Characterizing scale-dependent community assembly using the functional-diversity–area relationship

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Abstract. Phenotypic traits mediate organisms' interactions with the environment and determine how they affect and are affected by their biotic and abiotic milieu. Thus, dispersion of trait values, or functional diversity (FD) of a community can offer insights into processes driving community assembly. For example, underdispersion of FD suggests that habitat "filtering" of species with unfavorable trait values restricts the species that can exist in a particular habitat, while even spacing of FD suggests that interspecific competition, or biotic "sorting," discourages the coexistence of species with similar trait values. Since assembly processes are expected to vary as a function of spatial scale, we should also expect patterns of FD to reflect scale dependence in filtering and biotic sorting. Here we present the concept of the functional-diversity–area relationship (FAR), which is similar to the species–area relationship but plots a measure of phenotypic trait diversity as a function of spatial scale. We develop a set of null model tests that discriminate between FARs generated predominantly by filtering or biotic sorting and indicate the scales at which these effects are pronounced. The utility of the FAR for addressing long-standing issues in ecology is illustrated with several examples. A multi-scale examination of FD and its pattern relative to null expectations provides an important tool for ecologists interested in understanding the scale dependence of community assembly processes.

Key words: abiotic filtering; biotic sorting; community assembly; functional diversity; functional-diversity–area relationship; null models; spatial scale; species–area relationship; traits.

INTRODUCTION

Current community assembly theory posits that multiple, interacting factors like interspecific competition, sorting of species along environmental gradients, and disturbance operate in a scale-dependent manner that determines the number and types of species occurring in a given area (Shmida and Wilson 1985, Turner and Tjørve 2005, McGill 2010). This scale-dependent, multi-causal hypothesis of diversity is based on the implicit assumption that species respond differently to their biotic and abiotic environment because they have different phenotypic traits (e.g., body size,

cold tolerance, nitrogen use efficiency). For example, species with traits that make them strong competitors might be common in undisturbed patches, while good dispersers may be primarily found in disturbed patches (Grime 1977). Small areas are likely to contain just one type of patch, and therefore less variation in trait values, whereas large areas may contain both patch types and therefore greater variation in trait values, which we refer to here as "functional diversity" (FD).

The abiotic and biotic factors affecting an organism are mediated by its traits, which in turn determine how the organism influences its abiotic and biotic environment. FD among species often captures important dimensions of variation in ecological strategy (Westoby et al. 2002), vital rates (Poorter et al. 2008), and responses to abiotic conditions (Sandel et al. 2011). In

a community context, patterns of FD can reveal the action of ecological processes such as competition for resources (Ricklefs and Travis 1980, Stubbs and Wilson 2004), habitat filtering (Cornwell et al. 2006), trophic interactions (Díaz et al. 2001), or the combined action of multiple processes (Kraft et al. 2008). However, analyses of community assembly using FD typically show strong scale dependence (Cavender-Bares et al. 2006, Swenson et al. 2006, Swenson and Enquist 2009, Kraft and Ackerly 2010, Algar et al. 2011, Wang et al. 2013), suggesting that the spatial pattern of traits can be used to infer the type and characteristic scale of processes driving community assembly.

Here we present the concept of the functional-diversity–area relationship (FAR), which describes the change in a measure of among-species trait variation (e.g., range, variance, number of functional categories) as a function of spatial scale. We believe that the FAR is a useful extension of recent work in trait-based community assembly (Weiher and Keddy 1999, Cornwell et al. 2006, Kraft et al. 2008, Swenson and Enquist 2009), and improves on current trait-based approaches because examining more than one or two scales simultaneously allows us to better understand scale dependence. We first present a general theory of the FAR and how it should be expected to reflect the scale-dependent influence of assembly processes such as interspecific competition and habitat filtering. Next we discuss the covariance between species diversity and trait diversity and present a method for disentangling them using null model tests. Finally, we illustrate the utility of the FAR in addressing some long-standing issues in ecology.

Scale Dependence in FD and Community Assembly

Given that traits are the interface between an organism and its environment, the identity and values of traits of individuals in a community should reflect factors that allow them to exist in their particular habitat (Wright et al. 2005, Shipley et al. 2006). Typically, studies of community assembly focus on several different processes, including the effects of interspecific competition or "biotic sorting" and "habitat filtering" of species with unfavorable traits (e.g., Cornwell and Ackerly 2009).

Under the biotic-sorting hypothesis, differentiation in trait values facilitates the coexistence of species that partition available resources, meaning that species with similar trait values will be unlikely to coexist (Brown and Wilson 1956, MacArthur 1958). Over short time spans, biotic sorting can lead to competitive exclusion of species with trait values too similar to competitively superior species (e.g., Pyke 1982), leaving the distribution of FD within a community more evenly spaced than would be expected by chance. Over long time spans it can lead to ecological character displacement as a result of evolutionary divergence of trait values, and thus facilitate coexistence (Dayan and Simberloff 2005).

Either process will lead to more evenly spaced gaps in the distribution of FD than expected by chance (Stubbs and Wilson 2004).

Alternatively, the habitat-filtering hypothesis states that the abiotic environment limits the successful establishment of all but a group of species with a specific set of trait values, resulting in a distribution of FD that has less variation than one generated from a random sample of trait values in the region (van der Valk 1981). For example, feeding guilds of temperate stream insects generally sort along the length of a river network, with some species only able to live in fast-moving, shallow, headwater channels and others in slower, deeper, outlet channels (Vannote et al. 1980), so no single site contains the diversity of traits of the entire riverine fauna.

These two processes can be expected to be pronounced at different spatial scales. Competition is often hypothesized to be most prominent at fine scales because organisms typically interact over short distances (Shmida and Wilson 1985, Soberón and Nakamura 2009). In contrast, abiotic factors like climate, topography, and soil type vary over larger distances, so habitat filtering should be more pronounced at coarser scales (Grime 2006, Soberón and Nakamura 2009). Hence, there is a need for an approach that explicitly tests the type and relative importance of scale-dependent assembly processes mediated through traits.

Null Expectations for the FAR

The FAR is not only analogous to but also related to the species–area relationship (SAR), because the number of species at each scale represents the number of "opportunities" to sample from the pool of trait values. From a strictly geometric viewpoint, species richness at a particular scale is determined by three "species-level" patterns (Fig. 1a; He and Legendre 2002, McGill 2011). First, the prevalence of each species represents the proportion of sites (e.g., cells in a gridded landscape) occupied by a species. Second, intraspecific aggregation reflects the tendency of individuals of the species to be positively or negatively associated with one another. Third, patterns of interspecific association determine which species are likely to be co-located with one another. In turn, species-level patterns are often related to certain traits. For example, intraspecific clustering of trees in tropical forests is correlated with seed dispersal mode (Siedler and Plotkin 2006) and bee species segregate spatially according to proboscis length (Pyke 1982).

The distribution of FD across a landscape has patterns analogous to the species-level patterns: prevalence (the frequency with which a given trait value occurs across sites in a landscape, regardless of species identity); spatial dispersion (the probability that nearby cells contain individuals with the same trait value, regardless of species); and trait "mixing," or the
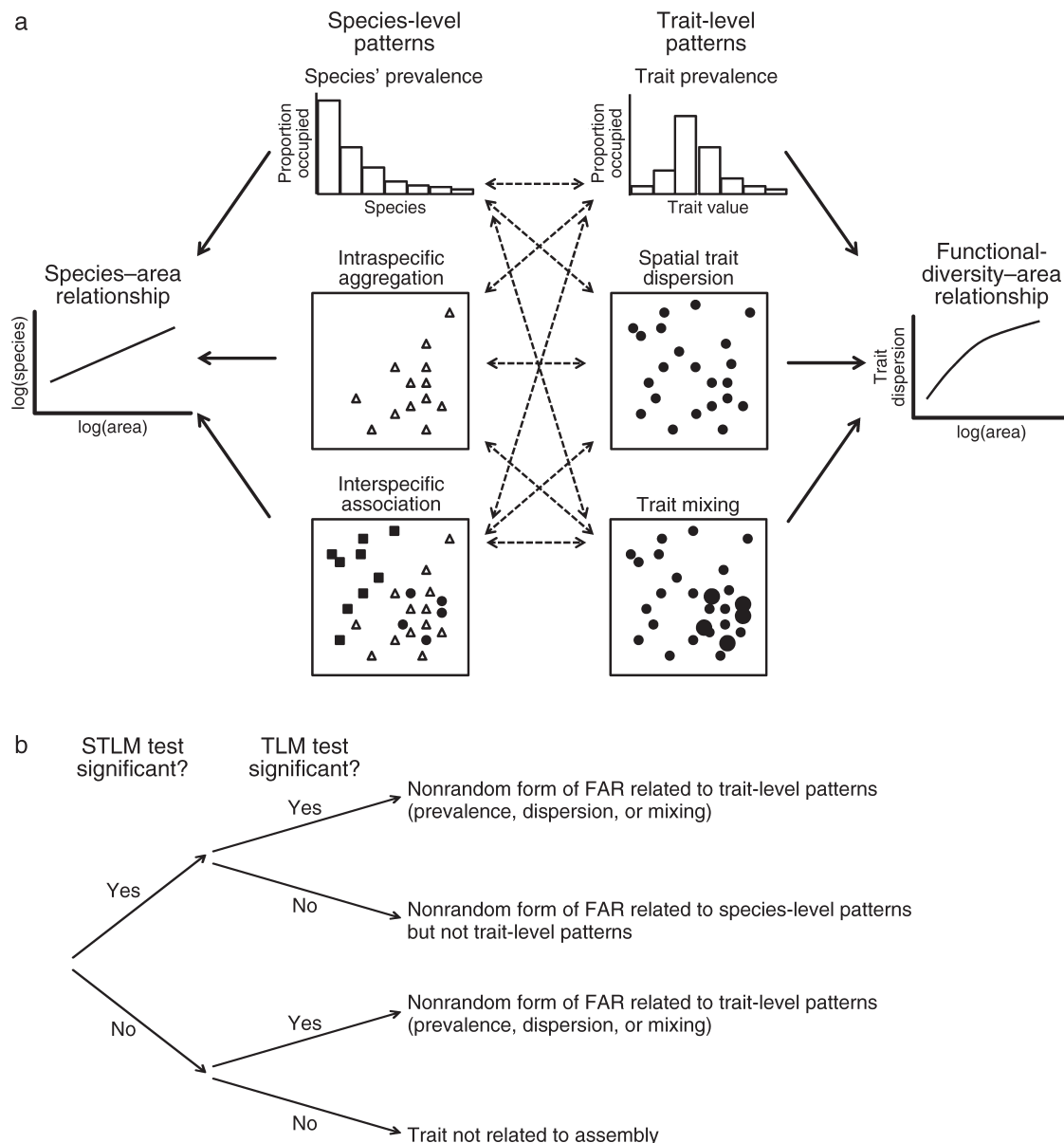
FIG. 1. (a) The relationship between species- and trait-level patterns that influence the species–area relationship (SAR) and functional-diversity–area relationship (FAR). The SAR (left side) is determined by the prevalence of species (proportion of cells occupied at a given scale), intraspecific clustering of individuals, and interspecific associations (probability different species are found in the same cell). Triangles, circles, and squares represent different species in the maps. The FAR (right side) is determined by trait prevalence (proportion of cells with a given trait value), spatial clustering of similar trait values, and trait mixing (spatial association between different values of a trait). Different sizes of the circles represent different trait values of the trait. The SAR can be an indirect function of trait-level patterns if these influence species-level patterns, and the FAR can be an indirect function of species-level patterns if these influence trait-level patterns. Solid arrows indicate direct relationships, and dotted lines indicate potential relationships. (b) Different combinations of significant species-trait-level model (STLM) and trait-level-model (TLM) tests can be used to infer whether species- or trait-level patterns influence nonrandom forms of the FAR. The STLM disrupts species- and trait-level patterns, while the TLM only disrupts the trait-level patterns but keeps species-level patterns untouched.

likelihood that individuals with divergent trait values will be found in the same site.

In general, we should expect FD to vary with area because an increase in species with area provides more opportunities to sample from the regional trait distribution. This does not imply the SAR is the more

"fundamental" relationship, but most workers have assumed that richness must be controlled for before examining FD (e.g., Stubbs and Wilson 2004, Cornwell et al. 2006, Swenson and Enquist 2009). Hence, when testing for nonrandom patterns of FD across multiple scales, we require a method that accounts for the

distribution of FD expected by chance at each scale as a function of the number of species.

Deviation of an observed FAR from the distribution of FARs generated by a random sampling process should reflect the importance of the given trait or suite of traits in community assembly. Furthermore, on the basis of arguments presented above, we expect certain patterns in the FAR to reflect biotic sorting and habitat filtering. These expectations lead to a null model approach for testing for patterns indicative of biotic sorting or habitat filtering while controlling for the passive sampling effect created by the SAR.

We propose two null model approaches that retain the observed SAR but randomize the species- and/or trait-level patterns expected to shape the FAR. First, the species- and trait-level model (STLM) randomly shuffles species' presences across the landscape but does not change the trait value associated with each species. The randomization operates on a species-by-site matrix where rows represent species and columns sites (we used the "proportional rows/fixed column sums" randomization of Gotelli [2000] to retain observed richness at each site; see also Gotelli and Graves [1996]). Second, the trait-level model (TLM) keeps species' spatial patterns as observed (the species-by-site matrix is unchanged) but shuffles trait values among species. In both null models, species richness at each scale is kept exactly as observed to control for sampling effects created by the SAR. The randomizations can be repeated a large number of times (we use 10 000) and FARs for measures of FD expected to be diagnostic of habitat filtering or biotic sorting can be calculated and plotted as 95% confidence envelopes and compared to the observed FARs calculated using the same metric of FD.

The STLM and TLM tests can be used in combination to further discern whether species- or trait-level patterns are related to nonrandomness in the FAR (Fig. 1b). The STLM retains species' mean prevalence but randomizes all other species- and trait-level patterns while the TLM retains all species-level patterns while shuffling the trait-level patterns. Hence, different combinations of significant and insignificant STLM and TLM tests can be used to infer the level of the pattern (species- or trait-level) related to nonrandomness in the FAR (Fig. 1b). Either null model can be calculated using any measure of FD. For simplicity, our examples use two metrics of FD. The first is the range of trait values (Cornwell et al. 2006), which, under the habitat-filtering hypothesis, should be reduced if the environment disallows species with traits that do not favor establishment (van der Valk 1981). Hence, if habitat filtering occurs, we expect the trait range FAR to fall below the STLM or TLM confidence envelope. Other indices of FD dispersion, such as variance, Rao's quadratic entropy, dendrogram distance, or trait-spacing metrics, could also be used (Rao 1982, Petchey and Gaston 2002, Kraft and Ackerly 2010). The second metric measures spacing between traits, and is calculated by binning the

observed trait values into discrete classes, each containing approximately the same number of species at the coarsest scale and tabulating the proportion of classes occupied at each finer scale. Under the biotic-sorting hypothesis, species more similar in trait values preclude each other. This means that the observed level of trait filling will fall below the null envelope since fewer bins are likely to be occupied when species' presences are more evenly spaced as a result of interspecific competition. Other "trait spacing" metrics could also be used (Stubbs and Wilson 2004, Kraft and Ackerly 2010).

Appendix A shows an example of null model calculation and Appendix B demonstrates that the null model approach is capable of detecting habitat filtering and/or biotic sorting in a simulated community with known levels of each. These simulations indicate that both TLM and STLM are most able to detect filtering and/or biotic sorting at fine scales and when sorting or filtering causes individuals to die or emigrate (vs. recolonize elsewhere on the landscape). Computer code written for R (R Development Core Team 2011) and tested on version 2.15.0 for implementing null model tests and simulating communities with various levels of sorting or filtering is available in Supplements 1 and 2.

DATA NECESSARY FOR CONSTRUCTING THE FAR

At minimum, constructing a FAR requires a spatially explicit record of species' presences and absences at some arbitrarily fine scale nested within a larger area and trait data for each species. The examples we use here have either Scheiner's (2003) Type IIa (contiguous, nested plots) or IIIa (disjunct plots) spatial design. To calculate the FAR, the mean of the FD metric being used is computed across all cells and recorded as a measure of trait diversity, cells are amalgamated with neighbors in pairs or quadruples to form the next-larger scale, the FD metric is calculated across these cells, and so on, until the last "cell" constitutes the entire plot.

AN EXAMPLE FAR: SERPENTINE GRASSLAND

We illustrate the concept with the FAR for seed mass of vascular plants in a serpentine grassland in California, USA (Fig. 2). The study plot is 8×8 m and subdivided into 256 0.5×0.5 m cells. In 2005, we recorded the presence of each species in each cell. Seed mass data was obtained from the Kew Gardens Seed Information Database and were available for 82% of the species in this plot (missing data were ignored in the calculations as they are in other examples in this paper; database *available online*).[6]

The observed FAR calculated using trait range falls below the null expectation for both null models at scales $\leq$2–4 m^2 but within the null expectations above this scale (Fig. 2a and b). Our simulations (Appendix B) suggest that, even when filtering is strong and removes a

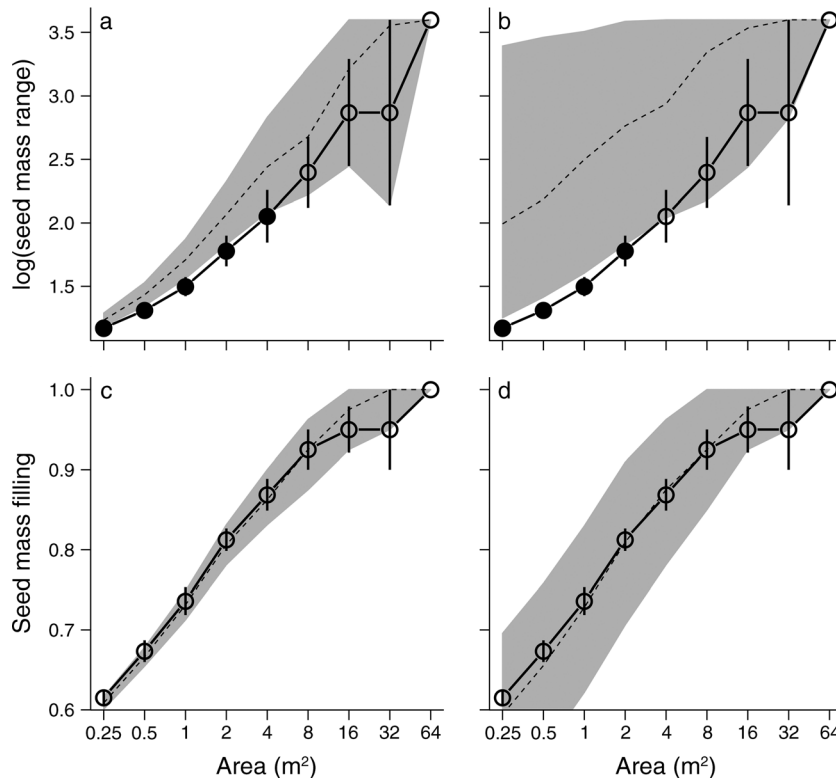---

[6] http://www.kew.org/data/sid

FIG. 2. The FAR for seed mass of vascular plants (measured in milligrams) of a serpentine grassland. In each panel, the solid line represents the observed FAR, the gray area the null model's 95% confidence envelope, and the dashed line the median null expectation. Solid circles on the observed FAR line indicate significant deviation from null expectation. Error bars represent standard errors. (a) The observed FAR calculated using trait range and the 95% confidence envelope of the STLM. (b) The observed FAR calculated using trait range and the 95% confidence envelope of the TLM. In either case, the observed FAR falls under the null expectation at fine scales, suggesting that filtering is the predominant community assembly process at scales ≤4 m². (c) The STLM test using the trait-space filling metric described in *Null expectations of the FAR*. (d) The TLM test using the trait-space filling metric. In neither case, is there evidence for biotic sorting operating on seed mass because the trait-space filling FAR always falls within the null envelope.

large proportion of individuals ($>\sim50\%$), the null model tests are less powerful at coarser scales. Others have also noted a general loss in statistical power as the size of the local community approaches the species pool against which it is compared (Kraft et al. 2007, Kraft and Ackerly 2010, de Bello 2012). At the coarsest scale there is but one subplot, the entire plot, so shuffling trait values among species does not change the range, but we include it in the figure because it represents a datum. In contrast to the trait-range FAR, the trait-space filling FAR does not deviate from the null envelopes of either test (Fig. 2c and d).

The lower-than-expected trait-range FAR in the STLM and TLM tests suggests that habitat filtering influences community membership and does so by affecting trait-level (vs. species-level) patterns (Fig. 1b). Serpentine soils are typically harsh edaphic environments to which few species in the larger region are adapted (Kruckeberg 1967). Hence, it is not surprising to find support for the filtering hypothesis in general. In contrast, the serpentine community seems not to be structured by biotic competition related to seed size

(Fig. 2b and c). These results concur with the general expectation that competition will be reduced in harsh environments where abiotic constraints dominate community assembly (Weiher and Keddy 1995).

APPLICATIONS OF THE FAR TO KEY ISSUES IN ECOLOGY

Body-size distributions

To a first approximation, body mass determines the mass-specific metabolic energy requirements of organisms and, in summation, entire ecosystems. Body-mass distributions at continental scales are often unimodal and right skewed (Hutchinson and MacArthur 1959), but relatively flat at finer scales (Brown and Nicoletteo 1991). A wide variety of hypotheses attempt to explain the discrepancy between local- and continental-scale distributions and the degree to which abiotic and biotic limitations shape the distribution (Brown 1995).

To examine these issues, we calculated the FAR for the body mass of non-domesticated mammals in a 2.2×10^6-km² portion of the western United States and southern Canada (Fig. 3; Appendix C shows a map of
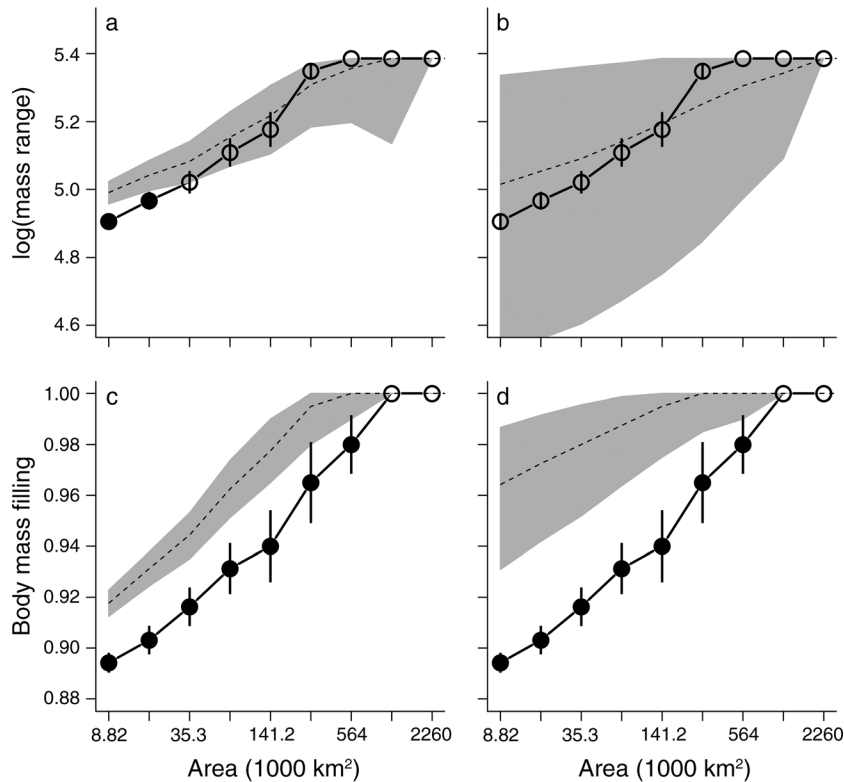
FIG. 3. Relationship between mammalian body mass range and area. Symbols are as in Fig. 2. (a) The STLM and (b) TLM tests using range of log(body mass) (measured in grams). The significant STLM test at scales $<\sim$17 000 km^2 combined with an insignificant TLM tests suggests that filtering occurs at finer scales by operating on species-level (vs. trait-level) patterns. The mean proportion of 25 body mass bins occupied by species within a cell vs. the null envelope calculated using (c) the STLM and (d) TLM. The nonrandom spacing of traits is strong across all but the coarsest scales and may be due to ecological character displacement or anthropogenic disturbance and persecution operating on trait-level patterns (cf. Fig. 1b).

the study area). The presence or absence of each species was determined using IUCN range maps, and body mass was obtained for all but one (99.5%) of the 218 species using Jones et al. (2009; range maps *available online*).[7]

The most striking contrast between the different null model tests is the departure of the trait-space filling metrics from the STLM and TLM null envelopes at all but the coarsest scales (Fig. 3c and d) but lack of departure for the trait range FAR except at $<\sim$17 000 km^2 for the STLM test (Fig. 3a; though this may be due to reduced statistical power at coarser scales). This suggests that biotic sorting plays an important role in assembling the community across nearly the entire scale range examined here, though the relatively small absolute difference between the observed FAR and the expected (median) value suggests it may not act very strongly. However, human activities could complicate the interpretation of the FAR. Anthropogenic impacts in this study area are most likely related to forestry, grazing, and conversion of native grassland to crops (Homer et al. 2004). Thus the pattern we see in the FAR

is possibly impacted by dramatic changes in land cover and use over the past century and half. (Only one of the species in the data set is nonnative, so introductions probably have little effect.) Additionally, a large proportion of large-bodied mammals went extinct in the end of the Pleistocene. Since these species no longer occur in the system it is not possible to use a modern FAR to detect historical influences on current species' distributions, but it opens the possibility of doing so with fossil data.

Disturbance and succession

Connell and Slatyer's (1977) seminal work on succession outlines three possible pathways that inherently appeal to a trait-based view of ecology based on whether species have traits that facilitate, tolerate, or inhibit establishment of other species. More recently, Weiher and Keddy (1995; see also Holdaway and Sparrow 2006) presented a conceptual model of trait dispersion as a function of two axes, one spanning a continuum from harsh abiotic conditions like those found in disturbed environments to intense biotic competition like those found in undisturbed environ-

[7] www.iucnredlist.org

ments, and the other the area of the regional pool of species.

To test Weiher and Keddy's (1995) model, we examined FARs for two sets of 4 × 4 m plots in a subalpine meadow in the Rocky Mountains of Colorado, USA affected by an earth flow in the 1920s. For our analysis we combined two sets of more disturbed plots ("heavily disturbed") and two sets of lightly or undisturbed plots ("lightly disturbed") from Carey et al. (2006) and show results averaged across each set of plots. Since we had more than one plot within each disturbance set, for the TLM test we sampled trait values from the distribution of observed trait values across all plots. Hence, the TLM null envelopes are not forced to collapse at coarse scales and the test is potentially more powerful at these scales. Seed mass data was obtained for 65% of the species from the Kew Gardens Seed Information Database (83% of occurrences; see footnote 6). Further details of the earth flow and study design are found in Carey et al. (2006).

Experimental work indicates that the abiotic environment of the more disturbed plots is harsher than the lightly disturbed areas (Curtin 1994). As a result, Weiher and Keddy's (1995) model predicts that the FAR of the lightly disturbed plots should display a signature indicative of biotic sorting but enter a zone of "randomness" as scale increases, which we interpret as a nonsignificant deviation from a null model envelope. In contrast, the observed trait-space filling FAR suggests that biotic sorting reduces spacing across the entire scale range by ~5–10% below the expected (mean) range in lightly disturbed plots (Fig. 4c). The discrepancy may arise from their hypothesis being based on observations that span several orders of spatial magnitude (vs. the relatively small scale range in these plots). Their model also predicts that heavily disturbed areas will show a signature of habitat filtering unchanging with scale while benign environments will display filtering only at fine scales. In this case, the trait-range FAR tends to support expectations, with the range of seed mass lower than the expected value by ~50% (on a non-log scale) in heavily disturbed plots over most of the scale range investigated here (Fig. 4h) and a reduction in seed mass range at fine scales in lightly disturbed plots (Fig. 4e).

EXTENDING THE FAR TO MULTIPLE TRAITS

An adequate assessment FD within a community will usually require examination of multiple traits since the success of an organism in a particular environment is likely dependent on more than one trait (Stubbs and Wilson 2004). Cornwell et al. (2006) introduced the convex hull volume (CHV) of multiple traits as an integrated index of trait diversity at a single scale. Here, the CHV is the volume of the smallest convex *n*-dimensional polyhedron enclosing a set of species with *n* traits in *n*-dimensional space (Preparata and Shamos 1985). CHV is fundamentally a measure of range, so

cannot be used to detect even trait spacing indicative of biotic sorting. We used log scaling of trait values since it weighs variation in each trait equally (Cornwell et al. 2006).

We illustrate use of the CHV FAR with a series of 16 2 × 2 m control plots in a larger experiment located at Point Reyes National Seashore, California, USA, described in Sandel et al. (2011). Trait data were collected for vascular plant species at these sites on height, specific leaf area (SLA), and seed mass using a combination of field sampling and database values. These traits were chosen to reflect the three primary spectra of plant life history strategies (Westoby 1998). Stem height relates to competitiveness in light-limiting environments and so reflects competitive ability (Moles et al. 2009). SLA correlates with procurement of resources, with higher values indicating a more aggressive "resource-seeking" strategy and lower values a conservative "resource-conserving" strategy (Díaz et al. 2004). Seed mass correlates positively with seedling success in stressful environments (Westoby et al. 1996). Each species was located in a three-dimensional trait space defined by these three traits. Full trait data were available for 100% of species in these plots. We chose to keep the three matched trait values (SLA, height, seed mass) for each species together when swapping values among species in the TLM test. For the TLM, we drew trait combinations from across all plots, meaning its null envelope does not collapse as scale becomes coarser, providing a potentially more powerful test at these scales.

Across all spatial scales, CHV was low relative to the null distribution, suggesting assembly mediated by habitat filtering, especially at the two coarsest scales (Fig. 5b). This pattern may relate to gradients in soil fertility, which is highly variable over fine scales at the site (B. Sandel, *unpublished data*), patchiness resulting from the action of large grazing Tule elk, or disturbance by gophers. Each of these factors could make a particular subplot unsuitable for species with certain trait values, producing lower-than-expected multivariate FD.

CONCLUSIONS

The FAR provides insight into processes and patterns that complement examination of species diversity. One might ask whether the FAR or SAR is the more "fundamental" relationship (Petchey and Gaston 2002), but we believe that each informs the other, though the relevance of the FAR or SAR will depend on the questions being asked. For example, when examining ecosystem function, the FAR may be a better indicator of the minimal size of a habitat necessary to provide a certain level of function than the SAR if traits influence function. Conservation typically focuses on the preservation of species diversity, but we foresee a role for the FAR given that an ecosystem's resilience and resistance to anthropogenic disturbance might depend at least in
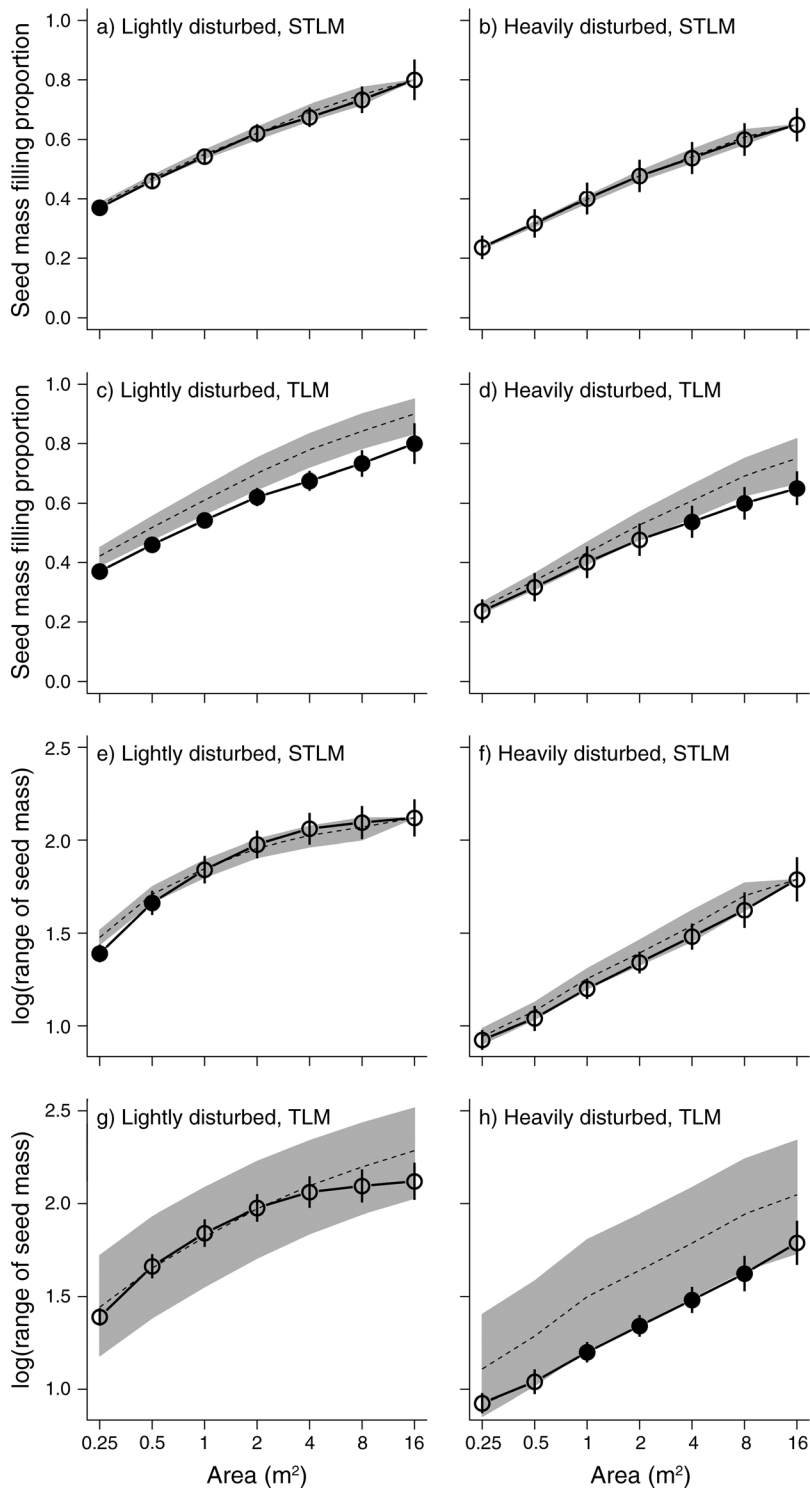
FIG. 4. The FAR for seed mass of vascular plants of a subalpine meadow as a function of disturbance intensity (harshness of the abiotic environment) tested using (a, b, e, f) the STLM and (c, d, g, h) the TLM tests. Lines and points are coded as per Fig. 2. Half of the plots were lightly disturbed (a, c, e, g) and half heavily disturbed (b, d, f, h). Generally the results support Weiher and Keddy's (1995) conceptual model, which suggests that harsh abiotic environments will show evidence for filtering across the scale range (h) while benign environments will only display filtering at fine scales (e). In contrast, Weiher and Keddy's (1995) model predicts that biotic sorting should occur at fine scales, but we found evidence for sorting across the scale range (c).
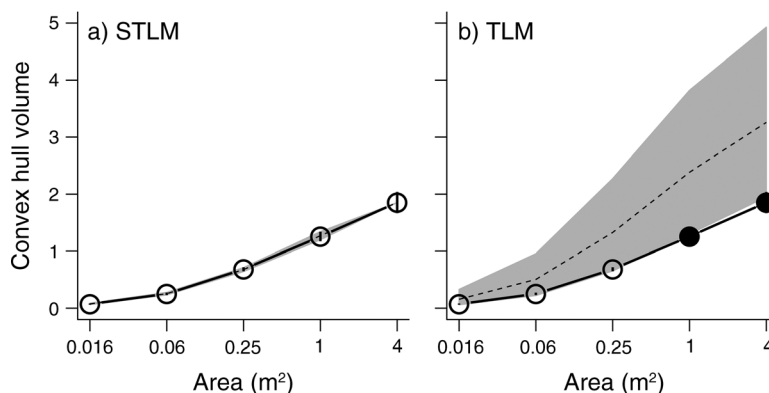
Fig. 5. Extension of the FAR to multiple traits using convex hull volume. Here, the convex hull volume FAR for the log range of three traits of vascular plant species in a coastal California grassland is shown for (a) the STLM test and (b) the TLM test. The results suggest that filtering occurs at coarse scale ranges and is related to trait-level patterns, but not species-level patterns. To construct a convex hull, each species is located at a point defined by its log(height), log(SLA), and log(seed mass). The minimum convex hull is the smallest convex polyhedron that encloses all points of all species at a particular scale. Lines and points are coded as per Fig. 2.

part on its diversity of traits (e.g., Lavorel 1999). The FAR also serves as a hitherto ignored "dimension" in macroecology, which has traditionally focused on species-level patterns to discern assembly processes (McGill 2011). At a deeper level we can ask whether causality runs from species richness to FD or vice versa. Regardless, our null models reflect the approach taken by others who assume that the SAR is the more fundamental relationship by retaining observed species richness in null models tests while allowing FD to vary (Cornwell et al. 2006, de Bello et al. 2009, Kraft and Ackerly 2010). Future directions might include alternatives like retaining observed FD but allowing richness to vary.

We have neglected fitting the empirical FARs with statistical models, such as the power or semilog functions, although this has been common practice for investigations of the SAR. Research has demonstrated that multiple mechanisms can create each of the commonly occurring statistical forms of the SAR (Hubbell 2001, Chave et al. 2002, He and Legendre 2002, among many others). As a result, any particular statistical form does not rule in favor of or against any particular mechanism. Hence, we have focused on the simplest expectation (higher or lower than a null envelope). Likewise, much debate revolves around which statistical model best fits the SAR (e.g., Fridley et al. 2005). However, we have found only slight differences in fits of statistical models to the empirical FARs in this paper. For example, of the 12 individual plots used in the earth flow analysis, differences between the R^2 of power and semilog functions for each plot were always ≤0.04, indicating very little statistical differentiation between the two.

As in any trait-based inquiry, researchers should have a firm basis for choosing the traits they focus upon (Westoby et al. 2002). Where there is no a priori reason to choose one over the other, the convex hull FAR may

better indicate relevant trends since each trait can be weighted equally. However, we caution that using multidimensional measures of FD like CHV could obscure trait differentiation along axes that allow coexistence of species or persistence in a habitat if other axes do not show such differentiation. Hence, we advise calculating both univariate and multivariate FARs to determine if different traits depart individually or jointly from null expectations along the scale gradient.

Here we have focused on the role of competition and habitat filtering since we have the best documentation of the effect of these processes on FD. However, as our understanding of the role of other processes like predation, facilitation, and disease in shaping community-level patterns of FD improves it will undoubtedly be valuable to broaden our framework. One important consideration is whether biotic sorting, like habitat filtering, should also be expected to reduce measures of trait dispersion (Mayfield and Levine 2010). We expect future work to shed more light on these expectations but in the meantime suggest caution when interpreting reduction in FD as unequivocal evidence for habitat filtering.

Our approach complements recent methodological advances. For example, Algar et al. (2011) present a method to partition variance in traits across scales, but their approach would become very complicated for more than a few scales. Future work should explore using prevalence- or abundance-weighted metrics of FD like Rao's quadratic entropy (Rao 1982) to account for changes in relative dominance of a trait; methods to further disentangle species- and trait-level patterns (Fig. 1); and trait-spacing metrics for multidimensional FD. Likewise, intraspecific trait dispersion could be examined using FARs in a manner analogous to range-area (scale-area) relationships for individual species (Kunin 1998, Harte et al. 2001). In conclusion, we encourage further integration of traits into community ecology.

While the focus of community ecologists will probably ultimately remain at the species level, a more catholic appreciation for all facets of diversity will better enable us to understand community assembly.

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SUPPLEMENTAL MATERIAL

Appendix A

An example of calculation of the null models for the functional-diversity–area relationship (FAR) (*Ecological Archives* E094-220-A1).

Appendix B

Testing the null models for the functional-diversity–area relationship (*Ecological Archives* E094-220-A2).

Appendix C

Map of the region used to create the mammalian body size FAR (*Ecological Archives* E094-220-A3).

Supplement 1

R scripts for trait-level model (TLM) and species-trait-level model (STLM) tests for nonrandom patterns in the functional-diversity–area relationship (*Ecological Archives* E094-220-S1).

Supplement 2

R scripts for simulating and testing functional-diversity–area relationships of communities with known levels of biotic sorting and abiotic filtering (*Ecological Archives* E094-220-S2).