

MORPHOLOGICAL DISPERSION OF *RHYTIDOPONERA* ASSEMBLAGES: THE IMPORTANCE OF SPATIAL SCALE AND NULL MODEL

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Abstract. A series of spatially nested assemblages of *Rhytidoponera* operational taxonomic units (OTUs) (Formicidae: Hymenoptera) from Sturt National Park, New South Wales, Australia, were examined for patterns of dispersion in multivariate morphological space. Morphological overdispersion within an assemblage, relative to a null model, is hypothesized to be a result of the structuring influence of interspecific competition. We compared up to 45 observed assemblages, from across multiple spatial scales, to two null models. Meta-analysis of the null model analyses indicated a general trend to morphological overdispersion, particularly so at restricted scales. Larger scale assemblages were overdispersed relative to only one of the two null models, which we tentatively interpret as being indicative of different competition-driven mechanisms operating at different spatial scales. We also demonstrate that the observed assemblages represent a larger number of species groups than expected by chance, and that this pattern of phylogenetic overdispersion is closely related to the observed morphological patterns.

Key words: *assembly rules; competition; ecomorphology; Formicidae; morphological dispersion; Rhytidoponera; Sturt National Park, New South Wales, Australia.*

INTRODUCTION

It is a general principle of ecomorphology that there is a correspondence between the phenotype of an organism and its ecological niche (Ricklefs and Miles 1994). Therefore, observed patterns of morphological variation among sets of co-occurring species should reflect niche differentiation, with the proviso that certain morphological characters, or combinations thereof, will more directly reflect niche separation than others. Given this premise, we can hypothesize that interspecific competition in ecological communities will result in a trend toward overdispersion in morphological space (Moulton and Pimm 1987).

Wilson (1999) recognizes two mechanisms by which morphological overdispersion may arise. The first mechanism, morphological assortment (or ecological sorting), is an assembly process where the most probable species combinations are those with maximal morphological differentiation. The second mechanism, morphological displacement (or character displacement), is an evolutionary process involving the divergence of one or more morphological characters. While both morphological assortment and displacement are purported to arise from the phenomenon of interspecific competition, they operate at different spatiotemporal scales (Dayan and Simberloff 1994). Nevertheless, it is quite possible for both mechanisms to be simultaneously influencing morphological dispersion of an assemblage (Brown et al. 2000)

Morphological dispersion in ecological communities has been investigated in both unidimensional and multidimensional space, that is, using a single character or a suite of characters to determine the morphological differentiation of species. A simple, commonly reported, unidimensional example is the putative phenomenon of equal spacing of body size ratios of co-occurring animal species, first reported by Hutchinson (1959), and critically assessed by Wiens (1982). Although examples of effectively random dispersion of body sizes within communities are common, there are several well-supported, recent studies (e.g., Losos 1990, Jones 1997, Gotelli and Ellison 2002), which indicate that significant patterns of overdispersion can occur in certain circumstances.

Analyses of dispersion in multidimensional morphological space are less common, particularly so for terrestrial invertebrate communities. Overdispersion in multidimensional space has been reported to occur under particular circumstances for communities of insular birds (Moulton and Pimm 1987, Lockwood et al. 1993), aquatic beetles (Juliano and Lawton 1990), and bats (Stevens and Willig 1999). These same studies also reported communities that were not significantly overdispersed. Similarly, Ricklefs and Travis (1980) and Weiher et al. (1998) reported no significant dispersion in communities of scrub birds or wetland plants, respectively.

Whether or not one finds that a community is morphologically overdispersed is dependent not only on whether interspecific competition has had a structuring influence, but also upon how that community has been circumscribed. Colwell and Winkler (1984) show that the more taxonomically inclusive the definition of a

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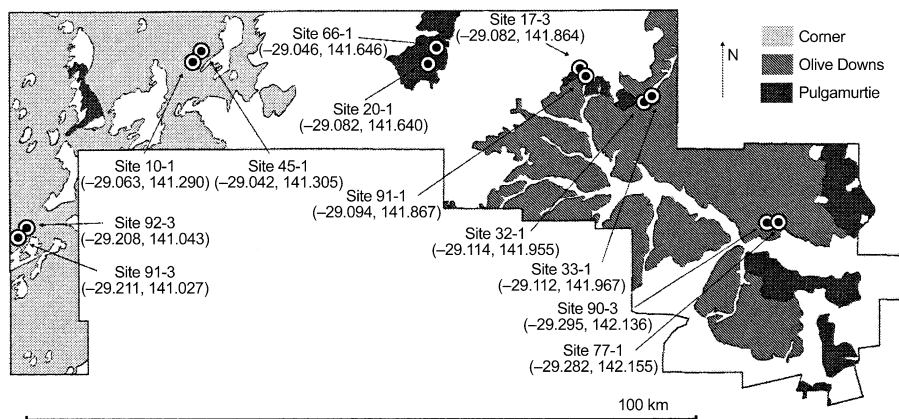


FIG. 1. Map of Sturt National Park, New South Wales, Australia, showing the location of sites and the extent of land systems sampled for this study. Sites are labeled with their geographic position in decimal degrees of latitude and longitude.

community, the less likely that the effects of competition will be detected. Similarly, Stevens and Willig (1999) reason that patterns of morphological overdispersion are only probable within, rather than across feeding guilds. Finally, we presume that interspecific competition will only occur at a spatial scale at which the component species of a community can be considered sympatric, that is, a scale at which the species of interest regularly interact.

Consequently, we here describe the analysis of morphological dispersion in a series of assemblages that are strictly constrained in terms of taxonomy, trophic structure, and spatial scale. These assemblages are based on a single genus of ant, *Rhytidoponera*, belonging to a single functional group (Andersen 1995). Also, these assemblages were constructed from spatially nested samples collected from Sturt National Park, allowing us to apply a variable spatial constraint to community membership.

Using this data, we asked the following questions: (1) Are any of the assemblages morphologically overdispersed? And, if so: (2) Under what circumstances (such as a particular spatial scale) does overdispersion occur? (3) What are the possible mechanisms contributing to overdispersion?

METHODS

The study site

Sturt National Park (NP) is a region of ~ 3500 km² located in northwestern New South Wales, Australia. The region has a warm, arid climate with an average annual rainfall of <250 mm. The eastern half of the park is an undulating landscape of exposed sedimentary bedrock, while the western half is an aeolean landscape of Neogene unconsolidated sediments. The entire land surface of the region has been classified into 23 “land systems” (Walker 1991), which are areas with a recurrent pattern of topography, soil, and vegetation (Christian 1958).

Ecological sampling

All the specimens examined for this paper were collected in 1997 as part of a separate study (Oliver et al. 1999, Oliver et al. 2004) from that described here. The previous study sampled a selection of land systems from Sturt NP using a spatially nested sampling regime for terrestrial invertebrates (Oliver et al. 2004). For the purposes of this paper, specimens of *Rhytidoponera* were examined from a subset of three of the land systems sampled by Oliver et al. (2004) (Fig. 1). The assemblages of the land systems were sampled from four sites, arranged in spatially proximate pairs (Fig. 1), while each site was divided into four plots, each with 16 pitfall traps. Each site sampled an area of 750×750 m, while each plot sampled an area of 250×250 m and was 250 m away from all neighboring plots. Each pitfall trap consisted of a 250 mL plastic container containing a solution of 70% ethanol and buried flush with the ground. Pitfall traps were left open for 10 d before collection. Specimens of *Rhytidoponera* recovered from the pitfalls were assigned to morphospecies (Oliver and Beattie 1996).

Of the 2725 workers of *Rhytidoponera* recovered from the pitfall traps, a subset of 446 specimens were carefully selected for the collection of morphometric data. For each of the 12 sites examined in this study, up to five specimens of each morphospecies collected from the site were randomly selected for measurement. From the four plots comprising a site, one plot was chosen as a “target plot” for additional sampling. For each target plot, up to five specimens of each morphospecies collected from the plot were randomly selected for measurement. From the 16 pitfalls comprising a target plot, one pitfall was chosen as a “target pitfall” for additional sampling. For each target pitfall, up to five specimens of each morphospecies collected from that pitfall were selected for measurement. In order to ensure assemblages of sufficient richness for meaningful analysis, target plots and target pitfalls were se-

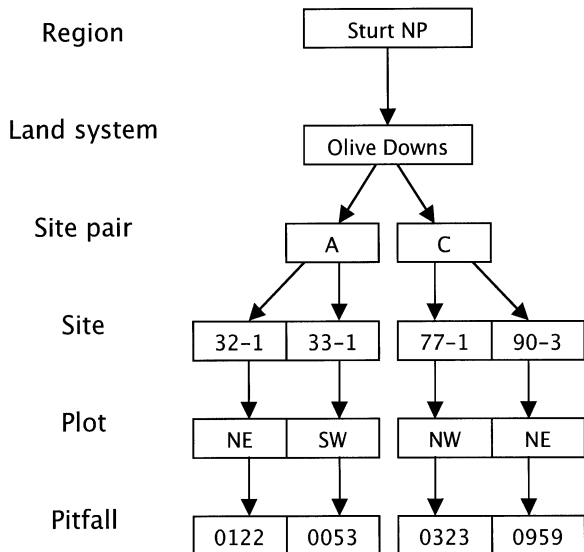


FIG. 2. Spatial hierarchy of *Rhytidoponera* assemblages investigated for morphological dispersion in this study. Only the nested arrangement for a single land system (out of three) is shown.

lected from among the richest available for each site and plot, respectively. In the case of site 92–3, with only one morphospecies occurring, no target plot or pitfall was chosen. By this means, a morphological sample of spatially nested assemblages of three land systems, six site pairs, twelve sites, eleven plots, and eleven pitfalls was investigated (Fig. 2).

Taxonomic verification

Of the 446 workers selected for measurement, a subset of 76 pinned specimens were verified by an experienced ant taxonomist (A. N. Andersen, *personal communication*). The taxonomic arrangement of specimens by A. N. Andersen was completed without reference to, or foreknowledge of, the morphometric data gathered for those specimens, nor the previous parataxonomic assignment of those specimens to morphospecies. Although none of the specimens could be confidently assigned to described species, we were able to ascertain that each of seven morphospecies could be considered an operational taxonomic unit (OTU; Appendix A). Moreover, these OTUs could be assigned to currently recognized species groups (Andersen 2000). A voucher series for the OTUs is held by the Tropical Ecosystems Research Centre, Commonwealth Scientific and Industrial Research Organization, Darwin, Northern Territory, Australia (in the care of A. N. Andersen).

Morphometrics

The specimens used in this study were measured for a set of nine numeric characters, based largely on the set used by Crozier et al. (1986) for their analysis of evolutionary patterns in *Rhytidoponera* (Appendix B).

All measurements were taken from digital images of the specimens using Carnoy software version 2.0 (Schols 2002). Digital images were acquired using a JVC KY-F70B digital video camera (JVC Australia, Kingsgrove, New South Wales, Australia) attached to an Olympus SZH10 dissecting microscope (Olympus Australia, Mount Waverley, Victoria, Australia). The digital camera was controlled with a Synoptics Prisms-PCI frame-grabber and Automontage software version 3.0 (Synoptics 1999).

Analysis

The procedure for the description of morphological patterns employed here largely follows that of Ricklefs and Travis (1980) and Moulton and Pimm (1987) where species are represented as centroids in a hyperdimensional morphospace, the axes of which are the common logarithms of the original morphometric measurements. A logarithmic transformation of morphometric data has many advantages (Thiele 1993, Ricklefs and Miles 1994) of which the most significant for this study is that distances in the morphospace correspond to factorial rather than additive differences, allowing for the statistical analysis of ratios.

The morphospace occupied by each assemblage was described by means of a principal component analysis (PCA) with principal components calculated from the covariance matrix rather than the correlation matrix (Ricklefs and Miles 1994). The PCA was recalculated for every assemblage and every species pool investigated in this study, using the mean values of each character for each OTU for each assemblage. From the PCA, a minimal spanning tree (MST) or Prim network was generated, which is the shortest possible network of lines connecting all points in the space (Prim 1957). An MST can be broken down into segments, which are the lines connecting adjacent points (in this case, species centroids) in the network (Fig. 3). The length of an MST segment connecting two species is equivalent to the Euclidean distance in morphospace between those two species. Both the PCA and the MST were calculated using PAST software version 1.09 (available online).²

We employ two indices to investigate the phenomenon of dispersion of *Rhytidoponera* assemblages in morphological space: variance in the length of the segments of the MST and total length of the MST. An unexpectedly low variance in segment length, relative to a null model, would correspond to an unexpectedly constant spacing of species in morphospace (Gotelli and Ellison 2002). However, segment length variance alone is an insufficient indicator of morphological dispersion. An overdispersed assemblage should not only be unexpectedly evenly distributed in morphospace, but also occupy an unexpectedly large area of morphospace. Hence, we adopted total length of the MST

² <http://folk.uio.no/ohammer/past>

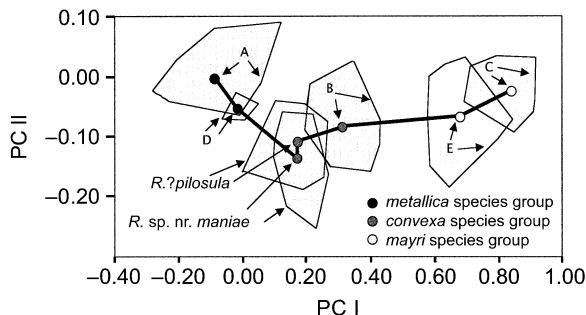


FIG. 3. Two-dimensional plot showing positions of the centroids and convex hulls of all OTUs of *Rhytidoponera* recorded from Sturt NP in a morphospace defined by the first and second principal components of nine log-transformed morphometric characters. The centroids are linked together by a minimal spanning tree (MST). The first principal component had an eigenvalue of 0.1074 and accounted for 90.86% of the total variance, while the second principal component had an eigenvalue of 0.0038 and accounted for 3.21% of the total variance. OTUs that are definitely not assigned to described species are given the letters A–E. *R. ?pilosula* is tentatively assigned to *Rhytidoponera pilosula*. “*R. sp. nr. maniae*” is considered similar to, but not conspecific with, *Rhytidoponera maniae*.

as an index of the size of the morphospace occupied by any particular assemblage.

We compared these two indices, as observed in the *Rhytidoponera* assemblages, to distributions generated from two distinct null models, herein referred to as the “random” model and the “pool” model. These two null models represented different hypotheses regarding the mechanism by which morphological overdispersion may have arisen in these assemblages. The random model assumes that all arrangements of morphometric centroids (representing species) within a morphospace are possible and equiprobable, with the single constraint that the length of the MST connecting these points is fixed for the entire null distribution and is equal to the MST length of the observed assemblage to which it is compared. In contrast, the pool model assumes that, given a pool of species that has already been constrained by biogeographic and habitat filters (Keddy 1992), all possible n -species combinations drawn from that pool are equiprobable. The random model, by allowing for any possible arrangement of points within a predefined morphospace, is modeling possibilities on an evolutionary timescale, whereas the pool model, by resampling the observed regional pool, is modeling possibilities on an ecological timescale.

It is important to note that, of the two indices of morphological dispersion investigated here, only variance in segment length was compared against both null models. Total length of the MST could not be compared to the random model, because the null distributions of that model are determined by the observed MST length.

To generate null distributions of the random model, a line equal in length to the observed MST for an assemblage is divided into $n - 1$ segments, where n

is the number of OTUs in the observed assemblage. The lengths of the individual segments are determined by randomly and equiprobably placing $n - 2$ points along the observed MST length. This procedure is repeated 1000 times to produce a null distribution of possible variances of segment length against which the observed variance is compared. When n was < 3 , no analysis was possible using this model as a single MST segment has no variance. We used the Size Overlap module of EcoSim software version 7.0 (Gotelli and Entsminger 2003) to generate this null distribution.

In the pool model, each observed assemblage was compared against all possible combinations of species of the same richness drawn from a species pool. The species pool consisted of all the operational taxonomic units recorded for a particular land system. Previous work in Sturt National Park (Oliver et al. 2004) had shown that there were strong differences in the ant faunas of the different land systems and we attribute these differences to variation in habitat requirements in the Sturt ant fauna. Consequently, in order to control for this variation, null distributions of the pool model were restricted to include only species thought to potentially co-occur. That is, those OTUs that co-occur at the land system scale. When the assemblage to be tested had the same number of OTUs as the pool, no analysis using this model was possible. Note that the null distribution for the pool model was not generated by using a computer algorithm to randomly draw species from a species pool, but rather by including the indices for all possible n -species combinations. This was done because the number of possible n -species combinations for the species pools was very limited (from four to 10) making the exhaustive compilation of the null distribution both feasible and essentially identical to that generated by a randomly assembling algorithm, while also ensuring that the null distributions contained no redundant data.

The OTUs of *Rhytidoponera* recorded from Sturt NP represent three species groups: *convexa*, *mayri*, and *metallica* (Andersen 2000). These informal taxa are presumed to represent monophyletic lineages (Crozier et al. 1986). Since there is little overlap in body size between these taxa, we surmized that an ecological assortment process might be in operation whereby assemblages with a highly equitable distribution of OTUs within species groups (Begon et al. 1990) would have a higher probability of occurring than assemblages with a low equitability. Such a process would lead to a pattern of phylogenetic overdispersion (Webb et al. 2002) in the observed assemblages. To test for this possibility, we compared the number of species groups present in an assemblage with a null distribution of the pool model as described previously.

All results produced by the null model analysis of the three indices (variance in MST segments, MST length, and number of species groups) were subjected to a meta-analysis closely following the methodology

TABLE 1. Meta-analysis of variance in MST segment length as an index of morphological dispersion in *Rhytidoponera* assemblages at varying scales, Sturt National Park, New South Wales, Australia.

Scale	Null model	Lower tail	Upper tail	Mean SES	SD of SES	<i>t</i>	<i>P</i>	Bonferroni <i>P</i>
Pitfall	random	3 (1)	0	-0.976	0.139	-12.187	0.007	0.07
	pool	3 (2)	0	-0.647	0.124	-9.010	0.012	0.12
Plot	random	9 (0)	0	-0.724	0.351	-6.197	0.000	0.001
	pool	6 (3)	1 (0)	-0.496	0.562	-2.333	0.058	0.58
Site	random	9 (1)	0	-0.666	0.400	-4.988	0.001	0.01
	pool	5 (5)	1 (0)	-0.450	0.939	-1.173	0.294	1.00
Site pair	random	4 (0)	1 (0)	-0.514	0.433	-2.655	0.057	0.57
	pool	2 (2)	1 (0)	-0.034	1.343	-0.044	0.969	1.00
Land system	random	2 (0)	1 (0)	-0.387	0.431	-1.557	0.260	1.00

Notes: The values in the columns "Lower tail" and "Upper tail" are the number of assemblages with an observed index respectively lower or higher than the mean index determined by the null model, while the number in parentheses indicates how many of these assemblages had significant patterns at 90% confidence limits ($P < 0.1$, one-tailed test). For each scale and null model, a one-sample *t* test was used to test the null hypothesis that the distribution of standard effect size (SES) values for that set of assemblages does not differ from zero.

of Gotelli and Ellison (2002). For each comparison of an observed index to a null distribution, a standard effect size (Gurevitch et al. 2001) was calculated. The standard effect size (SES) is the difference between the observed index and the average of the null distribution to which it is compared, standardized by the standard deviation of the null distribution (Gotelli and Ellison 2002). Sets of standard effect size values split by index, null model, and scale, were analyzed with a one-sample *t* test to determine whether the distribution of SES values differed from zero. Significant deviation of the SES distribution from zero would indicate that the set of assemblages as a whole showed a significantly consistent trend toward unexpectedly high or unexpectedly low index values. Meta-analyses were conducted within, rather than across, scales because the observed indices for assemblages spatially nested within larger assemblages were unlikely to be statistically independent of the observed indices of those larger assemblages. Consequently, we used multiple simple analyses rather than a single, multifactorial, and global test.

RESULTS

Principal component analysis

A PCA of all the specimens measured from Sturt NP, showed that a very large proportion (94%) of the total variance was explained by the first and second principal components. Moreover, different species groups occupied different sections of the first principal component (Fig. 3). We therefore interpret the first principal component as representing variation in body size, as is often the case in morphometric PCA analysis (Wiley 1981). Further details of the PCA of the entire Sturt assemblage are included in Appendix C.

Null model analysis

Variance in MST segment length of the entire Sturt assemblage of seven *Rhytidoponera* OTUs was found

to be 0.0147. When this index was compared to a null distribution generated by the random model, 211 of the 1000 iterations of the model were found to be lower than the observed index ($P = 0.211$), giving a standard effect size of -0.720 . The results for all other assemblages are summarized in the meta-analysis results.

Meta-analysis

The meta-analysis of variance in MST segment length as an index of morphological dispersion in the *Rhytidoponera* assemblages showed considerable variation in mean SES across scales and null models (Table 1). For most scales, there was a consistent trend toward observed indices being less than the mean index of the null model. For the random null model, this trend was significant (at 90% confidence limits, and after Bonferroni correction) for assemblages at the site scale and below. For the pool null model, the trend was not significant, after Bonferroni correction, at any scale. Additionally, for any particular scale, observed variance in MST segment length appears to be strongly dependent on the richness of that particular assemblage (Fig. 4).

The meta-analysis of total MST length as an index of morphospace size showed a general trend toward observed values being higher than the mean index of the pool null model. However, this trend was only significant at the site-pair scale (Table 2).

Following Moulton and Pimm (1987) and Dussert et al. (1987), we also investigated the relationship between the two indices describing the morphological space (MST length and variance in MST segment length) for both observed and simulated assemblages (using the pool model) for the site scale (Fig. 5). In general, when variance is converted to standard deviation values, there is a weakly positive linear relationship between the variables, with observed assemblages having among the largest MST lengths and the smallest

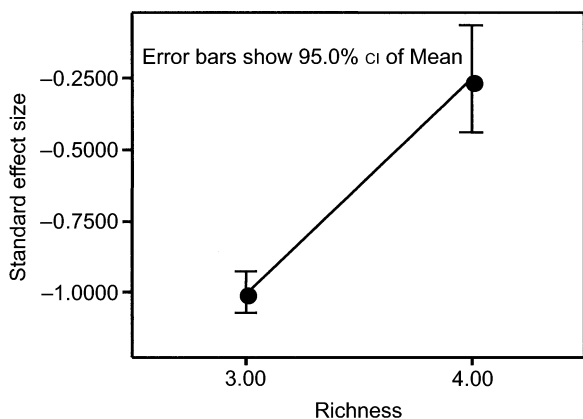


FIG. 4. Trend in morphological dispersion with richness for assemblages at the site scale, Sturt National Park, Australia. Morphological dispersion is expressed as the standard effect size (SES) of variance in MST segment length when compared to a null model of randomized segment lengths within a fixed total MST length.

standard deviations. Because of the mathematical tendency of MST length to covary with the number of nodes in the network (Dussert et al. 1987), analysis was restricted to assemblages with a common richness of three OTUs. Other combinations of scale and richness were not investigated because of a lack of data points.

The meta-analysis of the observed number of species groups as an index of phylogenetic dispersion showed patterns significantly different from expectation for scales at the site level and below (Table 3). Moreover, every assemblage at every scale had more species groups represented than the mean of all possible *n*-species combinations from an appropriate species pool.

DISCUSSION

Observed indices of morphological dispersion frequently deviated significantly from the null models. Moreover, there was a highly consistent trend toward morphological overdispersion in assemblages spatially nested within the land system pools. This trend often

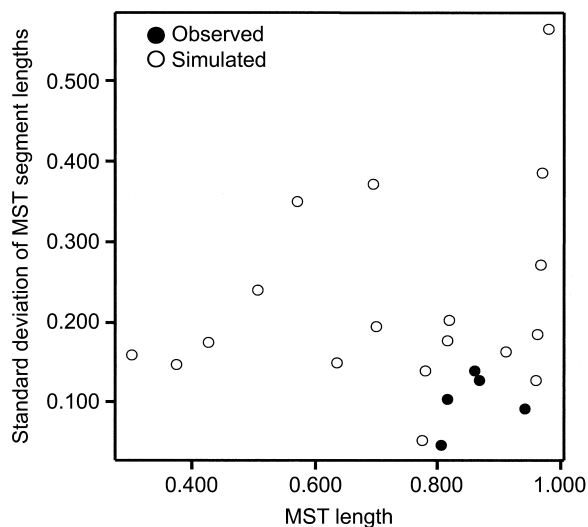


FIG. 5. Scatterplot of MST length and variance in segment length of observed three-species site-scale assemblages of *Rhytidoponera*, Sturt National Park, Australia, and the simulated assemblages to which they were compared for null model analysis. The simulated assemblages were constructed from all possible combinations of three species from the three land system pools. Pearson correlation between the two variables is 0.122 ($P = 0.578$, two-tailed).

proved statistically significant when meta-analyses were conducted.

The meta-analysis of MST segment variance reveals a pattern of increasing effect size with decreasing scale (Table 1). This pattern could be interpreted as the result of more intense competition at restricted scales, resulting in increasingly stronger ecological assortment and/or character displacement. Moreover, such an observation would not be unexpected given that whatever mechanism produces the observed pattern of morphological overdispersion, it would itself operate within a certain range of scale (Levin 1992). Interestingly, the meta-analysis of total length of the MST had an inconsistent relationship to scale (Table 2). Although MST length was generally larger than that predicted

TABLE 2. Meta-analysis of MST length as an index of morphospace size of *Rhytidoponera* assemblages at varying scales, Sturt National Park, Australia.

Scale	Lower tail	Upper tail	Mean SES	SD of SES	<i>t</i>	<i>P</i>	Bonferroni <i>P</i>
Pitfall	3 (0)	8 (4)	0.439	0.752	1.939	0.081	0.41
Plot	1 (0)	8 (4)	0.571	0.646	2.652	0.029	0.15
Site	2 (0)	6 (2)	0.564	0.653	2.443	0.045	0.23
Site pair	0	4 (1)	0.804	0.323	4.979	0.016	0.08

Notes: The MST length for each assemblage was compared to mean expectation, based on exhaustive sampling of the appropriate species pool. The values in the columns “Lower tail” and “Upper tail” are the number of assemblages with an observed index respectively lower or higher than the mean index determined by the null model, while the number in parentheses indicates how many of these assemblages had significant patterns at 90% confidence limits ($P < 0.1$, one-tailed test). For each scale, a one-sample *t* test was used to test the null hypothesis that the distribution of standard effect size (SES) values for that set of assemblages does not differ from zero.

TABLE 3. Meta-analysis of phylogenetic dispersion of *Rhytidoponera* assemblages at varying scales, Sturt National Park, Australia.

Scale	Lower tail	Upper tail	Mean SES	SD of SES	<i>t</i>	<i>P</i>	Bonferroni <i>P</i>
Pitfall	0	11	0.557	0.201	9.203	0.000	0.001
Plot	0	9	0.870	0.280	9.332	0.000	0.001
Site	0	8	0.781	0.306	7.214	0.000	0.001
Site pair	0	4	0.721	0.360	4.005	0.028	0.14

Notes: The number of species groups present in each assemblage was compared to mean expectation, based on exhaustive sampling of the appropriate species pool, and a standard effect size (SES) was calculated. The values in the columns “Lower tail” and “Upper tail” are the number of assemblages with an observed index respectively lower or higher than the mean index determined by the null model. A one-sample *t* test was applied at each scale for the null hypothesis that the distribution of SES values does not differ from zero.

by the null model (Fig. 5), the mean effect size for each scale was weak, with the exception of the site-pair scale.

It would appear that morphological dispersion is also influenced by the richness of the observed assemblage (Fig. 4), where four-species assemblages are consistently less evenly dispersed than three-species assemblages. Since the prevalence of four-species assemblages relative to three-species assemblages increases with spatial scale, this relationship alone may be sufficient explanation for an increase in morphological dispersion with decreasing scale. We recognize that by selecting the richest assemblages at each scale for our analyses, we have probably biased our meta-analyses. However, given that four-species assemblages were preferentially chosen over three-species assemblages, this bias would appear to have increased the likelihood of accepting, rather than rejecting, the null hypothesis.

The two null models chosen for this study produced often highly conflicting results for the one index (variance in MST segment length) to which they were both applied (Table 1). The pool model generally produced null distributions more similar to the observed index than the random model. A likely explanation for these results is that the models have quite different underlying assumptions about the mechanism and temporal scale of morphological dispersion. We hypothesize that overdispersion relative to the random model would indicate coevolutionary morphological displacement of the species of an assemblage, while overdispersion relative to the pool model would indicate morphological assortment.

However, there are other possible explanations for different results for different null models. The overall pattern of weaker effect sizes for observed assemblages compared to the pool model may be attributable to the restricted number of possible cases in the null distribution and thus, to the statistical power of the test. Null distributions for the pool model ranged in size from four to 35 cases, depending upon the particular species pool, and the number of species to be drawn from it. Additionally, the species pools themselves are trending toward overdispersion (Table 1). Therefore, though the

smaller scale assemblages were generally overdispersed when compared to the appropriate species pool (Fig. 5), the effect size would be weak when that pool itself tends to be overdispersed—the “Narcissus Effect” of Colwell and Winkler (1984).

The strongest pattern we observed in this set of assemblages was the unusually high number of species groups represented when compared to what could be expected from all possible *n*-species combinations from a pool (Table 3). One very important point we need to make is that the results of the meta-analyses in Table 3 only make sense in isolation from each other. Clearly, the species composition of any one of these assemblages is highly contingent on the composition of the larger scale assemblages in which it is nested. The mean effect sizes reported here rely on the assumption that, for any scale, all possible *n*-species combinations from an appropriate pool should be used to form simulated assemblages for that scale, rather than a pool formed from the larger scale assemblages within which the observed assemblages are nested. If one were to reject this line of reasoning and insist that the null distribution must be drawn from the larger assemblage in which the test assemblage is nested, the number of observed assemblages that could be tested is much smaller, resulting in loss of statistical power.

Regardless of this issue, all assemblages at all scales had the maximum possible number of species groups for a given number of OTUs. It would appear that there is an assembly rule in effect, which seeks to maximize the equitability of the distribution of OTUs in species groups. This would make sense if species groups in *Rhytidoponera* correspond to functional types or guilds.

The patterns in phylogenetic dispersion and morphological dispersion described here are clearly not independent of one another. The first principal component of the morphospace tended to discriminate between species groups while the second principal component tended to separate OTUs within species groups (Fig. 3). Sampled three-species assemblages, with a single representative in each species group (Shannon equitability index [*J*] of 1000), are consistently more

evenly dispersed in morphospace than assemblages with four species (Fig. 4) while also effectively occupying a large proportion of the potential morphospace (Fig. 3). Four-species assemblages must accommodate two species in a single species group (Shannon equitability index [J] of 0.946) without any increase in the range of body size, resulting in much less evenly dispersed assemblages.

The Sturt assemblage of *Rhytidoponera* as a whole, is unusually, but not significantly, evenly dispersed, relative to the random null model, and has a highly equitable distribution of OTUs within species groups (Shannon equitability index [J] of 0.982). The land system assemblages, taken as a group, are also weakly overdispersed (Table 1), and have Shannon equitability indices (J) ranging from 0.946 (four OTUs in three species groups) to 0.961 (five OTUs in three species groups). There appears, therefore, to be some structuring of the species pools, which may be attributable to the influence of interspecific competition (Brown et al. 2000). We find it difficult, however, to attribute these patterns to a mechanism of ecological assortment, especially given the assumption that the land systems function as habitat filters. Dayan and Simberloff (1994) suggest such patterns may result from a large-scale coevolutionary response, while Brown et al. (2000) describe how local interactions may contribute to the structuring of a regional pool. Given available evidence, we tentatively conclude that the patterns observed in the species pools are due to diffuse character displacement rather than ecological assortment. For assemblages at the site scale and below, we are more confident that the prevailing mechanism is ecological assortment. Despite an apparent Narcissus effect (Colwell and Winkler 1984), observed assemblages were consistently among the most overdispersed of all possible combinations of the pool model (Fig. 5).

Referring to our original research questions, it would appear that there is a consistent trend toward morphological overdispersion in *Rhytidoponera* assemblages in Sturt National Park. The pattern of overdispersion is strongest in assemblages with the following features: (1) at spatial scales below that of the land system, (2) with a single OTU in each species group, and (3) when compared to the null model assuming any possible arrangement of species within a predefined morphospace.

We also tentatively conclude that both morphological assortment and displacement, operating at different spatiotemporal scales, have contributed to the patterns reported here. We have no data with which to make an educated guess about the generality of either the pattern or the mechanisms by which it may have arisen. A more detailed understanding of the phylogeny, diversity, and evolution of *Rhytidoponera*, along with the systematic sampling of *Rhytidoponera* assemblages across the Australian continent, would certainly go a long way toward resolving these issues.

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APPENDIX A

Images of the operational taxonomic units of *Rhytidoponera*, and accompanying notes regarding their presumed species status, are available in ESA's Electronic Data Archive: *Ecological Archives* E085-086-A1.

APPENDIX B

Descriptions and images of the morphometric characters used, and accompanying notes on their possible ecological relevance, are available in ESA's Electronic Data Archive: *Ecological Archives* E085-086-A2.

APPENDIX C

The results of principal components analysis of the entire Sturt assemblage of *Rhytidoponera* OTUs are available in ESA's Electronic Data Archive: *Ecological Archives* E085-086-A3.

APPENDIX D

Morphometric data for each operational taxonomic unit for each assemblage tested in this study are available in ESA's Electronic Data Archive: *Ecological Archives* E085-086-A4.