anelosimus* social systems occur in all environments. Thus, only social *Anelosimus* occur in the lowland tropical rainforest, whereas higher elevations and latitudes and dry environments contain only subsocial and solitary species (23, 30). As reviewed in ref. 19, these patterns appear to reflect the effects of latitude and elevation on insect size distributions, precipitation intensity, and predation rate. Thus, social spiders are present where warm temperatures, high precipitation, and high productivity promote an abundance of large insects (23, 30–33), whereas subsocial and solitary species are excluded from areas of heavy rainfall and high predation (34, 35). Areas of intermediate characteristics harbor all social systems (15, 16, 23). This is thus a broad scale filter, with each of the filtered regions encompassing numerous communities and distributed across the continent (23).

Using the randomly assembled communities as the null model, we then considered whether the distribution of the two traits across the 53 observed communities was more overdispersed than expected by chance (as in refs. 36 and 37). Under the hypothesis that communities are assembled to reduce resource use overlap, we expect that co-occurring species with similar body sizes will differ in their social system or, conversely, species with similar social system will differ in body size. Communities could also differ along both dimensions, given that separation along one trait dimension may be exhausted as more species are added to a community.

Materials and Methods

Characterization of Local Communities and the Null Model. We gathered data from the literature and our own field observations on the occurrence of *Anelosimus* species across the Americas. After combining contiguous sites with identical species compositions to avoid pseudoreplication, we obtained a matrix of 53 sites (from 59 original sites) containing two or more co-occurring *Anelosimus* species (Fig. 1 and *SI Appendix*, Table S1-2), for a total of 23 species (*SI Appendix, Appendix S1*). We used the total body length of adult females to represent a species body size (*SI Appendix*, Table S1-1). We obtained a continuous measure of sociality, ranging from 0.0 (low sociality) to 1.0 (high sociality), by averaging with equal weight two components of the Avilés et al. (26) "sociality index"—the proportion of the life cycle spiders lived in groups and the proportion of nests in a population that contained multiple adult females. We had field estimates of the two components for more than half the species; for the others, we inferred a sociality index from their level of sociality reported in the literature (solitary, subsocial, intermediate, and social) and their phylogenetic position (*SI Appendix*, Table S1-1). We used the four discrete categories—solitary (index value 0.1), subsocial (0.3–0.6), intermediate (0.7–0.8), and social (0.9–1.0)—for the purposes of setting up the environmental filter for each of the communities.

To create our null communities we used as species pool the 23 species found across the 53 sites, plus two additional species, *Anelosimus analyticus* and *Anelosimus vierae* (*SI Appendix*, Table S1-1), which occur in singleton communities, but have geographic ranges contiguous to our focal communities and thus the opportunity to colonize them. We nonetheless ran the analyses with and without these additional species. Using these pools, we created 53 null communities, each mimicking one of the original communities in terms of the number of species they contained and accepting species based on restrictions imposed by the environmental filter—social only (6 species), solitary or subsocial only (16 species), from solitary to intermediate social (19 species), or any social (25 species) (*SI Appendix*, Table S1-2). Given such a filter, we filled each community by sampling with replacement from the section of the species pool corresponding to the social systems allowable in each habitat. Sampling was done with replacement under the assumption that existing species are mere instances of the combination of trait values (level of sociality and body size) that are possible in the genus, as represented by species in the American continent. This produced one replicate set of 53 random communities for which we calculated the average functional dispersion (FDis), as done in the original dataset (see *Trait Dispersion of Observed and Randomized Communities*). We then repeated the procedure 999 times to obtain a null distribution of the FDis test statistic.
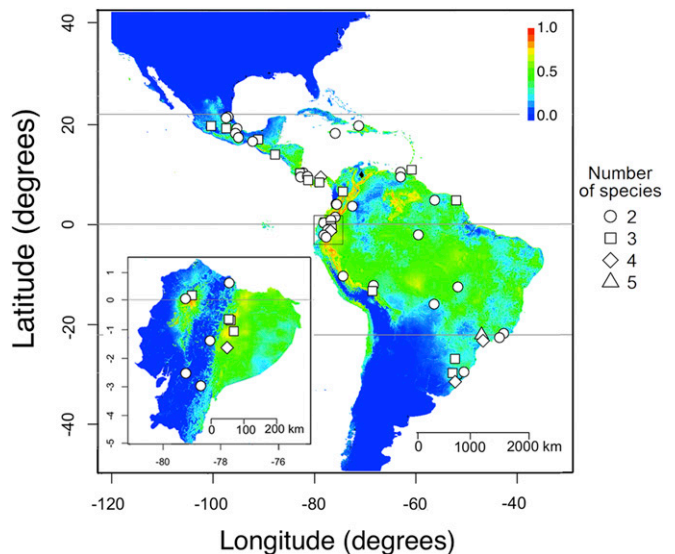
Fig. 1. Geographical location of the 53 communities included in the study and heat map (based on ref. 23) of the suitability of different regions across the Americas for *Anelosimus* species of different social systems. Blue regions are unsuitable for social species, whereas regions above 0.5 in the heat map scale (yellowish green to red) are unsuitable for solitary and subsocial species. Symbols mark locations of communities included in the analyses, all containing two or more recorded *Anelosimus* species. *Inset* represents sites in Ecuador.

Our choice of species pool follows the recommendations of Cornell and Harrison (38) of (*i*) including in the pool the same species used to derive local community richness, which these authors state is the "normal approach in null model analyses of local community structure"; (*ii*) restricting the pool to species that could potentially persist in a focal community, which we met by applying the environmental filter discussed above; and (*iii*) including species that could potentially disperse to a focal community. Regarding point *iii*, species in the genus *Anelosimus* appear to have strong dispersal abilities, as suggested by the worldwide distribution of the genus and the fact that species in some regions have their closest relatives in a different continent, rather than nearby (39). Furthermore, the habitats suitable for social and subsocial species have, or had in the past (40), a more or less continuous distribution, which would have facilitated colonization across the continent (23). This is reflected in several social and subsocial species in the Americas having distributions that span the entire region suitable for their social system (21, 23). Thus, some subsocial species (e.g., *Anelosimus studiosus* and *Anelosimus baeza*) occur from the southern United States or northern Mexico through to southern Brazil or northern Argentina. Likewise, several social species occur throughout the Amazon basin (*Anelosimus eximius*, *Anelosimus domingo*, and *Anelosimus rupununi*) and on both sides of the Andes (*A. eximius* and *A. domingo*) (21, 23). Finally, because the question of community composition should also allow for species arising de novo through speciation, it would have been possible to take an altogether different approach and consider all *Anelosimus* species across the globe as an example of the combinations of body size and level of sociality that can evolve in the genus. We did not take this approach, however, because the distribution of body sizes and social systems across the globe likely reflect the relative abundance of suitable and unsuitable habitat in different continents, which may not correspond to what is available in the Americas. Thus, limiting our pool to species in the Americas seemed the most appropriate approach both from an ecological and evolutionary perspective.

Contribution of Body Size and Sociality to Prey Size Divergence. We assessed the possibility that sociality and body size may contribute differentially to interspecific differences in resource use, thus requiring different weights in the trait dispersion analyses. For this, we used our own published and unpublished data on prey capture to characterize the prey size niches of *Anelosimus* species in communities in Brazil, Ecuador, and Panama (*SI Appendix*, Table S1-3). Our studies in Ecuador and Brazil documented the size distribution of insects captured by the natural range of colony sizes and age structures of all species in a community, which would have reflected the various species' levels of sociality and body size. In communities in Ecuador, colonies of all sizes and age structures are available year round. At Serra do Japi, Brazil, where species exhibit a seasonal phenology (15, 16), data were collected in early summer just before dispersal, which is the spiders' most active prey capture season. When data for more than one locality were available for a given species, we calculated simple averages across localities. The resulting dataset included nine species covering most of the body size range of *Anelosimus* species and all levels of sociality (*SI Appendix*, Table S1-3).

We analyzed the contribution of traits to prey capture patterns using phylogenetic generalized least squares (PGLS) regression to account for possible phylogenetic nonindependence of the data (41, 42). For this we used Agnarsson's (43) phylogenetic hypothesis for New World *Anelosimus*, which was developed using nuclear and mitochondrial gene markers (*SI Appendix*, Fig. S1-1). We included in our analyses the subset of species for which we had prey size data and used penalized likelihood rate smoothing to adjust branch lengths of the time-calibrated phylogeny. To allow comparison between the traits and control for their different ranges, we scaled them to have mean zero and unit variance before analyses. The sociality index was arcsine transformed before scaling; body size did not require a log transformation as the data were not skewed and the response was highly linear.

The slopes of the regressions of prey size on either level of sociality and body size indicate the rate at which the size of the prey captured increases per unit change in each of the traits. The ratio of these slopes can then be used to differentially weight the contribution of the two traits to prey size differentiation across species in our dispersion analyses (see below). For body size, we first obtained separate regressions for (*i*) solitary and subsocial species ($n = 4$) and for (*ii*) social species ($n = 3$), as these captured vastly different prey size ranges. We then ran both PGLS and linear model (LM) analyses, controlling for the two sociality categories (solitary/subsocial and social). This allowed us to obtain a single estimate of the slope, as the interaction between body size and the two sociality categories was not significant ($F_{1,3} = 4.41$, $P = 0.127$). Intermediate/social species were not included in the body size analyses as we had only two species in this category.

Trait Dispersion of Observed and Randomized Communities. To calculate the dispersion of the *n* species within a given community in the 2D trait space, we used the FDis method (36) with Gower dissimilarity coefficients (44, 45), as implemented in the FD R package (46). As noted in ref. 46, the FDis index has the advantage that "it can be computed from any distance or dissimilarity measure, it can handle any number and type of traits (including more traits than species), and it is not strongly influenced by outliers." Gower coefficients standardize variables before calculation and allow for mixed data types, as well as for differential weighting of the different variables. As before, we used arcsine-transformed sociality index values and untransformed body sizes. We made calculations considering both equal weighting of the two traits, as well as greater weighting of sociality, which we found to have a greater effect on resource use separation across species (see *Results*). Body size and sociality were also analyzed individually to assess the dispersion of each trait across our observed communities. We report the average FDis scores ($\pm$SE) across the 53 communities for the traits considered together and individually. Analyses did not consider species' relative abundances, since such information is unavailable for most species.

To obtain the expected trait dispersion under the null model, we estimated the trait dispersion of each set of 53 randomly assembled communities using the same relative weights for sociality and body size as above, extracted the mean across all sites, and repeated the procedure for the 999 replicate sets (using "sample" function in R software) (47). The observed mean trait dispersion was then compared with the distribution of trait dispersion values obtained under the null model. The *P* value was calculated as the proportion of iterations of the random null model that had an overall mean as extreme as, or more extreme than, the observed mean trait dispersion. A *P* value lower than 0.05 would suggest that co-occurring species have distributions of body size and sociality significantly more dispersed than expected by chance. This test was one tailed, since significant trait dispersion is expected to shift the observed dispersion above the random distribution mean. All analyses were conducted using the R software (47). The R code supporting this article has been uploaded as part of the supplementary material (Dataset S1).

Results

We found that the distribution of level of sociality and body size among co-occurring *Anelosimus* species in 53 communities across the Americas was more overdispersed than expected by chance. In areas where the environmental filter did not allow all social systems to be present, species tended to differ in body size, as in high latitude or high elevation communities where only solitary and subsocial *Anelosimus* occurred (e.g., Oaxaca, Mexico or Baños, Ecuador), or areas in the Amazonian rainforest with only social species (e.g., Jatun Sacha, Ecuador) (Fig. 2). In areas where all social systems were present, multiple species of similar body sizes occurred (e.g., Serra do Japi, Brazil; Fig. 2). Communities that differed in both body size and sociality tended to contain the largest number of species (average number of species in communities where both traits vs. only one of the traits differed: 2.85 vs. 2.24, $F_{1,51} = 12.6$, $P < 0.001$), possibly reflecting the ability for more species to be added to a community when the habitat filter allowed the presence of all social systems, and thus two dimensions along which differentiation could occur.

Contribution of Body Size and Sociality to Interspecific Prey Size Divergence. In addition to overdispersion in the two-trait parameter space, we also found that level of sociality was two to three times more important than body size in creating differences across species in the size of the prey captured. This was indicated by the slopes of the (PGLS) regressions of mean prey size on each of the traits (variables scaled, to be comparable): 2.78 ± 0.71 SE, for the effect of sociality ($t = 4.73$, $P = 0.006$, Fig. 3*A*) vs. 1.33 ± 0.36 SE, for the effect of body size on prey size divergence ($t = 3.75$, $P = 0.02$, Fig. 3*B*), the latter controlling for solitary/subsocial and social species in two categories (*SI Appendix*, Tables S1-4 and S1-5). These results indicate that level of sociality contributes more than twice as much as body size to the capture of larger prey across *Anelosimus* species: ratio of slopes = $2.78/1.33 = 2.08$, when solitary/subsocial and social species combined were considered; $2.78/0.82 = 3.40$, when only the solitary/subsocial species, which are less affected by differences in colony size and level of cooperation (15,
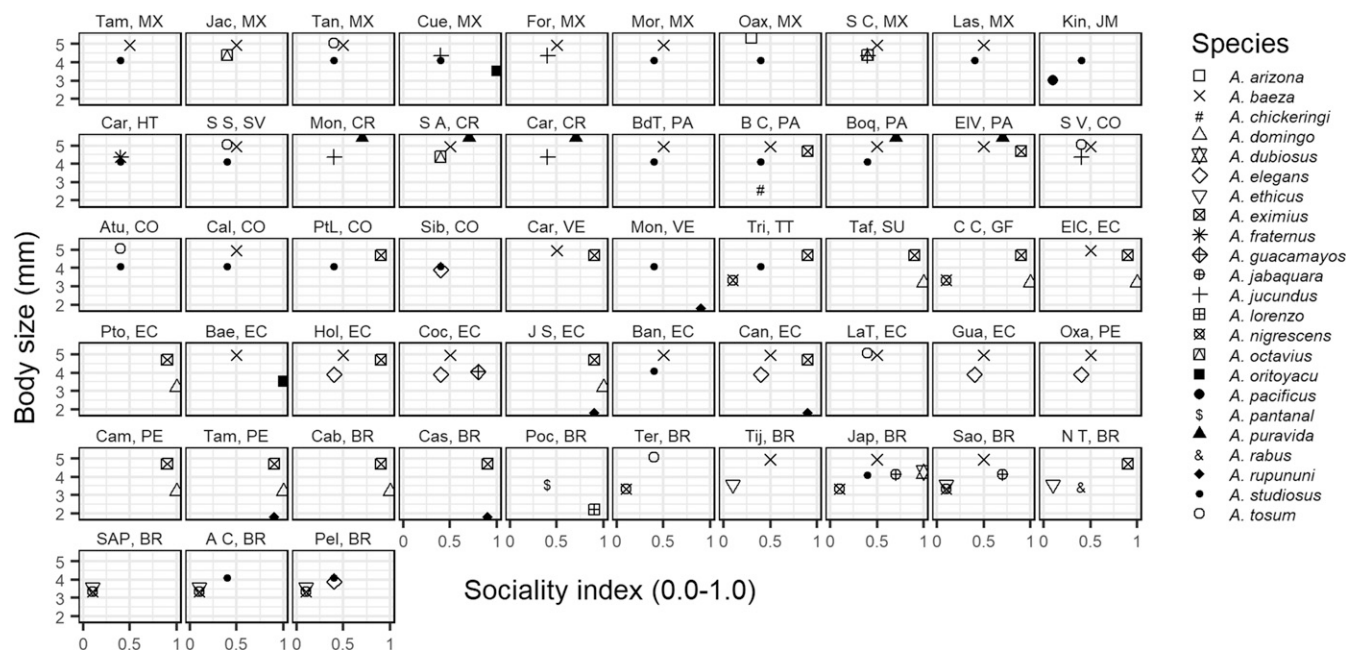
Fig. 2. Species composition in 53 sites across the Americas showing species according to their sociality index and body size. Sites are shown by country from north to south and west to east. Contiguous sites from the original dataset that had the same species composition were combined into one. For details on the localities, see *SI Appendix*, Table S1-2.

24), were considered (PGLS slope for solitary/subsocial species only: 0.82 ± 0.42; $t = 1.94$, $P = 0.19$) (Fig. 3).

Trait Dispersion in Null vs. Observed Communities. Estimated trait dispersion values across the 53 communities were significantly greater than expected by chance, whether sociality was assumed to be equally important or 3.4 times more important than body size in causing prey size divergence [$FD_{observed\ (obs)} = 0.132 \pm 0.070$ SD vs. $FD_{expected\ (exp)} = 0.113 \pm 0.008$ SD, $P = 0.013$, for the former, and $FD_{obs} = 0.127 \pm 0.083$ SD vs. $FD_{exp} = 0.103 \pm 0.009$ SD, $P = 0.005$, for the latter]. These findings demonstrate that *Anelosimus* communities across the 53 sites were more overdispersed than expected by chance in the 2D space of body size and level of sociality. When analyzing each trait individually, sociality was significantly more overdispersed than expected by chance ($FD_{obs} = 0.124 \pm 0.100$ SD vs. $FD_{exp} = 0.094 \pm 0.012$ SD, $P = 0.005$), whereas body size, for species of a given level of sociality, was not ($FD_{obs} = 0.142 \pm 0.076$ SD vs. $FD_{exp} = 0.135 \pm 0.012$ SD, $P = 0.29$). Excluding from the null model the two species that occurred only in single-species communities (*A. analyticus* and *A. vierae*) did not substantially change significance levels in any of the aforementioned analyses. We note that ours is a conservative test of the hypothesis of overdispersion as the power to detect nonrandomness in the makeup of local communities is expected to be low (high probability of type II error) when, as in our case, any given community consists of a small subset of species in the global pool (48).

Discussion and Conclusion

Co-occurring *Anelosimus* species across the Americas were more overdispersed than expected by chance in the 2D space of sociality and body size, with communities diverging in either one or both traits depending on the range of social systems present in individual communities as a function of the environmental filter. We further found that sociality had a greater contribution than body size to prey size divergence across *Anelosimus* species, pointing to a potentially greater role of this trait in structuring communities of social organisms.

That level of sociality may play a greater role separating species in trait space is not surprising, given that groups can vary in size much more broadly than individuals can. Thus, whereas adult *Anelosimus* females range from roughly 1.8–5.5 mm in length (*SI Appendix*, Table S1-1), colonies can range from one to tens of thousands of individuals, depending on the species (14, 15). Larger spider colonies have both more individuals available for prey capture (24) and larger webs (15). Our finding that the regression of mean prey size on spider body size had a slope close to 1.0 (Fig. 3B) is consistent with observations in both vertebrate and invertebrate systems that predator–prey size relationships tend to lie at or slightly under 1.0 (49–51). Dispersion as a function of individual size alone, therefore, appears limited in the degree of prey size separation it can create. Increasing group size, on the other hand, can create differences by orders of magnitude in the size of the prey captured (e.g., ref. 14). As a result, dispersion in our communities on the basis of level of sociality alone was just as significant as when we analyzed both traits combined, whereas for a given level of sociality, body size had a tendency to be more overdispersed than expected by chance, but not significantly so (*Results*).

Four mechanisms have been proposed to promote coexistence in ecological communities—resource partitioning, spatial and temporal heterogeneity, and natural enemies (6). Several studies within *Anelosimus* communities have found evidence linking body size or sociality to the first three mechanisms. The studies have also found that, in addition to differing in these two traits, species display a suite of behavioral and morphological traits suggestive of adaptation to particular niches within the communities. We have found, for instance, that the four most common *Anelosimus* species at Serra do Japi, Brazil, captured insects of increasing size not only as a function of the size of their webs (15), but also of the degree of cooperation among colony members (24). Differences in level of sociality in this community were also associated with differences in microhabitat use at multiple spatial scales (16). Thus, the two more social species had greater affinity for the forest interior where sturdier vegetation likely provides better support for their larger and longer-lived colonies, whereas the two least social species were more common on the herbaceous vegetation at the
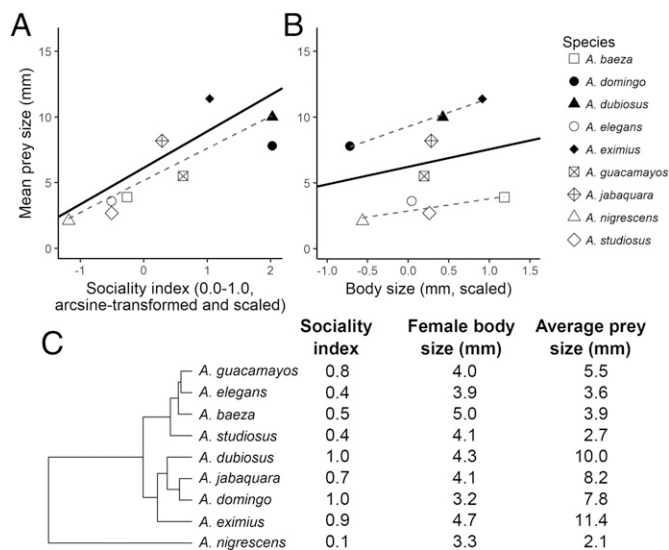
Fig. 3. Scatterplots of mean prey size (in millimeters) of *Anelosimus* species in relation to their (*A*) level of sociality and (*B*) body length, for solitary/subsocial (clear symbols, *n* = 4), intermediate/social (symbols with cross pattern, *n* = 2), and social (black symbols, *n* = 3) species. In *B*, the dashed lines correspond to the regressions for social (*Upper* line) and solitary/subsocial (*Lower* line) species considered separately; the solid line shows the common slope for these sociality categories combined (intermediate/social species not included, as there were only two species in this category). Solid lines are PGLS estimates and dotted lines are LM estimates. Slope values are as follows: (*A*) Solid line, 2.78 ± 0.71 SE; dotted line, 2.44 ± 0.62. (*B*) Solid line, 1.33 ± 0.36 SE; *Upper* dotted line, 2.16 ± 0.22 SE; *Lower* dotted line, 0.92 ± 0.47 SE. (*C*) Inferred phylogenetic relationships (based on ref. 46) of the species included in these analyses, which were the subset of species for which prey size estimates were available. For values of body size and level of sociality for the remaining species, see *SI Appendix*, Fig. S1-1 and Table S1-1 for a phylogeny including most of the additional species.

forest edge (16). Within microhabitats, species further differed in the position they occupied on the plant substrate, with those with larger and longer-lived nests (i.e., the more social species) occupying positions closer to the core of plants (16).

In the Amazonian lowland rainforest, where only social species occur, on the other hand, extreme body size differences are associated with differences in resource and microhabitat use. Here, an intermediate-sized species (*A. domingo*, 3.2 mm) occurs exclusively in the forest understory, whereas a large-sized one (*A. eximius*, 4.7 mm) occurs also at the forest edge (25). Both build webs with a basal sheet not suitable for prey capture, topped by a tangle of prey capture lines suspended from the vegetation above. The smallest of all *Anelosimus* species (*A. rupununi*, 1.8 mm in length), on the other hand, is a canopy specialist whose webs capture prey from all directions and appear better able to retain prey (27). We have further found that the intermediate species, which has its niche included within that of the larger one, is more efficient at capturing small prey by being generally faster, having greater density of individuals within the nests, and exhibiting greater participation of all age classes in prey capture activities (25). The three species, therefore, appear uniquely adapted to the niches they occupy, both in terms of the architecture of their webs and the behavior of the spiders.

In terms of temporal heterogeneity, we have found that species in the seasonal environment of Serra do Japi were offset in the peak of their reproductive seasons (16, 52), whereas in aseasonal tropical environments colonies of all age structures are present year round. Phenology appeared to be the main axis of differentiation in a community of 10 *Anelosimus* species in Madagascar where only subsocial species occur (18). Here, phenology was more overdispersed and evenly spaced than expected by chance, but neither body size nor a preference for close vs. open habitat was.

We are aware of only one other study, on sponge-dwelling shrimp (17), where the roles of both sociality and body size have been considered in the context of community assembly. There are some important differences, however. In the shrimp system there were only two social systems represented, solitary and eusocial, and body size and sociality played different roles in the assembly process, making it difficult to assess their relative importance. Body size was involved in habitat filtering, as solitary species assembled in communities based on their fit to the interstitial spaces of the sponges. Eusocial species, on the other hand, were involved in competitive exclusion, as only one of six eusocial species was present in any one community (17). Finally, in the shrimp system the habitat filter was inferred from the observed dispersion patterns, whereas in our case it was based on prior observations. Other studies have looked at the roles of body size or sociality separately, as in studies looking at the role of body size differences in ant assemblages (e.g., ref. 53) or dietary differences across predatory mammals of different social systems (54, 55).

Further studies are needed to assess the relative importance of the various coexistence mechanisms in structuring *Anelosimus* communities and more rigorously test their association with body size and sociality. A test of the habitat heterogeneity hypothesis, for instance, could involve manipulative experiments to test whether colonies of the various species have higher fitness in microhabitats to which they appear better adapted. No studies have yet directly tested for competition in *Anelosimus* communities, although competition for nest sites or resources among web building spiders has been experimentally demonstrated in some cases (56, 57). In the case of *Anelosimus*, we have observed that individuals dispersing from a common source tend to become established increasingly further away from the source as the season progresses, likely because nearby sites have already been occupied (58). There is also a pattern suggestive of competitive exclusion between the social *A. eximius* and *Anelosimus guacamayos*. In the close to 20 y since the discovery of *A. guacamayos* (31), we have never seen the two species occur in sympatry, even though they share an extensive boundary at the edge of their respective ranges in eastern Ecuador. The two species have almost identical nest architectures and similar body sizes, with *A. guacamayos* occurring at higher elevations than *A. eximius* (31).

The role of processes such as species sorting, character displacement (10), and sympatric speciation (59) in the assembly of *Anelosimus* communities also needs to be assessed. Species sorting occurs when multiple species colonize a region, but only those sufficiently different from one another become established. In such a case, we expect species to exhibit similar trait values across habitats of similar characteristics. With character displacement, on the other hand, species diverge once in sympatry, in which case we expect potential competitors to exhibit more extreme trait values when living together than in areas of no overlap. A third process, not often considered in studies of community assembly, is sympatric speciation leading to divergence in traits associated with resource use and reproductive isolation (59). Sympatric speciation appears a possiblity in at least two of our communities, which harbor sibling species pairs—*Anelosimus dubiosus* and *Anelosimus jabaquara*, in Serra do Japi, Brazil, and *A. guacamayos* and *Anelosimus elegans*, in Cocodrilos, Ecuador (*SI Appendix*, Fig. S1-1). In both cases, the species are almost identical in body size and morphology, but differ in level of sociality (21), with the more social species (*A. dubiosus* and *A. guacamayos*, respectively) having a much more limited geographical distribution, suggestive of a recent origin via sympatric speciation. That in both cases the species differ in level of sociality further suggests that sociality may be a faster and more effective way of separating species in niche space than differences in body size or morphology. Addressing this latter possibility, as well as the mechanism(s) by which the nonrandom composition of these communities may have come about, are promising directions for future research.

Despite the potential importance of behavioral traits in niche differentiation, there are remarkably few studies assessing the relative roles of behavior and morphology in community assembly. Behavioral traits, being more flexible and potentially more labile (60), may allow faster colonization of novel niches and greater flexibility in variable environments. Assessing the relative contributions of these two types of traits would thus enhance our ability to predict how animals will respond to novel habitats and rapid environmental change.

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