

Are regional effects on local diversity more important in marine than in terrestrial communities?

Jon D. Witman

J. D. Witman (jon_witman@brown.edu), Ecology and Evolutionary Biology Dept, Brown Univ., Providence, RI 02912, USA.

In a thought provoking article, Cornell and Harrison (2012) explore the reasons for different perspectives on the importance of the regional species pool in governing local species diversity on land vs the sea. I begin my commentary by underscoring the importance of regional processes in shaping local diversity then react to their explanations for the different system-based perspectives and conclude by proposing an experimental design to test for differences in regional enrichment of local species richness between marine and terrestrial systems.

That the number of species in a particular local community is at some level influenced by the diversity of species in the broader region is unarguable. For example, a cleared local patch of forest in the Amazon will contain more tree species after a period of community assembly than one of the same size in New England. This is partly due to the higher diversity of tree species outside the local patch (i.e. the regional species pool) in the Amazon available to colonize the patch. A vexing question at the heart of community ecology (Terborgh and Faaborg 1980, Cornell 1985, Ricklefs 1987, Cornell and Lawton 1992, Huston 1999) is, how important are regional processes 'relative' to local ones such as competition, predation, disturbance, facilitation, productivity, habitat complexity, local propagule supply and environmental factors that may ultimately increase, decrease, or impact local diversity in non-linear ways? A version of this question was originally formalized in an elegantly simple graphical model (Cornell 1985) known as local-regional richness (LSR–RSR) plots predicting that a linear relation between regional and local diversity indicates an unsaturated community where the regional species pool has an effect on local diversity corresponding to the magnitude of the correlation or the fit and slope of a regression line. In contrast, a curvilinear relation where local diversity leveled off with further increases in regional pool richness indicated that competitive species interactions were limiting local species richness, representing a saturated community. However elegant and heuristic, this interpretation turned out to be overly simplistic (Srivastava 1999, Huston 1999) as other factors besides local competition and regional pool size (e.g. disturbance, dispersal; Caswell and Cohen 1993, Shurin 2000, Mouquet and

Loreau 2003, Shurin and Srivastava 2005) can affect LSR–RSR relationships which are also sensitive to temporal variation, potentially switching from linear to curvilinear functions during community assembly (Mouquet et al. 2003, Belote et al. 2009).

Nonetheless, it is a legitimate and important effort, perhaps more so now than before (Lawton 2000) in this era of rapid global change to investigate the interplay of regional and local drivers of local diversity. Fruitful new avenues involve 1) an experimental macroecological approach (Witman and Roy 2009) where experiments manipulating local drivers of diversity across regional diversity gradients are combined with LSR–RSR analyses (Harrison and Cornell 2008, Canning-Clode et al. 2009, 2010, Belote et al. 2009, Freestone and Osman 2011) 2) analyzing multiple diversity structuring factors along with regional pool richness using multiple regression or structural equation modeling (Harrison and Cornell 2008) 3) investigating mechanisms linking the regional pool to local communities, such as propagule dispersal (Palmer et al. 1996, Shurin 2000, Merritt et al. 2010, Palardy and Witman 2011) and 4) studying the role of temporal variation (Fig. 1, Cornell and Harrison 2012, Belote et al. 2009, Canning-Clode et al. 2010) in determining the nature of LSR–RSR relations.

Cornell and Harrison (2012) suggest that the influence of the regional pool on local diversity is far better documented in the marine than terrestrial literature, providing three potential explanations.

Explanations 1 and 2 are related, that an emphasis on regional dispersal began earlier in marine communities 1) and that regional scale processes are actually more important in marine than terrestrial communities 2). The type of regional dispersal the authors are referring to is apparently the dispersal of reproductive propagules (i.e. Fig. 2, Cornell and Harrison 2012) such as fertilized embryos, larvae, asexual buds, spores and seeds. This is just one type of dispersal influencing LSR–RSR relations, which includes the migration of adults and juveniles as well as propagule dispersal (Holyoak et al. 2005). The distinction is important to the comparison of marine – terrestrial regional influences because some terrestrial LSR–RSR relationships are based

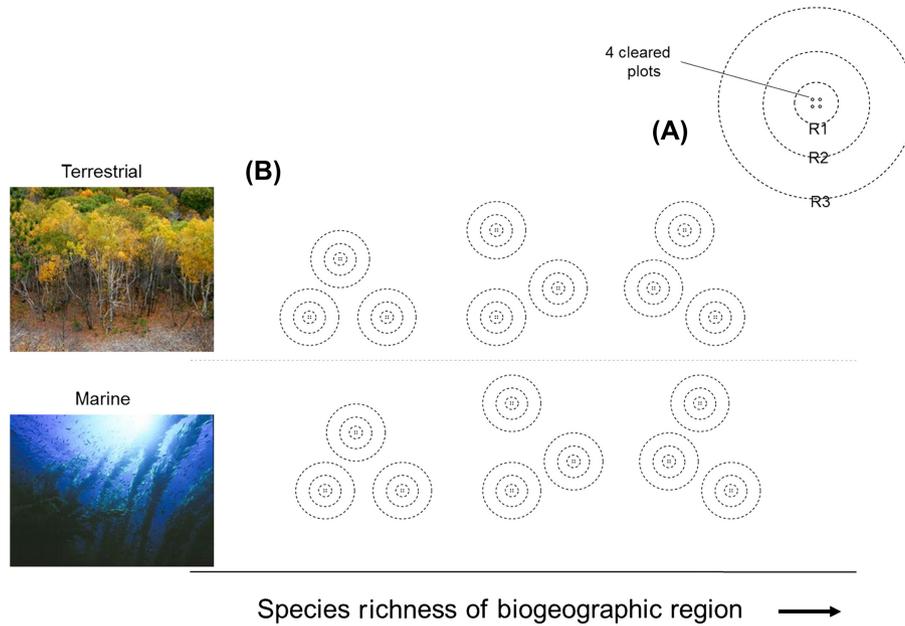


Figure 1. Diagram of an experimental design to test for differences in the extent of regional enrichment of local species richness between marine and terrestrial systems. The manipulation could be performed in a kelp forest underwater in a temperate forest on land by clearing four large plots of all vegetation and sessile fauna (at center of Fig. 1A) and monitoring the local species richness of the assembling community in the plots over time (Fig. 2). There would be an equal number of non-cleared control plots adjacent to the cleared ones (not shown). In this 'bull's-eye' colonization design, the cleared plots and controls are embedded in a regional species pool represented by the dashed circles. The number of species present in the surrounding region (pool) would be assessed at small, intermediate and large distances with regional pool habitat areas corresponding to the area of the inner circle defined by R1 and the area of the concentric rings R2–R3 in Fig. 1A. By replicating the bulls eye colonization experiments in multiple biogeographic regions, a wide range of regional richness would be sampled and included in LSR–RSR analyses, Fig. 1B. The experiments assume that propagule dispersal of sessile organisms (plants, benthic invertebrates) is the mechanism linking the regional pool to the local community. The design factors in the effect of dispersal distance from the regional pool, variation in regional pool richness and assembly time. The experiment could be designed so that the areas of the regional pools (concentric rings, inner area) are equivalent by using the equation below to solve for the radius r , representing the distance from the center of the 'bull's-eye' to the perimeter of each ring: $r = \sqrt{Ax/\pi}$, where A = area of the inner circle (e.g. contained in R1 of Fig. 1A) and x = number of rings plus the inner circle.

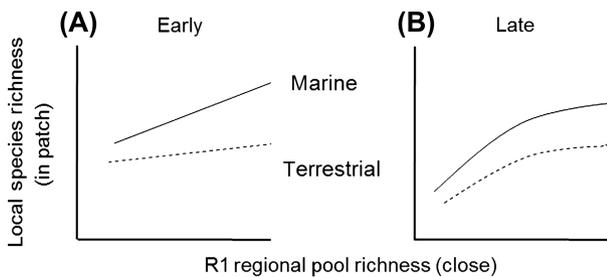


Figure 2. Two regional – local species richness plots that could result from the experimental manipulation depicted in Fig. 1, showing hypothetical effects of the duration of community assembly (early, late) on LSR–RSR relationships in marine and terrestrial systems. Results are shown only for the smallest distance class of regional pools, R1 (as in Fig. 1A). Analyses of regional (x) vs local (y) species richness would be analyzed separately by distance class (as shown here) because the regional pools defined by the distance classes are not independent. The LSR–RSR relationship may be linear and unsaturated early in community assembly (Fig. 2A) as the plots are colonized by propagules from the regional pool, becoming non-linear later on (Fig. 2B) as the community saturates and species interactions limit local richness (Mouquet et al. 2003, Belote et al. 2009). The lines and curves plotted to show a result consistent with Cornell and Harrison's (2012) hypothesis that the regional species pool has a greater influence on local species richness in marine than in terrestrial communities.

on mobile fauna such as birds (Terborgh and Faaborg 1980, Ricklefs 1987, Gaston and Blackburn 2000), and insects (Srivastava 2005, Fig. 3, Cornell and Harrison 2012) that can migrate from the region to local habitats.

The current emphasis on propagule dispersal in marine and terrestrial community ecology can be traced, at a minimum, back to early twentieth century investigations in fisheries biology of the role of oceanographic variability in fish recruitment (Hjort 1926) and to observations of seed dispersal in agricultural science (Clements 1916, Ridley 1930). Perhaps historians of science can weigh in on this issue as I find it difficult, as the authors do, to argue for the first explanation that terrestrial ecologists had their eyes fixed on local assemblages while marine ecologists were casting a broader gaze on regional propagule dispersal. The fisheries biologists' emphasis on the role of recruitment (Ricker 1954) in population regulation was largely unappreciated in marine ecology until key experiments began 'supply sided ecology' in the early 1980s (Paine and Levin 1981, Underwood and Denley 1984, Gaines and Roughgarden 1985). By the 1977 publication of Harper's book on the 'Population biology of plants', studying spatial variation in seed dispersal was a mainstream component of plant ecology. Considering the dispersal of adults rather than propagule dispersal as the regional – local

link blurs any marine-terrestrial differences in the chronology of emphasis on regional dispersal, as the regional-continental scale migration of fish, insects and mammals has fascinated scientists since the inception of ecology.

Part of the difficulty in evaluating explanation 2 (regional scale processes more important in marine communities) is that the definition of what constitutes a regional scale is fairly arbitrary (Srivastava 1999). What matters for LSR-RSR theory is that the physical scale of the region corresponds to the spatial scale of the regional source pool of potential colonists. A region can be anywhere between 2.0 and 2000 km distance of an intermediate spatial scale referred to as the mesoscale (Orlanski 1975). A region has been defined as 'a large area of habitat containing multiple localities and capable of supporting a metacommunity' – corresponding to the mesoscale of Holt (1993) in Holyoak et al. (2005) and also as an area > 200 and < 2000 km by Mittelbach et al. (2001). Some investigators consider substantially smaller regions, such as an individual fish (Aho and Bush 1993).

Although challenged by recent research (Puebla et al. 2009, Pinsky et al. 2010), a body of work suggests that the spatial scale of propagule dispersal in terrestrial plants (Harper 1977, Nathan 2006) is less than that of marine organisms (Richmond 1989, Kinlan and Gaines 2003, Reed et al. 2006) and is not typically at the mesoscale of a region. Long distance passive dispersal in plants is on the order of a few km for wind-dispersed conifer pollen (O'Connell et al. 2007) while 50 m is an average dispersal distance for tree propagules (Nathan 2006). Longer distance seed dispersal is achieved by animal vectors (Howe and Smallwood 1982) and extreme events (Nathan 2006), but even at these distances seed dispersal may only overlap the lower threshold of the regional scale of dispersal in marine propagules, which may occur over tens to hundreds of kilometers (Richmond 1989, Kinlan and Gaines 2003, Shanks et al. 2003). Genetic approaches of measuring dispersal suggest that the simulations used in Kinlan and Gaines (2003) overestimated the dispersal distance of coral reef fish larvae by an order of magnitude (Puebla et al. 2009). I generally agree however, with the authors that propagule dispersal on regional spatial scales is more common in marine than terrestrial communities (Carr et al. 2003), and may be a factor contributing to a greater recognition of regional effects in marine communities but clearly, more research using genetic and empirical methods is needed to refine estimates of actual dispersal distances. An experimental study of the effects of wind vs water dispersed propagules (seeds) on the diversity of riparian plant communities showed that treatments receiving only water dispersed seeds attained higher local species richness than those receiving wind dispersed seeds during early succession (Merritt et al. 2010) lending support to speculation that regional propagule dispersal may play a greater role in shaping local richness in aquatic and marine systems in general, than in terrestrial systems. Three mechanisms of long distance dispersal of plants and invertebrates warranting further consideration in LSR-RSR relations are 1) passive rafting (Thiel and Haye 2006, Winston 2012), 'hitchhiking' on or in vertebrates such as sea turtles, dolphins and birds (Spivey 1980, Harding et al.

2011, Gillespie et al. 2012) and 3) human transport of species, a major focus of invasion biology (Hulme 2009).

The last explanation offered for the perception that regional processes are more established in marine than in terrestrial community ecology is that recruitment from the regional pool is easier to study in marine vs terrestrial systems. This explanation is apparently conditional on the 2nd one; that is, if regional propagule dispersal (and ensuing recruitment) were more common in marine vs terrestrial systems, wouldn't it be more easily studied in marine communities? It may be that densely vegetated habitats on land such as forests provide more of an obstacle by serving as barriers to dispersal (Fig. 2, Cornell and Harrison 2012) or the permeability (Witman et al. 2004a) of propagule rain from the regional pool than in the ocean. A glance at the vast ocean gives the impression of an open system, yet the idea that barriers to dispersal are more common in marine vs terrestrial environments warrants closer examination as there is more habitat structure in deep benthic habitats (Levin and Dayton 2009) than meets the eye. Dawson and Hamner (2008) argue that an appropriate framework for marine-terrestrial comparisons should be based on similar physical environments, which are marine pelagic and aerial over land, and marine benthic and the surface of the land.

Can the main hypothesis of Cornell and Harrison's (2012) paper, that the regional species pool has a greater influence in marine than terrestrial communities be tested in the field by experimental manipulation? I think so. One potential approach that factors in the effects of the scale of propagule dispersal, the duration of community assembly (Jacquemyn et al. 2001, Belote et al. 2009) and variation in regional pool richness is proposed in Fig. 1 as a starting point. The manipulation involves clearing large (> 10 m²) replicate plots underwater in kelp forests and simultaneously in temperate forests on land. The experimental unit is a cleared plot, shown in Fig. 1A as four replicate small circles at the center of the 'bull's-eye'. An equal number of replicate control plots containing undisturbed vegetation would be randomly located near the cleared plots (not shown in diagram). In this bull's-eye colonization design, the cleared plots and controls are embedded in a regional species pool represented by the dashed circles. The number of species present in the surrounding region (pool) would be assessed at small, intermediate and large distances (concentric rings R1-R3 in Fig. 1A) from the cleared and control plots, while local species richness would be determined as the number of species colonizing the clearings. Because the small, intermediate and large distance classes of regional pools are not independent, regional (x) vs local (y) species richness would be analyzed separately for each distance class. For example, Fig. 2 shows a hypothetical LSR-RSR plot for the regional pool (R1 of Fig. 1A) closest to the cleared and control plots. A wide range of variation in the species richness of the regional pool (x-variable of LSR-RSR plots) would be sampled by replicating the bull's-eye colonization experiments in several biogeographic regions (Fig. 1). The effect of assembly time on the degree of regional enrichment and the form of the LSR-RSR functions would be determined by sampling the plots and regions early (months) and late (years) in succession. Temporal comparisons may indicate a linear

LSR–RSR relation in the early phase of community assembly but a non-linear one suggesting saturation later on (Fig. 2A–B). The null hypothesis of no difference in regional pool influences on local species richness between marine and terrestrial communities would be rejected if statistical metrics (slopes of the regression lines for linear fits, asymptotes of curvilinear functions, etc.) were significantly different. Differences in the regression coefficients of linear or non-linear LSR–RSR fits between the marine–terrestrial data would also indicate fundamental departures in the way that the regional species pool enriches local species richness in the two systems provided that the methodological problems potentially confounding LSR–RSR analyses are addressed (Srivastava 1999, Huston 1999, Witman et al. 2004b, Shurin and Srivastava 2005).

Is this experiment tractable? That depends on the amount of innovative thinking put into it to overcome the inherent difficulties of performing a logistically challenging, large-scale experiment in two systems where the colonizing species have radically different life histories, additional mechanisms of occupying space in the plots besides propagule dispersal (asexual re-growth, activation of seed banks in soil etc.) and where the source of the propagules colonizing the local plots is difficult to identify. Solutions to these challenges are available and include photographic monitoring of the plots to distinguish individuals that have re-grown asexually from those colonizing as propagules, using seed traps and recruitment substrates (Reed et al. 2006) to identify species colonizing as propagule rain and by using particle tracers (Levin et al. 1993) and genetic techniques (O’Connell et al. 2007, Puebla et al. 2009, Pinsky et al. 2010) to identify sources of propagules dispersing into the plots. Advances in metacommunity theory (Holyoak et al. 2005) and technology (e.g. remote sensing, high resolution GIS, acoustic methods of ocean current measurement, digital photography, molecular markers etc.) since regional diversity theory was developed in the 1980s have made it easier to test ecological theory at regional spatial scales. It is an exciting time to bring more experiments to bear on the question of how regional and local processes determines the number of species present in the local habitats we love to study and need to preserve.

Acknowledgements – Thanks to Editor Matt Bracken for improving the manuscript with their critical comments. Our LSR–RSR research was originally funded by the Biological Oceanography Program of the US National Science Foundation.

References

- Aho, J. M. and Bush, A. O. 1993. Community richness in parasites of some freshwater fishes from North America. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities: historical and geographical perspectives*. Univ. of Chicago Press, pp. 185–193.
- Belote, R. T. et al. 2009. Disturbance alters local–regional richness relationships in Appalachian forests. – *Ecology* 90: 2940–2947.
- Canning-Clode, J. et al. 2009. Local–regional richness relationship in fouling assemblages – effects of succession. – *Basic Appl. Ecol.* 10: 745–753.
- Canning-Clode, J. et al. 2010. Expanded view of the local–regional richness relationship by incorporating functional richness and time: a large scale-perspective. – *Global Ecol. Biogeogr.* 19: 875–885.
- Carr, M. H. et al. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. – *Ecol. Appl.* 13: 90–107.
- Caswell, H. and Cohen, J. E. 1993. Local and regional regulation of species area relation: a patch occupancy model. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities: historical and geographical perspectives*. Univ. of Chicago Press, pp. 99–107.
- Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. – Carnegie Inst. Wash., Publ. 355: 1–172.
- Cornell, H. V. 1985. Local and regional richness of cynipine gall wasps on California oaks. – *Ecology* 66: 1247–1260.
- Cornell, H. V. and Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities – a theoretical perspective. – *J. Anim. Ecol.* 61: 1–12.
- Cornell, H. V. and Harrison, S. P. 2012. Regional effects as important determinants of local diversity in both marine and terrestrial systems. – *Oikos* 122: 288–297.
- Dawson, M. N. and Hamner, W. H. 2008. A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. – *J. R. Soc. Interface* 5: 135–150.
- Freestone, A. and Osman, R. W. 2011. Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. – *Ecology* 92: 208–217.
- Gaines, S. and Roughgarden, J. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. – *Proc. Natl Acad. Sci. USA* 82: 3707–3711.
- Gaston, K. J. and Blackburn, T. M. 2000. *Pattern and process in macroecology*. – Blackwell.
- Gillespie, R. G. et al. 2012. Long-distance dispersal: a framework for hypothesis testing. – *Trends Ecol. Evol.* 27: 47–56.
- Harding, J. M. et al. 2011. Sea turtles as potential dispersal vectors for non-indigenous species: the veined rapa whelk as an epibiont of loggerhead sea turtles. – *SW Nat.* 2011: 233–244.
- Harper, J. L. 1977. *Population biology of plants*. – Academic Press.
- Harrison, S. and Cornell, H. V. 2008. Toward a better understanding of the regional causes of local community richness. – *Ecol. Lett.* 11: 969–979.
- Hjort, J. 1926. Fluctuations in the year classes of important food fishes. – *J. Conseil Int. L’Exploration Mer* 1: 5–18.
- Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities: historical and geographical perspectives*. Univ. of Chicago Press, pp. 77–88.
- Holyoak, M. et al. 2005. *Metacommunities: spatial dynamics and ecological communities*. – Univ. of Chicago Press.
- Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – *Annu. Rev. Ecol. Evol.* 13: 201–228.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. – *J. Appl. Ecol.* 46: 10–18.
- Huston, M. 1999. Local processes and regional patterns: appropriate scales for considering variation in the diversity of plants and animals. – *Oikos* 86: 393–401.
- Jacquemyn, H. et al. 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. – *J. Biogeogr.* 28: 801–812.
- Kinlan, B. and Gaines, S. D. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. – *Ecology* 84: 2007–2020.

- Lawton, J. H. 2000. Community ecology in a changing world. – *Ecol. Inst.*, Oldendorf.
- Levin, L. A. and Dayton, P. K. 2009. Ecological theory and continental margins: where shallow meets deep. – *Trends Ecol. Evol.* 24: 606–617.
- Levin, L. A. et al. 1993. Rare earth tagging methods for the study of larval dispersal by marine invertebrates. – *Limnol. Oceanogr.* 38: 346–360.
- Merritt, D. M. et al. 2010. Consequences of propagule dispersal and river fragmentation for riparian plant community diversity and turnover. – *Ecol. Monogr.* 80: 609–626.
- Mittelbach, G. G. et al. 2001. What is the observed relationship between species richness and productivity? – *Ecology* 82: 2381–2396.
- Mouquet, N. and Loreau, M. 2003. Community patterns in source–sink metacommunities. – *Am. Nat.* 162: 544–557.
- Mouquet, N. et al. 2003. Community assembly time and the relationship between local and regional species richness. – *Oikos* 103: 618–626.
- Nathan, R. 2006. Long-distance dispersal of plants. – *Science* 313: 786–788.
- O’Connell, L. M. et al. 2007. Extensive long distance pollen dispersal in a fragmented landscape maintains genetic diversity in white spruce. – *J. Hered.* 98: 640–645.
- Orlanski, I. 1975. A rational subdivision of scales for atmospheric processes. – *Bull. Am. Meteorol. Soc.* 56: 527–530.
- Paine, R. T. and Levin, S. A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. – *Ecol. Monogr.* 51: 145–178.
- Palardy, J. E. and Witman, J. D. 2011. Water flow drives biodiversity by mediating rarity in marine benthic communities. – *Ecol. Lett.* 14: 63–68.
- Palmer, M. A. et al. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. – *Trends Ecol. Evol.* 11: 322–327.
- Pinsky, M. L. et al. 2010. Using isolation by distance and effective density to estimate dispersal scales in anemonefish. – *Evolution* 64: 2688–2700.
- Puebla, O. et al. 2009. Estimating dispersal from genetic isolation by distance in a coral reef fish (*Hypoplectrus puella*). – *Ecology* 90: 3087–3098.
- Reed, D. C. et al. 2006. A metapopulation perspective on patch dynamics and connectivity of giant kelp. – In: Kritzer, J. P. and Sale, P. F. (eds), *Marine metapopulations*. Academic Press, pp. 353–386.
- Richmond, R. H. 1989. The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. – *Elsevier Oceanogr. Ser.* 52: 127–140.
- Ricker, W. E. 1954. Stock and recruitment. – *J. Fish. Res. Board Can.* 11: 559–623.
- Ricklefs, R. E. 1987. Community diversity – relative roles of local and regional processes. – *Science* 235: 167–171.
- Ridley, H. N. 1930. The dispersal of plants throughout the world. – L. Reeve and Co.
- Shanks, A. L. et al. 2003. Propagule dispersal distance and the size and spacing of marine reserves. – *Ecol. Appl.* 13: 159–169.
- Shurin, J. B. 2000. Dispersal limitation, invasion resistance and the structure of pond zooplankton communities. – *Ecology* 81: 3074–3086.
- Shurin, J. B. and Srivastava, D. S. 2005. New perspectives on local and regional diversity: beyond saturation. – In: Holyoak, M. et al. (eds), *Metacommunities*. Univ. of Chicago Press, pp. 339–417.
- Spivey, H. R. 1980. Occurrence of the balanomorph barnacle *Xenobalanus globicipitis* Steenstrup, 1851 (Coronulidae) on the Atlantic bottlenosed dolphin *Tursiops truncatus* in the Gulf of Mexico. – *Florida Sci.* 43: 292–293.
- Srivastava, D. S. 1999. Using local–regional richness plots to test for species saturation: pitfalls and potentials. – *J. Anim. Ecol.* 68: 1–16.
- Srivastava, D. S. 2005. Do local processes scale to global patterns? The role of drought and the species pool in determining treehole insect diversity. – *Oecologia* 145: 205–215.
- Terborgh, J. W. and Faaborg, J. 1980. Saturation of bird communities in the West Indies. – *Am. Nat.* 116: 178–195.
- Thiel, M. and Haye, P. A. 2006. The ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. – *Oceanogr. Mar. Biol. Annu. Rev.* 44: 323–429.
- Underwood, A. J. and Denley, E. J. 1984. Paradigms, explanations, and generalizations in models for the structure for the structure of intertidal communities on rocky shores. – In: Strong, D. L. et al. (eds), *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, pp. 151–180.
- Winston, J. E. 2012. Dispersal in marine organisms without a pelagic larval phase. – *Integra. Compar. Biol.* 52: 447–457.
- Witman, J. D. and Roy, K. 2009. Experimental marine macroecology: progress and prospects. – In: Witman, J. D. and Roy, K. (eds), *Marine macroecology*. Univ. of Chicago Press, pp. 341–356.
- Witman, J. D. et al. 2004a. The influence of physical processes, organisms, and permeability on cross-ecosystem fluxes. – In: Polis, G. A. et al. (eds), *Food webs at the landscape level*. Univ. of Chicago Press, pp. 335–358.
- Witman, J. D. et al. 2004b. The relationship between regional and local species diversity in marine benthic communities: a global perspective. – *Proc. Natl Acad. Sci. USA* 101: 15664–15669.