

META-
ANALYSIS



Does size matter for dispersal distance?

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ABSTRACT

Aim The aim of this study is to answer the questions: (1) do small organisms disperse farther than large, or vice versa; and (2) does the observed pattern differ for passive and active dispersers? These questions are central to several themes in biogeography (including microbial biogeography), macroecology, metacommunity ecology and conservation biology.

Location The meta-analysis was conducted using published data collected worldwide.

Methods We collected and analysed 795 data values in the peer-reviewed literature for direct observations of both maximal dispersal distance and mass of the dispersing organisms (e.g. seeds, not trees). Analysed taxa ranged in size from bacteria to whales. We applied macroecology analyses based on null models (using Monte Carlo randomizations) to test patterns relative to specific hypotheses.

Results Collected dispersal distance and mass data spanned 9 and 21 orders of magnitude, respectively. Active dispersers dispersed significantly farther ($P < 0.001$) and were significantly greater in mass ($P < 0.001$) than passive dispersers. Overall, size matters: larger active dispersers attained greater maximum observed dispersal distances than smaller active dispersers. In contrast, passive-disperser distances were random with respect to propagule mass, but not uniformly random, in part due to sparse data available for tiny propagules.

Conclusions Size is important to maximal dispersal distance for active dispersers, but not for passive dispersers. Claims that microbes disperse widely cannot be tested by current data based on direct observations of dispersal: indirect approaches will need to be applied. Distance–mass relationships should contribute to a resolution of neutral and niche-based metacommunity theories by helping scale expectations for dispersal limitation. Also, distance–mass relationships should inform analyses of latitudinal species richness and conservation biology topics such as fragmentation, umbrella species and taxonomic homogenization.

Keywords

Active dispersal, allometry, fragmentation, latitudinal species richness, mass, meta-community, microbial biogeography, neutral theory, passive dispersal.

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INTRODUCTION

Is dispersal distance a general function of size? Recent discussions on microbial biogeography centre around the idea that dispersal is allometric (e.g. Finlay, 2002; Martiny *et al.*, 2006). On the one hand are claims that ‘there is no biogeography for anything smaller than 1 millimeter’ (Finlay, 2002), and that for tiny organisms

‘dispersal is rarely (if ever) restricted by geographical barriers’ (Whitfield, 2005). This position is descended from a long-standing maxim of microbiology (de Wit & Bouvier, 2006) and supported by detailed analyses of diversity in selected sites (e.g. Finlay & Fenchel, 2004) and some molecular evidence collected among sites (e.g. Roberts & Cohan, 1995). On the other hand, studies using molecular techniques (e.g. Whitaker *et al.*, 2003; Green *et al.*,

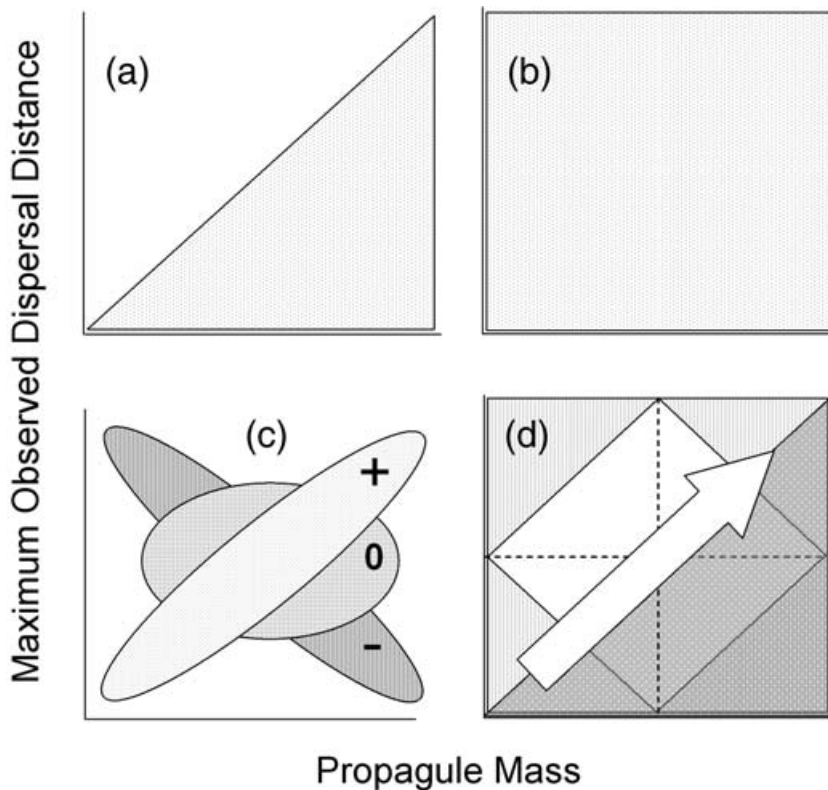


Figure 1 Hypothetical size–dispersal distributions for (a) active and (b) passive dispersers, and (c) three alternative hypotheses for both dispersal modes. Plot (d) depicts statistical tests described in the Methods and that collectively test the five hypotheses in plots (a)–(c) (see also Table 1). Plots (a) and (b) are based on Martiny *et al.* (2006).

2004; Horner-Devine *et al.*, 2004; Vos & Velicer, 2006) and novel analyses of morphotypes (e.g. Telford *et al.*, 2006) have revealed spatial structure in microbial diversity at multiple spatial scales. It appears that microbial biogeography may adopt some of what has been learned from studies of macroscopic organisms: biogeography is a complex tapestry woven from geological history, evolution and ecology (Lomolino *et al.*, 2005).

Discussions of the allometry of microbial dispersal join a longstanding and active inquiry of allometry for macroscopic organisms (e.g. Peters, 1986; West *et al.*, 1997; Woodward *et al.*, 2005). Though allometry is well-known for other traits (e.g. metabolic rate, etc.), allometry of dispersal distance has only recently been analysed for birds and mammals (Sutherland *et al.*, 2000; Bowman *et al.*, 2002). Martiny *et al.* (2006) considered lifetime dispersal capability related to mass attained at an organism's largest life stage for all organisms. Given these definitions, Martiny *et al.* hypothesized relationships for active and passive dispersers (Fig. 1a,b) and noted that neither pattern is well described by a general allometric equation. We anticipated that a meta-analysis of diverse taxa may be of service and relevant to diverse topics. We focus here on three sets of concepts: niche and neutral theories of macroecology, species richness gradients, and conservation biology.

Dispersal is an important component of neutral theory in macroecology (Hubbell, 2001) and is increasingly recognized to act in conjunction with local factors in determining community structure because it *may* be limiting, even for organisms once expected to be cosmopolitan (Bohonak & Jenkins, 2003). If passive dispersal is random and active dispersal is triangular

(Martiny *et al.*, 2006; Fig. 1a,b), then dispersal mode may help resolve the contrast (or continuum; Gravel *et al.*, 2006) between neutral and niche theories of macroecology (Holyoak *et al.*, 2006) and identify the relevant spatial scales.

Analyses of species richness gradients profit from explicit accounting for spatial scale (Rahbek, 2005) and organismal dispersal distance should be a determinant of the relevant spatial scale for analyses. If dispersal distance depends on body mass, then species richness gradients may be more clearly understood by accounting for body mass and/or dispersal. Hillebrand (2004) did just that in his comprehensive meta-analysis of latitudinal gradients of species richness and found that the general decrease in species richness with increasing latitude was steeper and clearer for organisms of greater body mass. Hillebrand concluded that dispersal type and body mass were 'clearly interlinked' and offered two hypotheses for the effect of body mass. First, smaller organisms may passively disperse at greater rates than larger, active dispersers (related to the hypothesis of Finlay, 2002). Hillebrand found mixed support for this hypothesis in his analyses. Secondly, latitudinal gradients in species richness may differ for ectotherms and homeotherms but covary with body mass. Thus, body mass affected latitudinal species richness gradients, and was in turn affected by dispersal or thermodynamics, or both. It would appear that a broad examination of dispersal–mass relationships may also serve analyses of species richness gradients.

Much of conservation biology is spatially based: topics such as habitat fragmentation (Fahrig & Merriam, 1994), the value of umbrella species concepts to designate protected areas (Simberloff, 1998) and biotic homogenization (Olden & Rooney, 2006)

all invoke distance and/or area as key components. If dispersal distance is a function of size, then some spatially-based conservation biology topics may be advanced by predictive models. For example, unknown dispersal distances for a rare or endangered species may be vital to effective habitat and corridor conservation: if such distances could be reliably estimated, conservation planning may be more efficacious. However, if size does not matter, then clear and effective conservation approaches may not transcend case-by-case efforts.

Definitions

Martiny *et al.* (2006) hypothesized the relationships between lifetime dispersal capacity and mass attained at an organism's largest life stage for active and passive dispersers (Fig. 1a,b, respectively). However, we viewed some details in their hypotheses differently, which substantially altered expected outcomes. Below, we explain these differences regarding dispersal, mass, and active and passive dispersal. The hypotheses and statistical analyses are graphical in essence, so we also attempt to explain them in graphical terms.

Dispersal

The analysis of lifetime dispersal capacity must await the availability of dispersal data recorded throughout the lifetime of multiple species of diverse sizes. Therefore, we used maximum observed dispersal distance as a practical, empirical proxy that reflects the state of the science, and with the expectation that maximum observed values are conservative estimates of lifetime capacity. Other measures (e.g. range size; Ottaviani *et al.*, 2006) may yield different results but the hypotheses of Finlay (2002) and Martiny *et al.* (2006) are best addressed with maxima. Also, distance measures yield a more direct test for size-based patterns among diverse taxa than an attempt to compare biogeographical distributions that result from multiple geological, historical and biological processes (Lomolino *et al.*, 2005). In most cases, spatial extent has been found to be positively related to mass (e.g. Reed, 2003), though not always (e.g. Murray & Hose, 2005). Disparities reflect differences among taxa as well as analyses that may account for life-history covariates (e.g. abundance, egg size; Murray & Hose, 2005) or phylogeny (e.g. Diniz-Filho & Torres, 2002; Ottaviani *et al.*, 2006). Though phylogenetic constraints have been found to be important for range–body size comparisons of some taxa (Diniz-Filho & Torres, 2002), we did not employ them because the hypotheses of Finlay (2002) and Martiny *et al.* (2006) were strictly based on size (i.e. phylogenetic differences were not considered).

Mass

Is mass of the dispersing organism (e.g. a seed) or mass attained at an organism's largest life stage (e.g. a tree) most appropriate for allometric analyses of dispersal distance? Here we departed from Martiny *et al.* (2006) and used mass of the dispersing organism (and hereafter we use 'propagule' to refer to a dispersing organism, regardless of its dispersal mode or metabolic state).

We used propagule mass for the following two reasons: (1) Many actively dispersing organisms (e.g. winged insects, birds, amphibians, reptiles, mammals, fish) travel farthest as adults and so the dispersing propagule is the largest life stage. Thus, our use of propagule mass is consistent with Martiny *et al.* (2006) for many active dispersers and maintains logical consistency in comparisons among taxa. (2) Many passive dispersers travel farther as smaller juveniles than as larger adults (e.g. most molluscs, corals, some reef fish, some stream insects, terrestrial plants). Thus maximum dispersal distance is driven by the smaller propagule and not the larger adult.

Active and passive dispersal

We defined active dispersal as occurring under self-propulsion, whereas passive dispersal requires no propulsion on the part of the propagule. Martiny *et al.* (2006) invoked trees, giant clams and corals as examples to justify the hypothesized wide range in dispersal distances for large active dispersers, and thus a triangular shape for the distance–mass distribution (Fig. 1a). Instead, we categorized such taxa as passive dispersers, given that the maximal dispersal distance for seeds and planktonic larvae is primarily a function of winds and water currents, respectively. Thus, our analyses of dispersal–mass distributions shifted expectations relative to those of Martiny *et al.* (2006), and we did not test their hypotheses as they stated them. Instead, we developed and tested alternative hypotheses (Fig. 1c) and the hypothesized size–distance distributions of Martiny *et al.* (2006; Fig. 1a,b) but with our definitions of distance, mass and dispersal categories as described below.

Caveats

This effort focused on the generality of distance–mass relationships for passive and active dispersers (Martiny *et al.* 2006; Fig. 1). We refrain here from comparing taxonomic groups for distance–mass relationships, which would require additional analyses (e.g. Warton *et al.*, 2006) beyond available space limits. As for any meta-analysis, we analysed what we found in the peer-reviewed literature; data we did not find or that are yet to be published may alter the results and conclusions.

Hypotheses

Active dispersers

A power curve with positive slope (Fig. 1c, +) should describe the distance–mass pattern, because range–mass trends are positively sloped (McNab, 1963; Peters, 1986), and range and dispersal distance can be correlated (e.g. Bowman *et al.*, 2002; Bowman, 2003). Alternatively, the distance–mass distribution may conform to a lower-right triangle (Fig. 1a; Martiny *et al.*, 2006), though we defined some taxa (e.g. trees, giant clams and corals) as passive dispersers, which should narrow the expected range of values for larger body mass. Finally, the null hypothesis is that patterns are not significantly different from random (Fig. 1c, 0).

Passive dispersers

The distance–mass pattern should be random but not fully fill the uniform distribution (Fig. 1c, 0) because passive dispersal data are either relatively rare for extremely low or large mass, or else data are numerous but centrally tending. Alternatively, the distance–mass pattern should not significantly differ from a random uniform distribution in the data space (Martiny *et al.*, 2006; Fig. 1b). Two other alternative hypotheses would be consistent with the expectation that small organisms are cosmopolitan dispersers (Finlay, 2002) while larger organisms are not: a negatively sloped regression; Fig. 1c, –) or a lower-left triangle. A lower-left triangle would require abundant data on microbial dispersal distances (a condition we doubted would exist; Foissner, 2006). Finally, we also considered the positive patterns described above for active dispersers (Fig. 1a or c, +) as alternatives, because phoretic dispersal may link passive and active dispersal distances (e.g. Bohonak & Whiteman, 1999; Wenny, 2001; Figuerola *et al.*, 2005).

We also assessed the effect that the distribution of available data may have on the ability to evaluate size–distance patterns for small organisms. Small organisms are more difficult to track through nature than large organisms; we expected that direct observations of long-distance dispersal by small organisms should be rarer than observations of larger organisms. This expected size-related constraint would affect the ability to test the ‘everything is everywhere’ argument for small organisms, which are presumed to disperse passively over long distances (Finlay, 2002; Hillebrand, 2004). Finally, if our underlying premises were correct in assigning taxa to active and passive-disperser categories, passive-dispersing propagules should be significantly smaller than active-dispersing propagules.

METHODS

We gathered literature data on maximum observed dispersal distance and propagule mass for diverse taxa and then \log_{10} -transformed all data. We included only data based on direct observation of maximum observed individual dispersal distance. We excluded indirect and assumed distances (e.g. genetic analyses or colonization of islands without known points of origin) and estimates from modelled dispersal kernels (e.g. Clark *et al.*, 1999). Clearly, these other means of estimating dispersal distance are valuable, especially given the difficulty in tracking some organisms over long distances. However, we chose to obtain the most direct, least assumption-laden data possible as the most definitive set of current evidence for maximum dispersal distance.

Because diverse investigators collected dispersal data for diverse taxa, we had to make some decisions. For example, body size for some taxa (e.g. amphibians) is typically reported as length rather than mass. In those cases, we applied length–mass regressions from the literature (e.g. Pough, 1980) to estimate mass. Also, many lengths are reported as a range: we used median length in those cases for input to the regressions. Some data for birds were reported only as mean and standard deviation (SD) of either natal or breeding dispersal distances. In those cases, we computed the mean +2 SD to represent the maximum dispersal

distance, and used the greater of either natal or breeding dispersal distance. We included data for pollen dispersal, though pollen is not an organismal propagule, because pollen is comparable in size to tiny organisms for which data are sparse. Given the broad size range of propagules being evaluated (from bacteria to whales), we considered potential errors in mass estimation by our methods to be minor for the purposes of this study.

All dispersers were first analysed together to test for a general pattern. More importantly for the hypotheses, we labelled data as either passive or active dispersal, according to information provided in the literature, and analysed active and passive dispersers separately. The distributions of mass and distance for both passive and active dispersers were also compared using descriptive statistics and Mann–Whitney tests.

Observed data were compared with randomized null models (10,000 iterations) using the macroecology analyses in EcoSim 7.0 (Gotelli & Entsminger, 2006; see Gotelli & Graves, 1996, for a full discussion on null-model approaches). Active-disperser data were compared with a data-defined randomization (i.e. distances were randomized among sizes, so that original variances and distributions of sizes and distances were retained). Passive dispersers were tested by comparison with data-defined randomizations and uniform random distributions (Fig. 1b; Martiny *et al.*, 2006). Several statistics (described below) were generated and examined for each of the above analyses, and in all cases were based on the distance–mass plot defined by the upper and lower limits of observed data on each axis. Considered together (Table 1), the null-model statistics permitted evaluation of all five hypotheses for distance–mass distributions (Fig. 1).

Dispersion index

Dispersion index is the variance in the number of points within quadrants of the data space, where quadrants are defined by the size and distance medians (dashed lines in Fig. 1d depict quadrants of a uniform random distribution). Active and passive dispersers should have index values significantly different from a uniform random distribution (Fig. 1b) if observed distributions follow Fig. 1(a) or (c). The range of available data may also affect this statistic, so passive dispersers were also tested against a random distribution defined by the bounds of the data (Fig. 1c, 0).

Linear regression

Linear regression tested the significance of the distance–mass slope (using \log – \log data; Warton *et al.*, 2006). Because slope significance was based on null-model simulations, normality of distance data was not required (Gotelli & Entsminger, 2006). The slope of \log – \log data corresponds to the exponent b of a power curve (distance = $a \times \text{mass}^b$). Active dispersers should have a significant, positive slope (e.g. the arrow in Fig. 1d), related to either a triangular or power-curve distribution. Passive dispersers should have a non-significant slope consistent with either a data-defined (Fig. 1c, 0) or uniform random distribution (Fig. 1b), though definitive evidence of that distribution also required statistics below.

Table 1 Null-model outcomes that cumulatively diagnose evidence relative to hypothetical distributions of maximal dispersal distance and propagule mass (see also Fig. 1d).

Hypothesis	Dispersion index	Slope	Triangle points & SS	Boundary points & SS
Triangle (Fig. 1a)	Sig.	Sig. +	Right, sig.>	Lower right, sig.>; upper left, sig.<
Uniform random (Fig. 1b)	NSD	NSD	NSD	NSD in all boundaries
Positive (Fig. 1c, +)	Sig.	Sig. +	Right, sig.<	Lower right, sig.<; upper left, sig.<
Neutral (Fig. 1c, 0)	NSD	NSD	NSD	Sig. in multiple boundaries
Negative (Fig. 1c, -)	Sig.	Sig. -	Left, sig.>	Upper right, sig.<; lower left, sig.<

Sig. = significantly different ($P \leq 0.05$) from random, NSD = not significantly different from random, SS = sum of squares, + and - refer to slope direction, and < or > refer to the direction of significance relative to null hypotheses. Triangles are oriented right or left (e.g. Fig. 1a is a right triangle), as are boundaries (grey corner zones in Fig. 1d), which may also be placed in an upper or lower quadrant.

Number of points within the lower-right or lower-left triangle

The number of observed data that fall within a triangle (e.g. the dotted area in Fig. 1d) was compared with the distribution of matching counts in null-model simulations. An observed count in the upper tail (> 95%) of that distribution indicates that data are significantly more triangular than expected at random. Active dispersers should have either a significantly greater (lower-right triangular distribution; Fig. 1a) or significantly lower (power curve; Fig. 1c, +) value than expected at random. Conversely, passive dispersers should yield a non-significant result (no more triangular than random) for either the data-defined or uniform random distribution. Alternatively, a significant value for passive dispersers would indicate one of the models described above for active dispersers, or the opposite if a lower-left triangle was observed.

Triangle sum of squares

The sum of squared vertical distances between the hypotenuse of the triangle and points within the triangle was compared with the distribution of matching values from null-model simulations. Values in the upper tail (> 95%) of the random distribution are significantly farther from the boundary than at random, and values in the lower tail are significantly closer to the boundary than at random. Considered with the number of points test (above), this test evaluates the fit of a triangular distribution to the data (Fig. 1a). Active dispersers with a triangular distribution should have a significantly greater value than expected at random, whereas a power-curve model would be indicated by a significantly lesser value. Passive dispersers should yield a non-significant result (no more triangular than random) for either the data-defined or uniform random distribution, whereas a significant value would indicate one of the models described above for active dispersers (lower-right triangle) or the opposite (lower-left triangle).

Number of points beyond a boundary

This statistic is the same as that for triangles except that a boundary is defined as the diagonal line between the midpoints of two

adjacent axes (e.g. striped corner zones in Fig. 1d). Active dispersers with a triangular distribution (Fig. 1a) would be indicated by significantly *fewer* points than expected at random above the upper left boundary and significantly *more* points than expected at random below the lower right boundary (consistent with the triangle sum of squares, above). Alternatively, active dispersers with a power-curve distribution would be indicated by significantly *fewer* points than expected at random beyond *both* the upper-left and lower-right boundaries. Lower-left and upper-right boundary tests also helped evaluate active-disperser distributions but did not directly test a hypothesis. Passive dispersers with a uniform random distribution (Fig. 1b) should have non-significant values in all four boundaries (i.e. data should be distributed equally in all boundary corners of the mass-distance space), while alternative hypotheses should have significant values in some (triangular) or multiple (central random) boundaries (Table 1).

Boundary sum of squares

This statistic is calculated as for the triangle sum of squares (above), except that distances of points inside the boundary are used. Active dispersers with a triangular distribution (Fig. 1a) should have significantly *lesser* values than expected at random for the upper-left boundary and significantly *greater* values than expected at random in the lower right boundary (consistent with the number of points, above). Alternatively, a power-curve distribution (Fig. 1c, +) for active dispersers would be indicated by significantly *lesser* values than expected at random in *both* the upper-left and lower-right boundaries (Table 1). Passive dispersers with a uniform random distribution (Fig. 1b) should have non-significant values in all four boundaries, while a centrally random tendency should have significantly lesser values than expected at random. Lower-left and upper-right boundary tests helped evaluate data distributions for active dispersers, but did not directly test a hypothesis.

RESULTS

Maximum observed dispersal distance and body mass data were obtained for 320 passively dispersed species and 475 actively dispersing species (total = 795 species), representing the Eubacteria,

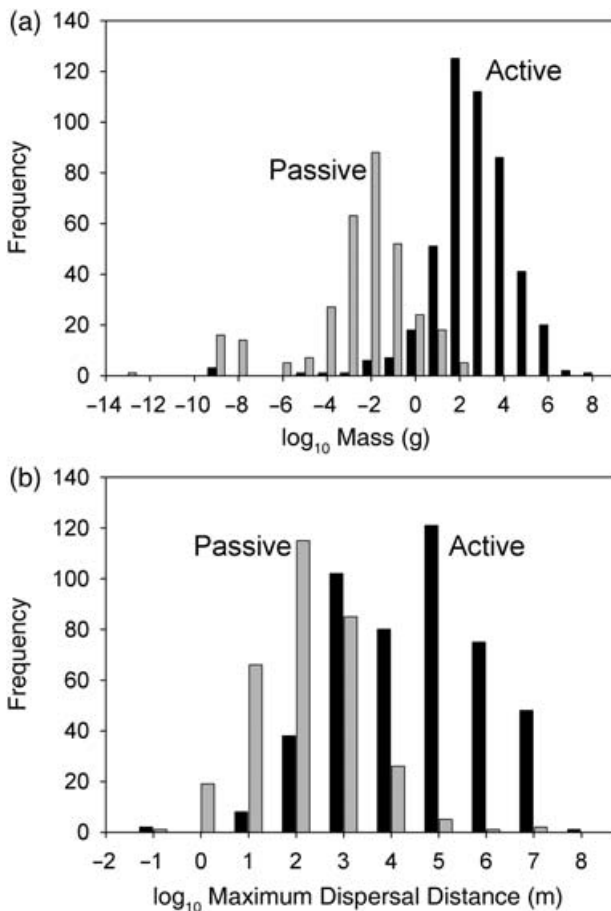


Figure 2 Frequency distributions of (a) propagule mass and (b) maximum observed dispersal distance. Note that categories are logarithmic. Active-disperser values were significantly greater than passive-disperser values for both mass and distance (Mann–Whitney, $P < 0.001$).

Protista, Fungi, Plantae and Animalia [ranging from Rotifera to the sperm whale (*Physeter macrocephalus*)]. Dispersal distance data spanned nine orders of magnitude, and mass data spanned 21 orders of magnitude (Fig. 2).

Though distributions appeared roughly normal (Fig. 2), neither propagule mass nor dispersal distance data were normally distributed (Table 2) and had heterogeneous variance ($P \leq 0.001$; Levene test). Mass for both active and passive dispersers had negative skewness and positive kurtosis: values tended to be located closer to respective upper ranges with a long tail towards smaller mass. Passive-disperser distances had a positive skew and kurtosis: values tended to be lower with a tail towards greater distances. Active dispersers were significantly larger and dispersed significantly farther than passive dispersers (Mann–Whitney tests; $P < 0.001$).

All dispersers: data-defined distribution

All statistical results were significant ($P < 0.01$) except for the number of points in the lower-left boundary (Table 3). The pattern was clustered (i.e. dispersion was not random), and

Table 2 Descriptive statistics for distributions of \log_{10} -transformed propagule mass and maximum observed dispersal distance for active ($n = 475$) and passive ($n = 320$) dispersers. All four distributions were significantly non-normal (Shapiro–Wilk, $P < 0.001$), and active-disperser distributions differed significantly from passive-disperser distributions for both mass and distance (Mann–Whitney, $P < 0.001$).

	Active dispersers	Passive dispersers
Log₁₀ propagule mass (g)		
Mean (SE)	2.16 (0.09)	−3.09 (0.13)
Skewness (SE)	−1.51 (0.11)	−1.19 (0.14)
Kurtosis (SE)	7.46 (0.22)	1.84 (0.27)
Log₁₀ max. dispersal distance (m)		
Mean (SE)	3.96 (0.07)	1.73 (0.06)
Skewness (SE)	−0.25 (0.11)	0.58 (0.14)
Kurtosis (SE)	−0.28 (0.22)	1.77 (0.27)

maximum observed dispersal distance increased with body mass with a significant slope (Fig. 3a). More points were located in the lower-right triangle (Fig. 3a) than expected at random, although those points were closer to the triangle diagonal than expected at random. Consistent with positive regression models, both the upper-left and lower-right boundaries had fewer points than expected at random and those points were closer to the boundary diagonals than expected at random. The overall pattern of all size–distance data was consistent with the positive regression hypothesis (Fig. 1c, +).

Active dispersers: data-defined random distribution

All macroecology statistics for active dispersers (Table 3) were significant ($P < 0.05$) except the number of points within the triangle: that value was not significantly different from data-based randomizations ($P = 0.51$). However, those points were closer to the triangle diagonal than expected at random. Dispersion was non-random and the points were fitted by a significant slope (Fig. 3b). Both the upper-left and lower-right boundaries had fewer points than expected at random and those points were closer to the boundary diagonals than expected at random. Considering all the above, the relationship between maximum observed dispersal distance and propagule mass for active dispersers was more consistent with the positively sloped alternative hypothesis (Fig. 1c, +) than with the triangular hypothesis (Fig. 1a).

Passive dispersers: uniform random distribution

All results for this comparison were significant ($P < 0.0001$) except the power-curve regression and lower right boundary points (Table 3). Compared with a uniform random distribution, passive-disperser data were significantly clumped (Table 3, Fig. 3c). However, there was no significant slope (i.e. body mass did not affect passive dispersal distance). More values were

Table 3 Macroecology statistics of the relationship between body mass and maximum observed dispersal distance. All values are standardized effect sizes (SES), which measure the calculated statistic's placement relative to the randomized null-model distribution, expressed in units of standard deviation. The sign of the SES indicates the direction of the effect. Active dispersers (Active) were analysed by comparison with data-defined randomizations. Passive dispersers were analysed by comparison with uniform random distributions (Passive: uniform) to test the prediction depicted in Fig. 1(b) (Martiny *et al.* 2006), and to data-defined randomizations for lower-right (Fig. 1a) and lower-left triangle distributions. Based on results for active and passive dispersers, all data (All) were analysed by comparison with data-defined randomizations.

Statistic	All	Active	Passive: uniform	Passive: data-defined, right (left)†
Dispersion	198.9**	31.9**	-4.3**	1.1
Regression slope‡	17.4**	10.8**	-0.4	-0.5
Triangle points	8.1**	0.3	14.0**	-1.8* (4.4**)
Triangle SS	-19.0**	-11.1**	4.7**	0.2 (-2.6**)
Lower right boundary points	-8.3**	-2.6**	-1.0	-2.5**
Lower right boundary SS	-4.0**	-1.8**	-3.8**	-3.3**
Upper left boundary points	-2.5**	-2.7**	-6.6**	0.9
Upper left boundary SS	-1.7**	-1.4**	-4.2**	-0.2
Lower left boundary points	0.3	2.6*	-6.5**	-0.8
Lower left boundary SS	4.4**	17.3**	-4.0**	0
Upper right boundary points	7.6**	2.0*	-6.0**	-0.2
Upper right boundary SS	14.8**	11.6**	-3.5**	2.0*
<i>n</i>	795	475	320	320

* $P \leq 0.05$; ** $P \leq 0.01$.

†Only triangle points and triangle sum of squares (SS) statistics differed for the lower-right or lower-left triangle tests for passive dispersers: all other statistics were identical.

‡Regression slope significance was calculated from comparisons with the randomized, null-model data.

located in the lower triangle and were distributed further from the triangle's upper edge than expected for a uniform random pattern. Fewer points occurred in the upper-left boundary than expected at random, and those few points were closer to the boundary diagonal than expected at random. Lower-right boundary points were also closer to the edge than random points, but no more occurred in that zone than at random. In addition, fewer points were located in lower-left and upper-right boundaries than expected for a uniform random distribution. Considered together, these results did not support the triangle (Fig. 1a), uniform random (Fig. 1b) or positive regression (Fig. 1c, +) hypotheses. The most parsimonious explanation (tested below) was that passive-disperser data were random but centrally tending and sparse at the edges of the mass and distance ranges, rather than uniformly random.

Passive dispersers: data-defined random distribution

Results of this comparison differed from those of the uniform random distribution. Data were randomly dispersed in the mass–distance space and did not follow a significant distance–mass slope (Table 3). Fewer points may have occurred within the lower-right triangle than at random ($P = 0.047$), though other iterations yielded barely non-significant outcomes (e.g. $P = 0.051$) due to randomization variance. Also, the points in the lower-right triangle were no closer to the diagonal edge of the triangle than expected at random. The number and positions of points in the lower-right boundary were significantly fewer and closer to the diagonal than expected at random, though all other boundaries were consistent with the data-defined random distribution

(Table 3). Finally, the passive-disperser distance–mass pattern clearly did not fit a lower-left triangle (as may be expected if smaller sizes disperse farther). Although more points existed in that triangle than expected at random (Table 3), this occurred because numerous values were in the lower-right portion of the plot (Fig. 3c) rather than a strong fit to a lower-left triangle (also note that boundary results are inconsistent with a lower-left triangle). To sum, the results supported the hypothesis that the distance–mass relationship for passively dispersed propagules was random but constrained relative to a uniform random distribution (Fig. 1c, 0). No support was given to the lower-right triangle hypothesis (Fig. 1a), the positive regression hypothesis (Fig. 1c, +), the negative regression hypothesis (Fig. 1c, -) or a lower-left triangle.

DISCUSSION

Does dispersal distance depend on body mass? In general, yes, and our hypotheses for active and passive dispersers were supported. Available data obtained by direct observation showed that active dispersers followed a positive dispersal–mass trend and that passive-disperser distances were random with respect to propagule mass. The two patterns combined yielded a pattern whereby larger organisms tended to achieve greater maximal dispersal distances. We think these results are relevant to several topics: the presence of allometric 'rules' of biogeography against which microbes purportedly rebel, the potential scaling of neutral and niche-based theories of metacommunities, the effect of distance–mass relationships on latitudinal patterns of species richness, and conservation biology.

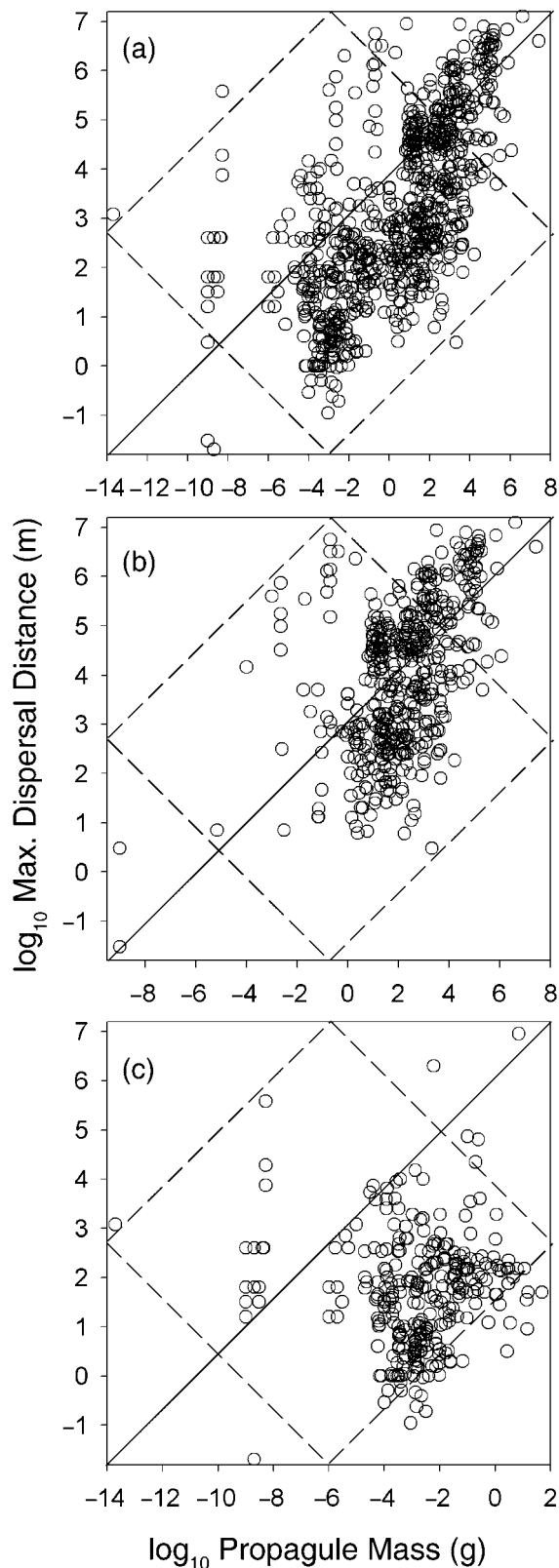


Figure 3 Maximum dispersal distance relative to propagule mass for (a) all data, (b) active dispersers and (c) passive dispersers. Diagonal lines denote the lower-right triangles and dashed lines denote boundaries. Note that axes are log-transformed and ranges change for each plot: boundaries and triangle dimensions were determined by empirical data ranges.

The allometry of dispersal

We began with the hypotheses of Martiny *et al.* (2006) regarding active and passive dispersal, but then changed the terms and introduced our own hypotheses to test. Thus, we did not test the Martiny *et al.* (2006) hypotheses *per se* because we thought it best to focus on dispersal distances and mass of the same objects (e.g. seeds) and because we labelled some species (e.g. trees) as passive dispersers rather than active. Despite a different approach, our results are consistent in the broad outlines with the Martiny *et al.* (2006) hypotheses, although necessarily different in the details. Active dispersal distance increases with mass, as it would for their hypothesis of a triangular shape (Fig. 1a). However, our analyses of redefined data did not support a triangular model. Passive dispersal data are random, as Martiny *et al.* (2006) hypothesized, although not uniformly so.

The distance–mass relationship for active dispersers is generally consistent with empirical relationships of home range and mass (Peters, 1986) and an assumption that individual dispersal distance correlates with home range size (Bowman *et al.*, 2002). Our results suggest that this assumption is generally valid, although range size may correlate with maximum dispersal distance better for some taxa than others (Bowman, 2003).

The allometry of sparse data

Collected data were notably sparse for tiny propagules. A hypothetical uniform random distribution for passive dispersers was not met (in part) because data were sparse for small organisms. Given that several million prokaryotic species are likely to exist (Curtis *et al.*, 2002), that protistan diversity exceeds the combined diversity of Fungi, Plantae and Animalia (Sogin *et al.*, 1986), and that 5–10 million arthropod species may exist (Ødegaard, 2000), it is obvious that too few direct observations of dispersal distance exist for small organisms. A second factor that probably constrains the data distribution is that we used only data obtained by direct observation of dispersal distance: we did not include data based on genetic analyses or models. Results analysed here surely underestimated potential dispersal for some taxa. However, it is also possible that dispersal distances of tiny taxa are linked to dispersal distances of large taxa via phoresis (e.g. Figuerola *et al.*, 2005): if so, then active dispersal distances of some larger taxa may predict passive dispersal distances of some smaller taxa.

Microbial biogeography

Our results generally support Martiny *et al.* (2006): there should be a great diversity of dispersal distances for microbes of similar size, reflecting a vast breadth of life histories, ecological roles and access to dispersal vectors in diverse systems. The distance–mass relationship for passive dispersers was random, and although it was dominated by plant seed data, 30 data points existed for organisms weighing 10^{-8} – 10^{-9} g. Maximum observed dispersal distances of these organisms ranged over nearly eight orders of magnitude. Diverse spatial patterns for microbes observed recently (e.g. Whitaker *et al.*, 2003; Green *et al.*, 2004; Horner-

Devine *et al.*, 2004; Telford *et al.*, 2006; Vos & Velicer, 2006) are consistent with a wide-ranging dispersal–mass distribution for passive dispersers. In other words, we expect that microbes are likely to be consistent with the pattern of other passively dispersed propagules and will not be monolithic in their cosmopolitanism. To unravel *why* some microbes of similar size disperse different distances will require more knowledge of microbial ecology.

Much of what is written regarding dispersal of tiny organisms is inherited myth of *potential* dispersal and lacks supporting data on *realized* dispersal (Bohonak & Jenkins, 2003), though multiple investigators are working to overcome this using novel approaches (Bilton *et al.*, 2001; Figuerola *et al.*, 2005; Macneale *et al.*, 2005). This condition severely limits our ability to test the hypothesis that tiny organisms have no biogeography (e.g. Finlay, 2002; Fenchel & Finlay, 2004). Indeed, the hypothesis has recently been considered untestable given the current state of the science (Foissner, 2006). An analysis of calibrated genetic data among diverse taxa may provide the best test, but must rely on indirect estimates of dispersal distance with their requisite assumptions (Bohonak, 1999; Avise, 2004) and genetic estimates of microbial species identity, despite the misgivings of Fenchel (2005). Until that is possible, existing dispersal data cannot resolve the debate (Finlay, 2002; Foissner, 2006) on whether small organisms disperse so far as to be cosmopolitan, though existing data provide a hint.

The above expectations mimic a similar conceptual transition — from ‘black-box’ generality to more sophisticated resolution — that has been occurring for freshwater zooplankton (e.g. Hebert & Wilson, 1994; Havel & Shurin, 2004; Gomez, 2005). Similar conceptual shifts occurred for tropical canopies (Erwin, 1983) and marine benthos (Grassle & Maciolek, 1992): biogeographical diversity was underestimated until investigators looked closely *and* broadly. We expect that microbial biogeography will not be found to be an oxymoron, but will extend and contribute importantly to the knowledge built from the biogeography of macroscopic organisms.

Neutral and niche-based theory

Neutral and niche-based theories of macroecology or metacommunity structure (Hubbell, 2001; Chase & Leibold, 2003) are more complex than can be summarized here, but one key difference is that neutral theory assumes dispersal limitation while niche-based theory does not. The two theories are not immediately reconciled, though that is a goal (Gravel *et al.*, 2006).

Dispersal limitation depends on the distance among habitats relative to the distance an organism can disperse. Support for neutral or niche-based theories may depend on metacommunity spatial scale relative to dispersal distance, propagule mass and the taxa being studied. For example, Gravel *et al.* (2006) considered neutral and niche-based theories as extremes of a continuum by analysing (among other variables) the probability m that a recruit to a community is an immigrant from the metacommunity. Based on our results, larger active dispersers are more likely to have greater values of m than small active dispersers in a given landscape, whereas m should not vary predictably with propagule

mass for passive dispersers. Thus, our results may help to gauge the scales of metacommunity processes and the applicability of niche and neutral theories on a propagule-mass continuum.

Latitudinal patterns in species richness

Species richness generally decreases with increasing latitude, and this trend is steeper and clearer for organisms of greater body mass (Hillebrand, 2004). Dispersal mode (active or passive) and organismal thermodynamics (ectotherm or homeotherm) interact with body mass to affect the general pattern. To explain this pattern, Hillebrand (2004) hypothesized that: (1) smaller organisms may passively disperse at greater rates than larger, active dispersers; or (2) latitudinal gradients in species richness may differ for ectotherms and homeotherms but covary with body mass. Our results do not support the first of these hypotheses: small, passive dispersers achieved significantly shorter distances than large, active dispersers. Though this conclusion may change with the availability of more data for small dispersers, it currently appears that the second hypothesis is more likely, and would be consistent with knowledge of the relationship between metabolic thermodynamics and range size (McNab, 1963; Peters, 1986). Therefore, our results suggest further inquiry into allometric differences among ectotherms and homeotherms as a basis for predicting latitudinal species richness.

Conservation biology

Our results potentially apply to three topics in conservation biology: habitat fragmentation, umbrella species and biotic homogenization. Habitat fragmentation is a spatial process, and the scales of landscape spatial structure need to be considered relative to the dispersal distances of the subject organisms (Fahrig & Merriam, 1994). More and better data on dispersal distances may lead to quantitative, allometrically-based predictions of habitat fragmentation effects, in addition to other species-specific traits that drive functional connectivity in fragmented landscapes (e.g. Ueza *et al.*, 2005).

Distance–mass relationships are implicitly part of the umbrella species approach (e.g. Simberloff, 1998; Fleishman *et al.*, 2001; Roberge & Angelstam, 2004) because ‘charismatic megafauna’ are often identified as umbrella species, due in part to their large range sizes. Problems arise with this approach when the space under the umbrella is patchy for other, smaller species (Roberge & Angelstam, 2004). Based on our results, the umbrella species concept may apply best when restricted to active dispersers; it may be less successful when applied across active and passive dispersal modes because they differ in their allometries of dispersal distance.

How fast is the ‘Homogocene’ approaching (Olden & Rooney, 2006)? That question may best be answered by comparison of accelerated taxonomic homogenization rates with background rates and distance functions, especially relative to natural barriers (e.g. trans-oceanic distances for terrestrial fauna). Our results represent conservative size-based estimates of natural dispersal distances: many observations of arrivals that can only *assume* a point of origin were excluded — obviously, various species have

arrived at distant islands or ports and must have traversed long distances. The approach employed here may help estimate natural dispersal distances for comparison to enhanced, anthropogenic distances.

CONCLUSIONS

Does size matter for active and passive dispersal? Based on direct observational data, the answer is affirmative for active-dispersing organisms but negative for passive-dispersing organisms. Passively dispersed propagules tend to be smaller than active dispersers, and disperse less far overall. Our results do not support the hypothesis that tiny organisms disperse far, though many more data are needed for organisms <1 g to fully test that hypothesis. Our results are relevant to diverse ecological concepts, including neutral and niche-based metacommunity theories, latitudinal variation in species richness, and conservation biology.

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BIOSKETCHES

The authors were members of a biogeography course: this paper is a product of work conducted during that course. Though having approached this topic from diverse perspectives and backgrounds, we now view our specializations through a broader lens and aspire to be labelled as biogeographers one day.

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