

# Functional trait assembly through ecological and evolutionary time

James C. Stegen · Nathan G. Swenson

Received: 18 September 2008 / Accepted: 25 February 2009 / Published online: 3 April 2009  
© Springer Science + Business Media B.V. 2009

**Abstract** A classic community assembly hypothesis is that all guilds must be represented before additional species from any given guild enter the community. We conceptually extend this hypothesis to continuous functional traits, refine the hypothesis with an eco-evolutionary model of interaction network community assembly, and compare the resultant continuous trait assembly rule to empirical data. Our extension of the “guild assembly rule” to continuous functional traits was rejected, in part, because the eco-evolutionary model predicted trait assembly to be characterized by the expansion of trait space *and* trait/species sorting within trait space. Hence, the guild rule may not be broadly applicable. A “revised” assembly rule did, however, emerge from the eco-evolutionary model: as communities assemble, the range in trait values will increase to a maximum and then remain relatively constant irrespective of further changes in species richness. This rule makes the corollary prediction that the trait range will, on average, be a saturating function of species richness. To determine if the assembly rule is at work in natural communities, we compared this corollary prediction to empirical data. Consistent with our assembly rule, trait

“space” (broadly defined) commonly saturates with species richness. Our assembly rule may thus represent a general constraint placed on community assembly. In addition, taxonomic scale similarly influences the predicted and empirically observed relationship between trait “space” and richness. Empirical support for the model’s predictions suggests that studying continuous functional traits in the context of eco-evolutionary models is a powerful approach for elucidating general processes of community assembly.

**Keywords** Community assembly rules · Body size · Functional diversity · Morphological space · Nearest-neighbor difference · Adaptive dynamics

## Introduction

With the goal of understanding the processes responsible for the observed distribution and abundance of species, community ecologists have sought rules governing the assembly and structure of ecological communities. Although discussions of the processes constraining community assembly date back at least to Clements (1916, 1936) and Gleason (1917, 1926), Diamond (1975) was the first to coin the term “community assembly rule.” Diamond (1975) examined patterns of island communities with respect to coexistence (and lack thereof) of various bird species. From these analyses, Diamond (1975) inferred that some combinations of species are not possible (but see Connor and Simberloff 1979) and referred to these constraints as “community assembly rules.” This pioneering study stimulated a great deal of work looking for (and refuting) assembly rules (e.g., Adams 2007; Bangert and Whitman 2007; Belyea and Lancaster 1999; Brown et al. 2002; Connor and Simberloff 1979; Feeley 2003; Fox and Brown 1993; Gotelli and

**Electronic supplementary material** The online version of this article (doi:10.1007/s12080-009-0047-3) contains supplementary material, which is available to authorized users.

J. C. Stegen (✉)  
Department of Ecology and Evolutionary Biology,  
University of Arizona,  
Tucson, AZ, USA  
e-mail: stegen@u.arizona.edu

N. G. Swenson  
Arnold Arboretum,  
Center for Tropical Forest Science—Asia Program,  
Harvard University,  
Cambridge, MA, USA

McCabe 2002; Piechnik et al. 2008; Stone et al. 1996; Temperton et al. 2004; Weiher and Keddy 1995, 1999).

In order to elucidate the processes responsible for community assembly and structure, it is useful to adopt a functional trait approach to community ecology (Fukami et al. 2005; Hoinghaus et al. 2007; Holdaway and Sparrow 2006; McGill et al. 2006; Petchey and Gaston 2002; Weiher and Keddy 1995). This is because species names alone provide little information regarding how constituent species interact to limit or promote the distribution and abundance of one another (Foote 1997; Roy and Foote 1997; Vileger and Mouillot 2008; Weiher and Keddy 1995). As pointed out by Weiher and Keddy (1995), assembly rules based on species names are likely to become intractably complex with increasing species richness but rules based on traits can provide simple broadly applicable statements (e.g., Fox 1987, 1999; Fox and Brown 1993). In turn, the generality of assembly rules is lost when focusing on species identities but can potentially be gained with an emphasis on functional traits (Fukami et al. 2005; McGill et al. 2006).

Embracing the functional approach allowed Fox (1987) to hypothesize a general guild assembly rule: species are added to a community from those guilds not represented at a given time, and only after all guilds are represented do additional species from any given guild persist in the community (see also Fox 1989, 1999; Fox and Brown 1993, 1995; Fox and Kirkland 1992). The Fox (1987) hypothesis has received some support in small mammal communities (Brown et al. 2000, 2002; Fox 1999; Fox and Brown 1993, 1995; but see Simberloff et al. 1999; Stone et al. 1996, 2000). However, testing the Fox hypothesis requires that species be placed in discrete guilds and, while this has been a useful starting point, developing community assembly rules in the context of continuous functional traits may provide a more quantitative and general approach (McGill et al. 2006).

Here, we have four primary goals: (1) conceptually extend the Fox hypothesis to continuous functional traits; (2) compare the predictions of this conceptual hypothesis with an eco-evolutionary model of community assembly; (3) if needed, provide a revised community assembly rule for continuous functional traits; and (4) compare the predictions of the revised rule to empirical data.

#### Extending Fox's rule to continuous traits

Fox (1987) hypothesized that species are added to a community first from unrepresented guilds, and after all guilds are represented additional species can be added within guilds. Extending this hypothesis to the assembly of continuous functional traits provides four related predictions. (1) As a community assembles, the range of functional trait values will increase directly with species

richness to a maximum and subsequently remain relatively constant. This prediction is parallel to the guild hypothesis in that Fox's hypothesis predicts that the number of guilds will increase to a maximum. (2) The trait range will increase strongly with species richness during the early stage of community assembly, but this relationship will diminish as community assembly proceeds. Again, this parallels the guild hypothesis in that Fox's hypothesis predicts that only that initial accumulation of species will result in additional functional groups. (3) As a corollary to the first two predictions, the trait range is expected to be a saturating function of species richness but only when richness is sampled across the majority of its potential range. (4) The relationship between the nearest-neighbor trait distance and species richness will initially be relatively weak, and as community assembly proceeds this relationship will strengthen and become more negative. This fourth prediction assumes support for our first three predictions: the trait range will become decoupled from richness as assembly proceeds such that fluctuations in richness will lead to the "packing and unpacking" of trait space. This is in contrast to the alternative scenario whereby increases and decreases in species richness lead to expansion and contraction of the trait range, respectively, throughout all stages of community assembly.

These four predictions suggest how continuous functional traits should assemble within a community if Fox's guild assembly rule holds. However, these predictions are useful primarily as a point of departure. Their utility is limited because they are based on conceptual intuition rather than a formal model of community assembly. It is thus necessary to compare these conceptual predictions to more rigorous predictions that emerge from an explicit model of the assembly of continuous functional traits. Doing so will determine if Fox's rule is expected to translate directly to continuous functional traits and, if it does not translate, allow for a revised continuous trait assembly rule. The following section describes such a model.

#### Eco-evolutionary community assembly

As in Diamond (1975), studies of community assembly commonly examine patterns of community structure and infer assembly rules and the processes generating these rules *post hoc*. Weiher et al. (1998) captured the philosophy of this approach and stated that "In order to find and define any assembly rules for communities, we must first investigate the patterns among species assemblages." This "top-down" approach has been useful and has provided a rich array of hypotheses (e.g., Cody 1999). A complementary, and potentially useful, "bottom-up"

approach would make use of theoretical frameworks that define ecological interactions from organismal-level processes and that allow for the dynamic diversification/assembly of continuous functional traits. Community assembly rules would thus be predicted *a priori* and emerge through the dynamic interplay of ecological interactions and phenotypic diversification.

The goal of community ecology in general, and work on assembly rules in particular, should be to provide a process-based understanding of community assembly and structure. A “bottom-up” approach, as described above, can help elucidate key processes and is thus a necessary component of assembly rule research. Eco-evolutionary models (e.g., Doebeli and Dieckmann 2000; Ferriere et al. 2002, 2004) provide one approach for realizing this “bottom-up” approach. These models describe the influence of functional traits on organismal-level processes such that community-level patterns emerge as a consequence of dynamic feedbacks between ecological interactions, the evolution of novel phenotypes, and ecosystem context (Fussmann et al. 2007).

Although evolution is not addressed in some community assembly research (e.g., Weiher and Keddy 1999; but see Foote 1997; Urban et al. 2008), the structure of natural communities emerges from the combined effects of ecological *and* evolutionary processes and historical contingencies (Brooks and Wiley 1988; Drake 1990a, b; Drake et al. 1996; Lawler 1993; Roughgarden 1989). In addition, experimental studies have demonstrated that evolution works on timescales relevant to ecological phenomena, including community structure (Bohannan and Lenski 2000; Hairston et al. 2005, 2007; Thompson 1998; Venail et al. 2008; Yoshida et al. 2007; also see discussions in Ricklefs 2007). Eco-evolutionary models allow the combined influences of ecology, evolution, history, and ecosystem context to dynamically emerge as model communities assemble. Pursuing eco-evolutionary models will thus help extend community assembly theory beyond the influence of biotic and abiotic “filters” (Poff 1997) to also include the dynamic interplay between these filters and the selective pressures they place on organismal functional traits. This class of model therefore provides a powerful theoretical framework for generating *a priori* expectations for community assembly rules.

Here, we use a modified version of an eco-evolutionary model of size-structured interaction webs (Loeuille and Loreau 2005, 2006). Using this model, we provide predictions for the temporal dynamics of functional trait assembly within communities. These predictions are first compared to the conceptual predictions outlined in the previous section. We subsequently use the eco-evolutionary predictions to define a revised community assembly rule for continuous functional traits and compare empirical data to

the predicted relationships between the trait range and species richness. More generally, we aim to develop theoretical expectations for how functional traits are “packed” as communities assemble through ecological and evolutionary time. Doing so will further elucidate how organismal-level processes influence functional trait assembly which may, in turn, allow more informed predictions for the response of communities to environmental change.

### Model description

We built upon and modified a recently published eco-evolutionary model (Loeuille and Loreau 2005, 2006) to evolve dynamic interaction networks. In the model, species interactions are defined as functions of species’ body sizes and body size is allowed to evolve. In turn, the assembly of whole communities can be followed from a single consumer to complex species-rich networks. No direct constraints are placed on community assembly or structure. Rather, these are emergent properties of a given community that result from dynamic feedbacks between inter- and intra-specific competition (exploitative and interference), inter-specific trophic interactions, and consumption of and recycling into an inorganic nutrient pool. The model represents a significant advance over previous interaction network models, which are too complex to allow inference (e.g., McKane 2004) or do not explicitly define organismal functional traits (e.g., Cattin et al. 2004; Cohen et al. 1990; McKane and Drossel 2006; Williams and Martinez 2000). Furthermore, the model allows for biotic modification of a community’s niche structure and, in turn, allows biotic modification to drive community assembly (Glasser 1982).

In the model, feeding rate is determined, in part, by a Gaussian feeding function defined by the difference between predator and prey body sizes (Suppl. Fig. 1). For a given predator body size, there is an optimal prey body size around which feeding rate declines: a concept consistent with empirical data and other trophic models (Andersen and Beyer 2006; Cozar et al. 2008; Loeuille and Loreau 2005, 2006; Sala and Graham 2002). In addition, mass-specific feeding rate has been shown to scale with body size to the  $-0.25$  power (Hansen et al. 1997; Moloney and Field 1989; Peters 1983). Feeding rate is thus modeled as a function of predator,  $M_i$ , and prey,  $M_j$ , body sizes:  $f(M_i, M_j) = f_0 M_i^{-0.25} s^{-1} (2\pi)^{-0.5} \exp\left(-\frac{(M_i - M_j - d)^2}{s^2}\right)$ . Here,  $f_0$  is a constant independent of body size;  $s$  is the standard deviation of the Gaussian function, and  $d$  is the optimal predator–prey body size difference (Suppl. Fig. 1). Intrinsic, mass-specific mortality has likewise been shown to scale with body size such that:  $m(M_i) = m_0 M_i^{-0.25}$ , where  $m_0$  is a constant independent of body size (Savage et al. 2004).

In addition to exploitative competition, which emerges in the model due to population dynamics and resource consumption, interference competition is an important aspect of trophic dynamics (Skalski and Gilliam 2001). Interference competition is modeled following Loeuille and Loreau (2005, 2006) as a truncated uniform distribution such that:  $\alpha(M_i, M_j) = \begin{cases} \text{if } (|M_i - M_j| > \beta) \dots 0 \\ \text{if } (|M_i - M_j| < \beta) \dots \alpha_0 \end{cases}$ . Similarly

sized species are assumed more likely to interfere such that  $\beta$  is the threshold body size difference beyond which species  $i$  and  $j$  do not interfere and  $\alpha_0$  is the mass-specific rate of interference.

Species are modeled as pools of biomass and, for an increasing order of body sizes, where basal nutrients are denoted with a subscript 0, change in the biomass of species  $i$  is given as:

$$\frac{dN_i}{dt} = N_i \left( \varepsilon \sum_{j=0}^{i-1} f(M_i, M_j) N_j - m(M_i) - \sum_{j=1}^n \alpha(M_i, M_j) N_j - \sum_{j=i+1}^n f(M_j, M_i) N_j \right)$$

Only a fraction of consumed biomass is assimilated ( $\varepsilon$ ) and this is assumed constant with respect to body size (Peters 1983). The nutrient pool increases due to nutrients entering the system at a constant rate ( $I$ ) and as a proportion ( $\nu$ ) of

recycled nutrients from mortality and inefficient feeding. Nutrients leave the system at a mass-specific rate ( $\gamma$ ) and decline due to direct consumption. Change in nutrient biomass is thus given as:

$$\frac{dN_0}{dt} = I - N_0 \gamma + \nu \left( (1 - \varepsilon) \sum_{i=1}^n \sum_{j=0}^{i-1} f(M_i, M_j) N_i N_j + \sum_{i=1}^n m(M_i) N_i + \sum_{i=1}^n \sum_{j=1}^n \alpha(M_i, M_j) N_i N_j \right) - \sum_{i=1}^n f(M_i, M_0) N_i N_0$$

Novel body sizes enter the interaction network via mutation. Mass-specific mutation rate is assumed to scale with body mass to the  $-0.25$  power (Gillooly et al. 2005, 2007). Realized mutation rate for species  $i$  is thus given as:  $\lambda_i = N_i \lambda_0 M_i^{-1/4}$ , where  $\lambda_0$  is a normalization constant independent of body size. The value  $\lambda_0$  was chosen to give a mutation probability of  $10^{-4}$  for a body size of 5 kg; the approximate median body size of interaction webs evolved under a body-size-independent mutation probability of  $10^{-4}$ . As in Loeuille and Loreau (2005, 2006), mutations were assumed to result in small changes in body size such that a mutant's body size was taken as a proportion, drawn from a uniform distribution between 0.8 and 1.2, of its ancestor's body size. Other parameters were set to values similar to those producing realistic interaction webs in Loeuille and Loreau (2005, 2006; Table 1).

Sensitivity analyses were performed on the two parameters shown to strongly affect interaction web structure in Loeuille and Loreau (2005, 2006): the strength of interference competition and niche breadth ( $s^2/d$ ). In particular, these parameters strongly influence patterns of trait packing (see Fig. 2 in Loeuille and Loreau 2005). Three replicates were run for each of the four combinations of the maximum and minimum interference competition and niche width parameter values. Additional sensitivity analyses were performed across a range of nutrient influx rates (Table 1) as Loeuille and Loreau (2005) found this parameter to affect the maximum body size and species richness. Nutrient influx

rate sensitivity analyses were run with  $\alpha_0=0.1$  and  $s=1$ . Model simulations were run in the program R (<http://www.r-project.org/>) for ten million time steps. This was sufficient time for interaction web species richness to reach a dynamic equilibrium across all parameter values (Suppl. Fig. 2). However, results are presented up to two million time steps to allow visualization of the early stages of community assembly, and patterns did not vary greatly beyond two million time steps.

#### Model analysis

Interaction networks were initialized with a single consumer (body size=2 kg) and an initial nutrient pool (body size=0 kg). Consumer body size evolution and speciation proceeds via a mutation-selection process whereby novel mutants have either a negative population growth rate and immediately go extinct or increase and remain in the system as a new species. The fitness landscape, and thus population growth and speciation, is determined by the current species assemblage and population sizes and varies through time due to speciation and extinction. Established species are assumed to go extinct if their population size falls below a minimum threshold ( $1e-20$ ), which is equal to the population biomass of a new mutant. Hence, a dynamic speciation–extinction process emerges that is dependent on the contribution of novel phenotypes and temporal variation in the ecological context of the evolving interaction network.

**Table 1** Parameter values used in model simulations

Parameter	Description	Value (units)
$\lambda_0$	Mutation rate normalization	0.00015 (mutation $\times$ mass <sup>-3/4</sup> $\times$ time <sup>-1</sup> )
$v$	Ecosystem nutrient retention efficiency	0.5 (unitless)
$y$	Nutrient loss rate	0.1 (time <sup>-1</sup> )
$I$	Nutrient influx rate	0.71, 1.15, 1.83, 2.85, 4.4, 6.68, 10.0, 14.79, or 21.6 (mass $\times$ time <sup>-1</sup> )
$\beta$	Interference competition max. body size difference	0.25 (mass)
$\alpha_0$	Interference competition rate constant	0.1, 0.3, or 0.5 (time <sup>-1</sup> )
$m_0$	Mortality rate normalization	0.1 (mass <sup>0.25</sup> time <sup>-1</sup> )
$f_0$	Feeding rate normalization	1.189 (mass <sup>0.25</sup> time <sup>-1</sup> )
$s$	Feeding function standard deviation	1, 2.25, or 3.16 (mass)
$d$	Optimal body size difference	2 (mass)
$\varepsilon$	Assimilation efficiency	0.25 (unitless)

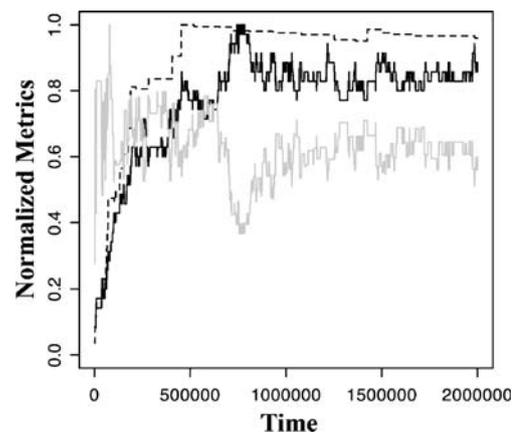
These evolving interaction webs were sampled every 1,000 time steps and for each sample, species richness, the range in body sizes, and mean nearest-neighbor body size difference were calculated. Species richness was taken as the number of unique body sizes in the community. The range in body sizes was the difference between maximum and minimum sizes. Mean nearest-neighbor difference was found by first finding the minimum body size difference between each species and all other species in the community. The mean value of these minima was then taken as mean nearest-neighbor difference. This provides a continuous metric of trait “packing” such that smaller values indicate tighter “packing” of body sizes and thus great functional similarity.

### Comparing conceptual and eco-evolutionary predictions

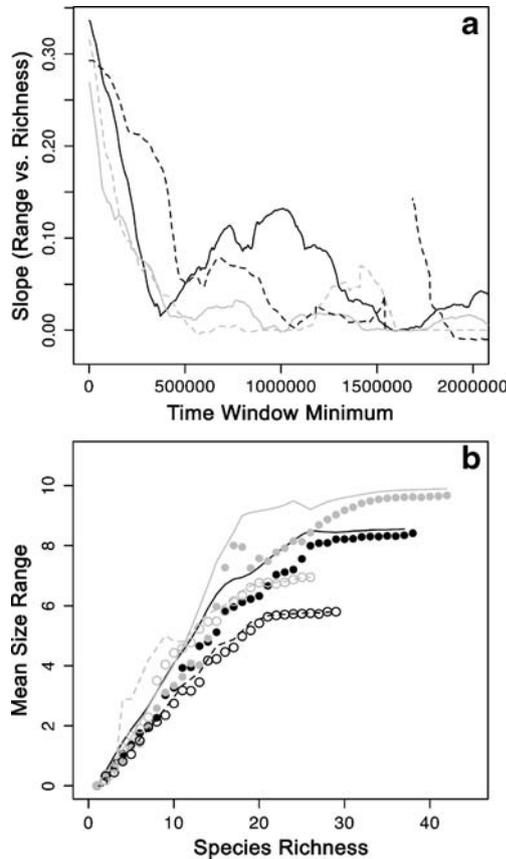
Consistent with the first prediction of our conceptual continuous trait extension of Fox’s assembly rule, across all combinations of interference competition and niche breadth and across all rates of nutrient influx, body size range first increased and abruptly reached a relatively consistent maximum (Fig. 1; Suppl. Fig. 2). The eco-evolutionary model also predicts maximum body size range to be larger when interference competition is weaker, niche breadth is broader, and nutrient influx is greater (Suppl. Fig. 2). Species richness similarly increased through time, but reached a “dynamic equilibrium” rather than a consistent maximum (Fig. 1). Richness during the dynamic equilibrium phase increased with niche breadth and nutrient influx, but interference competition had a relatively small and inconsistent effect (Suppl. Fig. 2).

Consistent with the second prediction of our conceptual assembly rule, the trait range initially increased with species richness and this relationship diminished as community assembly progressed. More specifically, the

linear slope of the regression relating the trait range to species richness, within a given time window, declined through time (Fig. 2a). This pattern was generally consistent across all combinations of interference competition and niche breadth and across all rates of nutrient influx (Suppl. Fig. 3). There were, however, important departures from the expectation that the slope would consistently decline towards zero as community assembly progressed. In some cases, the slope declined and subsequently increased and in other cases relatively steep negative slopes emerged. Nonetheless, the slope always converged towards zero as community assembly progressed (Fig. 2a, Suppl. Fig. 3).



**Fig. 1** Temporal dynamics of body size range (*dashed*), species richness (*solid black*), and mean nearest-neighbor body size distance (*gray*). Note that species richness and nearest-neighbor distance appear to be “mirror images” of each other after the body size range has reached its maximum. All three metrics were normalized to their maximum values for visualization. Parameter values as in Table 1, and  $\alpha_0=0.5$ ;  $s=3.16$



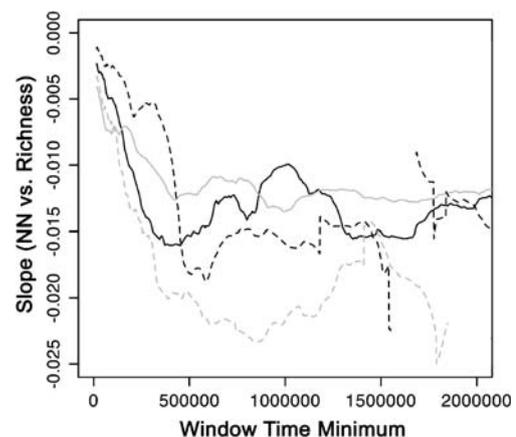
**Fig. 2** **a** Ordinary least squares slope for the regression between the body size range and species richness within a continuously moving window of 500,000 time steps. The choice of window size is somewhat arbitrary, and shorter or longer windows produce less or more smooth temporal trajectories. Lines represent the mean slope within a given time window for three replicates of each parameter combination: *solid black* ( $\alpha_0=0.5$ ,  $s=3.16$ ); *solid gray* ( $\alpha_0=0.1$ ,  $s=3.16$ ); *dashed black* ( $\alpha_0=0.5$ ,  $s=1$ ); *dashed gray* ( $\alpha_0=0.1$ ,  $s=1$ ). Regressions were not conducted if the richness range within a time window was less than four, and relatively large regions of interpolation were removed from the figure; **b** individual data points are the mean body size range for a given species richness within a given parameter combination and are based on three replicates for each parameter combination. Lines represent two standard deviations above the mean size range. Parameter combinations are the same as in part **a**, where *open symbols* correspond to *dashed lines*

When evaluated across the entire range of species richness observed within a community, instead of through time, the trait range was a saturating function of species richness (Fig. 2b). This saturating pattern emerged across all combinations of niche breadth and interference competition and across all nutrient influx rates (Suppl. Fig. 4) and was consistent with the third prediction of our continuous trait assembly rule. However, there was a variation in the trait range for a given value of species richness (Fig. 2b), which was not expected and was inconsistent with our assembly rule.

The final prediction of our conceptual assembly rule states that the relationship between the nearest-neighbor trait distance and species richness will initially be relatively weak and that this relationship will become more negative as assembly proceeds. Patterns emerging from our eco-evolutionary model are roughly consistent with this prediction (Fig. 3). A consistent temporal decline in the nearest neighbor–richness slope did not, however, emerge across our sensitivity analyses (Suppl. Fig. 5). The emergent temporal patterns of the nearest neighbor–richness slope are thus inconsistent with our continuous trait assembly rule.

### A revised continuous trait assembly rule

Patterns that emerged from the eco-evolutionary model of community assembly are not entirely consistent with the predictions made by our conceptual extension of Fox's guild assembly rule. Specific departures include (1) temporal fluctuations in the slope relating the trait range to species richness; (2) variation in the trait range for a given level of richness; and (3) temporal fluctuations in the slope relating nearest-neighbor trait distance to richness. These departures are significant enough that we reject our extension of Fox's assembly rule, and we construct a new assembly rule from the most consistent patterns that emerged from our eco-evolutionary model.



**Fig. 3** Ordinary least squares slope for the regression between the nearest-neighbor body size distance and species richness within a continuously moving window of 500,000 time steps. Lines represent the mean slope within a given time window for three replicates of each parameter combination. Line types correspond to parameters as in Fig. 2. Regressions were not conducted if the richness range within a time window was less than four, and relatively large regions of interpolation were removed from the figure

The most consistent pattern of assembly that emerged from the eco-evolutionary model was the initial increase and subsequent plateau of the trait range. Our revised assembly rule is thus: the assembly of continuous functional traits should be characterized initially by a general increase in the trait range, followed by a period of transition whereby the trait range may increase in relatively discrete steps, and upon reaching a maximum the trait range will remain relatively constant irrespective of further fluctuations in species richness. This is similar to the first prediction of our conceptual assembly rule but allows for departures from a strict relationship between the trait range and species richness during community assembly. This allows for expansion of the trait range or trait packing within the trait range at any point in time. Our assembly rule thus predicts that on average the trait range will be a saturating function of species richness and that variation around this relationship is likely (e.g., Fig. 2b). Empirical data characterized by a saturating relationship between the trait range, or morphological space, diversity, etc., would thus provide indirect support for our eco-evolutionary continuous trait assembly rule.

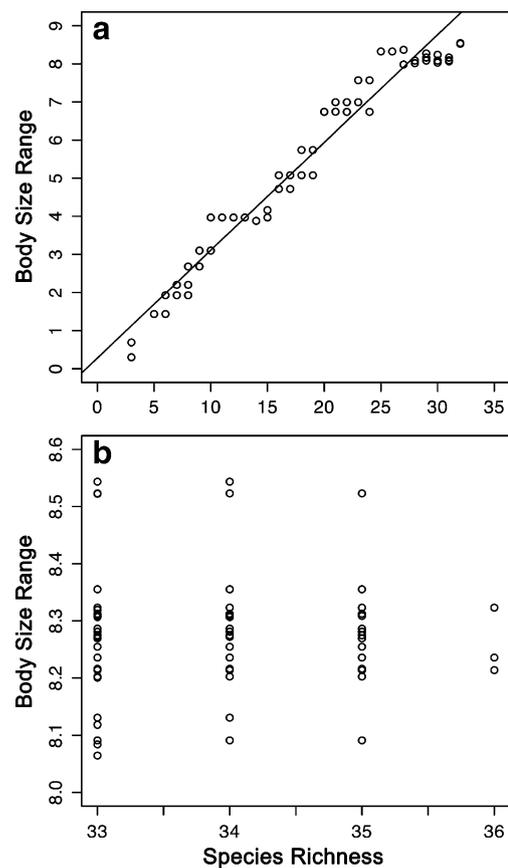
### Empirical trait range–richness relationships

To test our continuous trait assembly rule, we next compare empirical data to the prediction that trait space will be a saturating function of species richness. Before discussing the empirical data, it is important to note that for the current purposes we consider measures of trait or morphological range, space, volume, diversity, etc. to be conceptually consistent with each other and we generally use these terms interchangeably.

A number of empirical studies have examined the relationship between the range in morphological space and species richness, thus allowing for an indirect comparison of our eco-evolutionary assembly rule to empirical data. The range in morphological space occupied by functional traits has been observed to be uncorrelated with (Foote 1993; Weiher et al. 1998), to increase with (Cornwell et al. 2006; Petchey et al. 2007; Ricklefs and Miles 1994), or to saturate with species or taxonomic richness (McClain et al. 2004; Roy et al. 2001). While appearing divergent, these empirical patterns may be consistent with each other and our eco-evolutionary assembly rule. Saturating relationships between the trait range and richness consistently emerged from our eco-evolutionary model (Fig. 2b, Suppl. Fig. 4) such that linear and null relationships are likely under our assembly rule if species richness is sampled only below or above, respectively, the richness at which the trait range is maximized.

To demonstrate the likelihood of observing linear and null trait range–richness relationships, we found, within model communities, the species richness at which the trait range was maximized and split trait range and richness data into those below and above this richness value. Regressing the trait range against richness within each data group shows strongly linear and extremely weak relationships for values below and above the richness value corresponding to the maximum trait range, respectively (Fig. 4). The mean regression slope and  $R^2$  values for these two data groups across our sensitivity analyses were, respectively, 0.34 and 0.87 for values below and 0.026 and 0.067 for values above the richness value corresponding to the maximum trait range. Our eco-evolutionary assembly rule is thus at least consistent with saturating, linear, and null empirical relationships between the trait range and species richness.

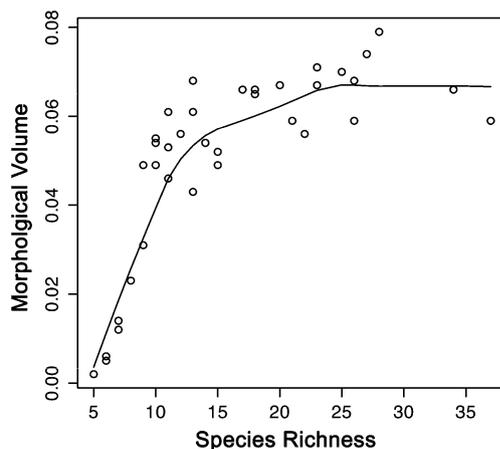
Our eco-evolutionary model predicts saturating, linear, and null relationships between the trait range and richness depending on whether or not the trait range is maximized



**Fig. 4** Body size range as a function of species richness for  $\alpha_0=0.5$  and  $s=3.16$ . The data are split between those below (a) and equal to or above (b) the maximum size range. The solid line in a is the ordinary least squares regression line. No regression line is provided in b: the regression was not significant ( $p>0.05$ )

across the sampled range of species richness. A detailed investigation of published empirical datasets provides general support for this prediction. Ricklefs and Miles (1994) examined a number of studies that related various measures of morphological space or diversity to species richness. These authors concluded that there is a general increase in morphological space with species richness but did not examine the form of this relationship. We collated data from the studies cited in Ricklefs and Miles (1994) and examined the form of the morphological space–richness relationship for each study. There is a broad range in the quality and applicability of data in these empirical studies and we do not address seven of the 13 cited studies. We excluded these seven studies because they were not accessible; they provided very few data points (<5); the species richness range was five or less, and/or they did not provide specific data on morphological range, space, etc. We did, however, augment the studies cited in Ricklefs and Miles (1994) with six additional studies.

Travis and Ricklefs (1983) was the only study cited in Ricklefs and Miles (1994) that provided a relatively large number of data points that evenly sampled a relatively large species richness range. Data from Travis and Ricklefs (1983) are consistent with our assembly rule such that morphological volume saturated with increasing species richness (Fig. 5). The other five studies cited in Ricklefs and Miles (1994) are less than ideal as they have few data points (~5) and/or provide no data across the middle or high ends of the range in species richness (Suppl. Fig. 6). Nonetheless, Suppl. Fig. 6 provides plots of morphological range, volume, etc. against species richness from four of the



**Fig. 5** Empirical data from Travis and Ricklefs (1983) relating community morphological “volume” to species richness. The morphological volume metric used was “...the geometric average distance across the morphological space occupied by a community...” See Travis and Ricklefs (1983) for additional details. The *solid line* represents a smoothed curve fit to the data

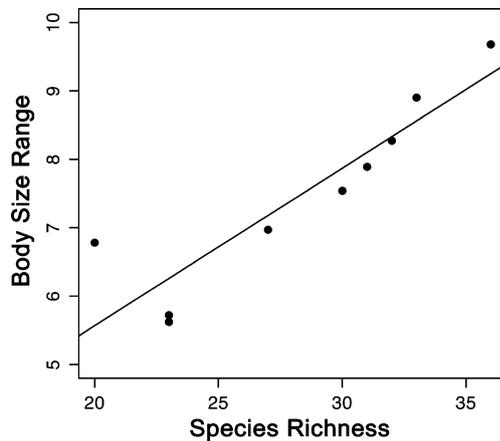
studies and Foote (1993). In general, saturating functions are commonly observed (e.g., Findley 1976; Roy et al. 2001; McClain et al. 2004) and linear relationships are observed when maximum species richness is relatively small (e.g., Ricklefs and Travis 1980; Cornwell et al. 2006) or when the middle range of species richness is not sampled (e.g., Blondel et al. 1984). Winemiller (1991) and Petchey et al. (2007) provide an exception: non-saturating morphological/functional space/diversity–richness relationships across relatively broad and uniformly sampled ranges of species richness. This departure may be due to sampling: Winemiller (1991) and Petchey et al. (2007) sampled species across multiple orders. In contrast, data from Travis and Ricklefs (1983) are constrained to passerine birds and are characterized by a saturating function.

Empirical patterns suggest that our model should predict a linear relationship between morphological space and species richness when species are sampled across relatively divergent taxonomic groups. A potentially analogous scenario in the context of the eco-evolutionary model would be to analyze the trait range–richness relationship across model communities that differ in organismal trait values. Consistent with empirical patterns, the model predicts a non-saturating function between the trait range and species richness among communities that differ in organismal trait values (Fig. 6).

We suggest that nearly all empirical patterns examined to this point are generally consistent with the predictions of the eco-evolutionary model and thus our continuous trait community assembly rule. However, in plant communities, Weiher et al. (1998) found no relationship between morphological space and species richness even though their species richness range (~2–19) was well sampled. These authors suggested that a null relationship might have resulted because they examined plant communities whereas studies prior to Weiher et al. (1998) had examined animal communities. However, Cornwell et al. (2006) demonstrated a positive relationship between morphological volume and species richness across plant communities. Our eco-evolutionary model is based on trophic interactions and thus applies most directly to animal communities. The departure from our model’s predictions in Weiher et al. (1998) and the lack of consistent patterns between Weiher et al. (1998) and Cornwell et al. (2006) suggest that plant-specific theoretical work is needed in the context of trait assembly.

## Discussion

Attempts to develop community assembly rules often describe an empirical system at one point in time and define assembly rules *post hoc* in terms of species names or sometimes functional guilds (see Weiher and Keddy 1999; Temperton et al. 2004). While useful within narrowly



**Fig. 6** The body size range as a function of species richness at the end of community assembly (i.e., at time step 10,000,000). Each data point is a single community representing a unique combination of  $\alpha_0$  and  $s$ , where  $\alpha_0$  is equal to 0.1, 0.3, or 0.5 and  $s$  is equal to 1, 2.25, or 3.16. Given the difference in organismal trait values, this analysis is more closely aligned to empirical studies that sample species relatively broadly in terms of taxonomy (e.g., across multiple orders)

defined systems, this approach limits the generality of assembly rules. More generalized and dynamic assembly rules are needed for broad understanding of biological systems and for applied issues such as the restoration of ecological communities (Temperton and Hobbs 2004).

Here, we have worked towards more general assembly rules by focusing on the dynamic assembly of a continuous functional trait, body size, in the context of an eco-evolutionary model built from organismal-level processes. We began by conceptually deriving predictions for the assembly of continuous functional traits from Fox's (1987) guild assembly rule. We subsequently used an eco-evolutionary model of community assembly to rigorously distill these conceptual predictions into an *a priori* continuous functional trait assembly rule. This predicted assembly rule was then compared to empirical patterns of community functional trait composition.

Our extension of Fox's (1987) assembly rule provided conceptual predictions for the interrelationships between species richness, the range in trait values, and nearest-neighbor trait distance. These predictions were commonly upheld across our sensitivity analyses, but a number of important departures emerged. For example, variation in the trait range was observed for any given value of species richness. This variation rejects our conceptual extension of Fox's hypothesis because it shows that functional traits can be added to the periphery of or packed and unpacked within trait space at any given time. The only prediction that was consistently upheld was the temporal increase in the trait range to a maximum that subsequently remained relatively

constant (Fig. 1, Suppl. Fig. 2). We subsequently tested this assembly rule by noting a corollary prediction: the trait range is a saturating function of species richness (Fig. 2b, Suppl. Fig. 4). This corollary prediction was generally supported empirically, with important departures observed in plant communities and for analyses that sampled across relatively broad taxonomic groups (e.g., across multiple bird orders). In turn, we extended predictions of the eco-evolutionary model to more closely address studies that use broader taxonomic sampling. In this extended case, the prediction of our model again matched the empirical relationship between morphological space, diversity, etc. and species richness (Fig. 6).

Predictions arising from the eco-evolutionary model appear to be broadly consistent with empirical communities. We suggest that our community assembly rule may thus be a general rule across animal communities that are relatively constrained taxonomically. The degree of sampled taxonomic or phylogenetic "breadth" beyond which the expected relationship between morphological space and richness transitions from saturating to linear is, however, not clear. Future studies that couple theoretical and empirical analyses to predict/quantify the taxonomic-scale dependence of trait assembly will be useful in further generalizing our assembly rule.

To this point, we have addressed community assembly in the context of Fox's assembly rule, but the eco-evolutionary model makes additional predictions that go beyond our extension of Fox's rule. The model predicts that greater resource supply, broader consumer niche breadth, and weaker interference competition allow a larger trait range (Suppl. Fig. 4). Loeuille and Loreau (2005) similarly showed that maximum body size increases with production efficiency and nutrient supply. A broader consumer niche causes lower feeding rates and a flatter feeding function (Suppl. Fig. 1). The broadest trait ranges are thus predicted to emerge when resource supply is highest, ecological interactions (trophic and competitive) are weakest, and when organisms are the most ecologically similar to each other. Thus, the more productive and closer a community is to being "neutral" (*sensu* Bell 2000, 2001; Hubbell 2001, 2006), the broader the functional trait range should be. If supported empirically, a relationship between morphological space and the relative influence of neutral/stochastic processes (e.g., Gravel et al. 2006; Chase 2007) may provide a tool through which underlying community-level processes can be inferred.

In conclusion, we have provided theoretical predictions for how functional traits are assembled as communities emerge through ecological and evolutionary time and provided a general community assembly rule for continuous functional traits. As communities assemble, the functional trait range, space, volume, diversity, etc. are

expected to increase, reach a maximum, and subsequently remain relatively constant even if species richness continues to increase or fluctuate. This assembly rule is supported indirectly through empirical analyses of the relationship between morphological space, diversity, etc. and species richness and may thus be a general assembly rule across animal communities.

**Acknowledgements** We thank Regis Ferriere, Brian Enquist, and Nicolas Loeuille for insightful comments related to the interpretation of our modeling results and Molly Stegen for her continued support. NGS was supported by a National Science Foundation Post-Doctoral Fellowship in Bioinformatics (DBI-0805618) while working on this project.

## References

- Adams DC (2007) Organization of Plethodon salamander communities: guild-based community assembly. *Ecology* 88:1292–1299. doi:10.1890/06-0697
- Andersen KH, Beyer JE (2006) Asymptotic size determines species abundance in the marine size spectrum. *Am Nat* 168:54–61. doi:10.1086/504849
- Bangert RK, Whitman TG (2007) Genetic assembly rules and community phenotypes. *Evol Ecol* 21:549–560. doi:10.1007/s10682-006-9135-7
- Bell G (2000) The distribution of abundance in neutral communities. *Am Nat* 155:606–617. doi:10.1086/303345
- Bell G (2001) Neutral macroecology. *Science* 293:2413–2418. doi:10.1126/science.293.5539.2413
- Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. *Oikos* 86:402–416. doi:10.2307/3546646
- Blondel J, Vuilleumier F, Marcus LF et al (1984) Is there ecomorphological convergence among Mediterranean bird communities of Chile, California, and France? In: Hecht MK, Wallace B, Prance GT (eds) *Evolutionary biology*, vol 18. Plenum Press, New York, pp 141–207
- Bohannan BJM, Lenski RE (2000) Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. *Ecol Lett* 3:362–377. doi:10.1046/j.1461-0248.2000.00161.x
- Brooks DR, Wiley EO (1988) *Evolution as entropy: toward a unified theory of biology*, 2nd edn. Chicago University Press, Chicago
- Brown JH, Fox BJ, Kelt DA (2000) Assembly rules: desert rodent communities are structured at scales from local to continental. *Am Nat* 156:314–321. doi:10.1086/303385
- Brown JH, Kelt DA, Fox BJ (2002) Assembly rules and competition in desert rodents. *Am Nat* 160:815–818. doi:10.1086/343882
- Cattin MF, Bersier LF, Banasek-Richter C et al (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature* 427:835–839. doi:10.1038/nature02327
- Chase JM (2007) Drought mediates the importance of stochastic community assembly. *Proc Natl Acad Sci U S A* 104:17430–17434. doi:10.1073/pnas.0704350104
- Clements FE (1916) *Plant succession: an analyses of the development of vegetation*. Carnegie Institute, Washington D.C
- Clements FE (1936) Nature and structure of the climax. *J Ecol* 24:252–284. doi:10.2307/2256278
- Cody ML (1999) Assembly rules at different scales in plant and bird communities. In: Weiher E, Keddy P (eds) *Ecological assembly rules: perspectives, advances, retreats*. Cambridge Univ Press, Cambridge
- Cohen JE, Briand F, Newman CM (1990) *Community food webs: data and theory*. Springer, Berlin
- Connor ER, Simberloff D (1979) The assembly of species communities: chance or competition. *Ecology* 60:1132–1140. doi:10.2307/1936961
- Cornwell WK, Schilck DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology* 87:1465–1471. doi:10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2
- Cozar A, Garcia CM, Galvez JA et al (2008) Structuring pelagic trophic networks from the biomass size spectra. *Ecol Modell* 215:314–324. doi:10.1016/j.ecolmodel.2008.02.038
- Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Harvard Univ Press, Cambridge
- Doebeli M, Dieckmann U (2000) Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am Nat* 156:S77–S101. doi:10.1086/303417
- Drake JA (1990a) Communities as assembled structures: do rules govern pattern. *Trends Ecol Evol* 5:159–164. doi:10.1016/0169-5347(90)90223-Z
- Drake JA (1990b) The mechanics of community assembly and succession. *J Theor Biol* 147:213–233. doi:10.1016/S0022-5193(05)80053-0
- Drake JA, Huxel GR, Hewitt CL (1996) Microcosms as models for generating and testing community theory. *Ecology* 77:670–677. doi:10.2307/2265489
- Feeley K (2003) Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. *Oecologia* 137:104–113. doi:10.1007/s00442-003-1321-5
- Ferriere R, Bronstein JL, Rinaldi S et al (2002) Cheating and the evolutionary stability of mutualisms. *Proc R Soc B Biol Sci* 269:773–780. doi:10.1098/rspb.2001.1900
- Ferriere R, Dieckmann U, Couvet D (2004) *Evolutionary conservation biology*. Cambridge Univ Press, Cambridge
- Findley JS (1976) The structure of bat communities. *Am Nat* 110:129–139. doi:10.1086/283053
- Foote M (1993) Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* 19:185–204
- Foote M (1997) The evolution of morphological diversity. *Annu Rev Ecol Syst* 28:129–152. doi:10.1146/annurev.ecolsys.28.1.129
- Fox BJ (1987) Species assembly and the evolution of community structure. *Evol Ecol* 1:201–213. doi:10.1007/BF02067551
- Fox BJ (1989) Small mammal community pattern in Australian heathland: a taxonomic rule for species assembly. In: Morris DW, Abramsky Z, Fox BJ et al (eds) *Patterns in the structure of mammalian communities*. Texas Tech Museum Special Publication Series, Lubbock, pp 91–103
- Fox BJ (1999) The genesis and development of guild assembly rules. In: Weiher E, Keddy PA (eds) *Ecological assembly rules*. Cambridge University Press, Cambridge, pp 23–57
- Fox BJ, Brown JH (1993) Assembly rules for functional groups in North American desert rodent communities. *Oikos* 67:358–370. doi:10.2307/3545483
- Fox BJ, Brown JH (1995) Reaffirming the validity of the assembly rule for functional groups or guilds. *Oikos* 73:125–132. doi:10.2307/3545735
- Fox BJ, Kirkland GL (1992) North American sorcid communities follow Australian small mammal assembly rule. *J Mammal* 73:491–503. doi:10.2307/1382015
- Fukami T, Bezemer TM, Mortimer SR et al (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecol Lett* 8:1283–1290. doi:10.1111/j.1461-0248.2005.00829.x
- Fussmann GF, Loreau M, Abrams PA (2007) Eco-evolutionary dynamics of communities and ecosystems. *Funct Ecol* 21:465–477. doi:10.1111/j.1365-2435.2007.01275.x

- Gillooly JF, Allen AP, West GB et al (2005) The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc Natl Acad Sci U S A* 102:140–145. doi:10.1073/pnas.0407735101
- Gillooly JF, Mccoy MW, Allen AP (2007) Effects of metabolic rate on protein evolution. *Biol Lett* 3:655–659. doi:10.1098/rsbl.2007.0403
- Glasser JW (1982) On the causes of temporal change in communities: Modification of the biotic environment. *Am Nat* 119:375–390. doi:10.1086/283916
- Gleason HA (1917) The structure and development of the plant association. *Bull Torrey Bot Club* 53:7–26. doi:10.2307/2479933
- Gleason HA (1926) The individualistic concept of the plant association. *Bull Torrey Bot Club* 53:7–26. doi:10.2307/2479933
- Gotelli NJ, McCabe DJ (2002) Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83:2091–2096
- Gravel D, Canham CD, Beaudet M et al (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecol Lett* 9:399–409. doi:10.1111/j.1461-0248.2006.00884.x
- Hairston NG, Ellner SP, Geber MA et al (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett* 8:1114–1127. doi:10.1111/j.1461-0248.2005.00812.x
- Hansen PJ, Bjornsen PK, Hansen BW (1997) Zooplankton grazing and growth: scaling within the 2–2,000- $\mu$ m body size range. *Limnol Oceanogr* 42:687–704
- Hansen SK, Rainey PB, Haagensen JAJ et al (2007) Evolution of species interactions in a biofilm community. *Nature* 445:533–536. doi:10.1038/nature05514
- Hoeninghaus DJ, Winemiller KO, Birnbaum JS (2007) Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *J Biogeogr* 34:324–338. doi:10.1111/j.1365-2699.2006.01587.x
- Holdaway RJ, Sparrow AD (2006) Assembly rules operating along a primary riverbed–grassland successional sequence. *J Ecol* 94:1092–1102. doi:10.1111/j.1365-2745.2006.01170.x
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton Univ Press, Princeton
- Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. *Ecology* 87:1387–1398. doi:10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2
- Lawler SP (1993) Direct and indirect effects in microcosm communities of protists. *Oecologia* 93:184–190. doi:10.1007/BF00317669
- Loeuille N, Loreau M (2005) Evolutionary emergence of size-structured food webs. *Proc Natl Acad Sci U S A* 102:5761–5766. doi:10.1073/pnas.0408424102
- Loeuille N, Loreau M (2006) Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecol Lett* 9:171–178. doi:10.1111/j.1461-0248.2005.00861.x
- McClain CR, Johnson NA, Rex MA (2004) Morphological disparity as a biodiversity metric in lower bathyal and abyssal gastropod assemblages. *Evol* 58:338–348
- McGill BJ, Enquist BJ, Weiher E et al (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185. doi:10.1016/j.tree.2006.02.002
- McKane AJ (2004) Evolving complex food webs. *Eur Phys J B* 38:287–295. doi:10.1140/epjb/e2004-00121-2
- McKane AJ, Drossel B (2006) Models of food web evolution. Oxford Univ Press, Oxford
- Moloney CL, Field JG (1989) General allometric equations for rates of nutrient-uptake, ingestion and respiration in plankton organisms. *Limnol Oceanogr* 34:1290–1299
- Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecol Lett* 5:402–411. doi:10.1046/j.1461-0248.2002.00339.x
- Petchey OL, Evans KL, Fishburn IS et al (2007) Low functional diversity and no redundancy in British avian assemblages. *J Anim Ecol* 76:977–985. doi:10.1111/j.1365-2656.2007.01271.x
- Peters RH (1983) The ecological implications of body size. Cambridge Univ Press, Cambridge
- Piechnik DA, Lawler SP, Martinez ND (2008) Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order. *Oikos* 117:665–674. doi:10.1111/j.0030-1299.2008.15915.x
- Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J N Am Benthol Soc* 16:391–409. doi:10.2307/1468026
- Ricklefs RE (2007) History and divergence: explorations at the intersection of ecology and evolution. *Am Nat* 170:S56–S70. doi:10.1086/519402
- Ricklefs RE, Miles DB (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright PC, Reilley SM (eds) *Ecological morphology*. University of Chicago Press, Chicago
- Ricklefs RE, Travis J (1980) A morphological approach to the study of avian community organization. *Auk* 97:321–338
- Roughgarden J (1989) The structure and assembly of communities. In: Roughgarden J, May RM, Levin SA (eds) *Perspectives in ecological theory*. Princeton Univ Press, Princeton, pp 203–226
- Roy K, Foote M (1997) Morphological approaches to measuring biodiversity. *Trends Ecol Evol* 12:277–281. doi:10.1016/S0169-5347(97)81026-9
- Roy K, Balch DP, Hellberg ME (2001) Spatial patterns of morphological diversity across the Indo-Pacific: analyses using strombid gastropods. *Proc R Soc Lond B Biol Sci* 268:2503–2508. doi:10.1098/rspb.2000.1428
- Sala E, Graham MH (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. *Proc Natl Acad Sci U S A* 99:3678–3683. doi:10.1073/pnas.052028499
- Savage VM, Gillooly JF, Brown JH et al (2004) Effects of body size and temperature on population growth. *Am Nat* 163:429–441. doi:10.1086/381872
- Simberloff D, Stone L, Dayan T (1999) Ruling out a community assembly rule: the method of favored states. In: Weiher E, Keddy P (eds) *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 58–74
- Skalski GT, Gilliam JF (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology* 82:3083–3092
- Stone L, Dayan T, Simberloff D (1996) Community-wide assembly patterns unmasked: the importance of species' differing geographic ranges. *Am Nat* 148:997–1015. doi:10.1086/285968
- Stone L, Dayan T, Simberloff D (2000) On desert rodents, favored states, and unresolved issues: scaling up and down regional assemblages and local communities. *Am Nat* 156:322–328. doi:10.1086/303384
- Temperton VM, Hobbs RJ (2004) The search for ecological assembly rules and its relevance to restoration ecology. In: Temperton VM, Hobbs RJ, Nuttle T et al (eds) *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice*. Island Press, Washington DC, pp 34–54
- Temperton VM, Hobbs RJ, Nuttle T et al (2004) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington DC
- Thompson JN (1998) Rapid evolution as an ecological process. *Trends Ecol Evol* 13:329–332. doi:10.1016/S0169-5347(98)01378-0
- Travis J, Ricklefs RE (1983) A morphological comparison of island and mainland assemblages of neotropical birds. *Oikos* 41:434–441. doi:10.2307/3544103

- Urban MC, Leibold MA, Amarasekare P et al (2008) The evolutionary ecology of metacommunities. *Trends Ecol Evol* 23:311–317. doi:10.1016/j.tree.2008.02.007
- Venail PA, MacLean RC, Bouvier T et al (2008) Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. *Nature* 452:210–214. doi:10.1038/nature06554
- Villeger S, Moullot D (2008) Additive partitioning of diversity including species differences: a comment on Hardy & Senterre (2007). *J Ecol* 96:845–848. doi:10.1111/j.1365-2745.2007.01351.x
- Weiher E, Keddy PA (1995) Assembly rules, null models and trait dispersion: new questions from old patterns. *Oikos* 74:159–164. doi:10.2307/3545686
- Weiher E, Keddy PA (1999) *Ecological assembly rules*. Cambridge University Press, Cambridge
- Weiher E, Clarke GDP, Keddy PA (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309–322. doi:10.2307/3547051
- Williams RJ, Martinez ND (2000) Simple rules yield complex food webs. *Nature* 404:180–183. doi:10.1038/35006555
- Winemiller KO (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecol Monogr* 61:343–365. doi:10.2307/2937046
- Yoshida T, Ellner SP, Jones LE et al (2007) Cryptic population dynamics: rapid evolution masks trophic interactions. *PLoS Biol* 5:1868–1879. doi:10.1371/journal.pbio.0050235