Assembly Models

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Introduction

Understanding the processes that drive the assembly of a community has been a central theme of ecology since the foundation of the discipline. It concerns basic questions such as how do we start from a regional species pool to assemble a structured community? How many species should be found at a given location? What is the relationship between community structure and the environment? Studying the different drivers of community assembly is not only interesting for its own sake, but is also essential for a predictive ecology. The different processes involved in the assembly of a community will also be the ones driving the response to future environmental changes. The theme of community assembly is a huge area including an immense amount of theoretical, experimental, and observational studies. This article and bibliography will attempt to cover the main aspects of the discipline with a special attention to assembly models. It starts with a section defining the domain of the article and then sets the stage with the presentation of historical backgrounds. The next section addresses the community assembly dynamics in space and time. Conceptual aspects of the empirical investigation of community assembly are then presented with a section on the war over assembly rules, which launched the tradition of null model testing in community ecology. The article ends with the subject of the future of community assembly and an outlook on three fields that have gained considerable interest over the last decade: ecophylogenetics, trait-based assembly, and network ecology. The focus is mainly on the ecology of community assembly and therefore the reader interested by its evolutionary counterpart should consult the theme of adaptive radiation.

Definitions

Several definitions of community assembly have been proposed, some more stringent than others. Given its central role in ecology, the study of community assembly shares historical landmarks with several other themes such as the niche, the Competitive Exclusion Principle, and species distribution over environmental gradients (see Historical Background). The term "assembly rules" nonetheless came later, when Diamond 1975 introduced it to refer to a set of empirically derived regular aspects of community structure. After years of debate over the existence of such rules, the theme of community assembly became much broader in scope. Keddy 1992 generalized it as follows: "the objective of assembly rules is to predict which subset of the total species pool for a given region will occur in a specified habitat" (p. 158). The idea that communities are samples from a regional species pool gained further interest as it made its presence felt in the proposition of the Neutral Theory of biodiversity and Metacommunity Ecology. Nowadays the term "community assembly" is commonly employed to refer to "any constraint on species coexistence," as in Götzenberger, et al. 2012. Fukami 2010 also emphasizes its dynamic aspects, with explicit consideration of the buildup of the community through sequential establishment of colonists and the development of their population. In his seminal book on biogeography, MacArthur 1972 proposed four essential ingredients of community assembly: the structure of the environment, species morphology, the economics of its behavior, and population dynamics. Vellend 2010 focuses on how these fundamental ingredients still hold today as major drivers of community assembly, with the addition of dispersal and evolutionary processes.

Diamond, Jared. 1975. Assembly of species communities. In *Ecology and evolution of communities*. Edited by Martin L. Cody and Jared Diamond, 342–444. Cambridge, MA: Belknap.

This book chapter launched the idea that there are some "assembly rules" based on an interpretation of years of field work on bird assemblages near New Guinea. Rules are derived from well-defined patterns of species co-occurrence and assume strong interspecific interactions.

Fukami, T. 2010. Community assembly dynamics in space. In *Community ecology: Processes, models, and applications*. Edited by Herman A. Verhoef and Peter J. Morin, 45–54. Oxford: Oxford Univ. Press.

Synthesizes the dynamics of community assembly with special attention to the effect of assembly history and spatial dynamics; distinguishes deterministic from historically contingent community assembly; and discusses the impact of patch size, patch isolation, and environmental heterogeneity on these types of assembly.

Götzenberger, Lars, Francesco de Bello, Kari Anne Bråthen, et al. 2012. Ecological assembly rules in plant communities: Approaches, patterns and prospects. *Biological Reviews* **87.1: 111–127.**

Critical and up-to-date review of the evidence for Diamond's assembly rules in plant communities. A survey and a meta-analysis are reported and suggest that nonrandom co-occurrence of plant species is not a general phenomenon. Includes a discussion of methodological limitations and proposition of a set of guidelines for future research on assembly rules. Available online for purchase or by subscription.

Keddy, Paul. 1992. Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science* **3.2: 157–164.**

Begins with a review of the controversy over assembly rules and the lack of generalities in community ecology. Develops the argument that assembly rules provide a unifying framework for community ecology, and emphasizes that functional traits should be used to make general predictions across systems with different species pools. Available online for purchase or by subscription.

MacArthur, R. H. 1972. *Geographical ecology: Patterns in the distribution of species.* **Princeton, NJ: Princeton Univ. Press.**

Last publication by MacArthur, this book presents a synthesis of his theoretical work on species coexistence and distribution. The most accessible and achieved description of the niche theory. Discusses the fundamental principles underlying species distribution.

Vellend, Mark. 2010. Conceptual synthesis in community ecology. *Quarterly Review of Biology* **85.2: 183–206.**

Vellend asks: What are the fundamental processes in community ecology? Inspired by the ones found in population genetics, he proposes that selection, drift, speciation, and dispersal are sufficiently general to encompass all theoretical and conceptual models in community ecology. Interesting and potentially controversial perspective that is well suited for discussion in a journal club or in a graduate course. Available online for purchase or by subscription.

Historical Background

The history of community assembly study essentially maps onto the major landmarks in ecology. This section first reviews the naissance and maturation of the niche concept, followed by its relationship with the Competitive Exclusion Principle. These themes are dominant in the study of community assembly, and particularly the assembly rules that are the subject of the War over Assembly Rules.

DEFINITION OF THE NICHE

Not surprisingly, community assembly shares its historical background with several other themes of ecology. The first discussions on community assembly were initiated by the view advanced in Clements 2010 (originally published in 1916) that communities are essentially "complex organisms." Following his studies of the dynamics of plant succession (see also Ecological Succession), Clements proposed that communities are the end result (climax) of a deterministic development series of the assemblages best fitting the local conditions. This view became influential in several fields of ecology, especially in phytosociology. He was nonetheless rapidly challenged by Gleason 1926, which instead argued for an individualistic perspective, where the community is a "coincidence" resulting from the different characteristics of species that could inhabit a location and the interactions among them. The development of the niche concept was somewhat independent of this debate but rapidly provided mechanisms to support Gleason's individualistic perspective. The original formulation of the niche is usually attributed to Grinnell 1917, a seminal paper on the distribution of the California Thrasher. The Grinnellian niche refers to the set of environmental conditions (biotic and abiotic) necessary for an organism to sustain a population.

Hutchinson 1957 later defined the niche as the n-dimensional hypervolume of environmental conditions required for a species to maintain a population. The niche concept has since been used to understand species distribution over environmental gradients, for example in the study of the vegetation of the Smoky Mountains in Whittaker 1956. The Grinnellian niche is now commonly used in niche modeling (also named species distribution modeling as in Peterson, et al. 2011) to describe the actual relationship between the distribution of species and the environment, and, most of all, to forecast their future distribution in response to environmental change. Although Grinnell is credited with the first usage of the term, Elton 2001 (originally published in 1927) was the first one to formally define it. The Eltonian niche refers to the "place" of a species in the community where it is found. Because of the original confusion generated by these different perspectives of the niche, the concept has drifted considerably over the years and encountered much criticism. Chase and Leibold 2003, an influential textbook, finally put an end to the confusion, clarified the definition, and reconciled the different perspectives. The niche concept was defined as the "joint description of the environmental conditions that allow a species to satisfy its minimum requirements . . . along with the set of per capita effects of that species on these environmental conditions" (Chase and Leibold 2003, p. 15). For more information, see the *Oxford Bibliographies* in the Ecology article, "Niches" by Dan Warren and Nichole Bennett.

Chase, Jonathan M., and Mathew A. Leibold. 2003. *Ecological niches: Linking classical and contemporary approaches*. Chicago: Univ. of Chicago Press.

Graduate-level presentation of the history of the niche concept, the divergences in definition and finally the proposition of a contemporary definition. Covers novel aspects of the niche such as temporal variability, spatial dynamics, and trophic interactions.

Clements, Frederic E. 2010. *Plant succession: An analysis of the development of vegetation*. Charleston, NC: Nabu.

This monograph presents a holistic viewpoint of community assembly, with a special focus on plant communities. Clements analogizes community development to a complex organism undergoing a life cycle and culminating in its climax. Originally published in 1916 (Washington, DC: Carnegie Institution of Washington).

Elton, C. S. 2001. *Animal ecology*. Chicago: Univ. of Chicago Press.

A classic and foundational textbook in ecology. Outlines the principles of animal behavior and life history, feeding relationships (e.g., food chains) and definition of the ecological niche. Emphasizes the role of a species in the community. Originally published in 1927 (London: Sidgwick and Jackson).

Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53.1: 7–26.

Gleason proposes that there are no definite plant associations, that communities are the end result of the individual response of their different constituent species to the local environment and biotic interactions. Available online for purchase or by subscription.

Grinnell, Joseph 1917. The niche-relationships of the California Thrasher. *Auk* 34:427–433.

Grinnell was the first to propose the term "niche." He provides some insights on competitive exclusion with the assertion that "no two species regularly established in a single fauna have precisely the same niche relationships" (p. 433). Emphasizes the environmental aspect of the niche.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.

The first rigorous definition of the niche, proposing that the niche is an n-dimensional hypervolume allowing the development of sustainable populations, and distinguishing between the fundamental and the realized niche. Available online for purchase or by subscription.

Peterson, Andrew T., Jorge Soberon, Richard G. Pearson, et al. 2011. *Ecological niches and geographic distributions*. **Princeton, NJ: Princeton Univ. Press.**

Up-to-date synthesis of the development of species distribution models (also called niche models, climatic envelopes, or habitat suitability models). Discussion of the underlying principles, assumptions, and critical limitations of these models.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* **26.1: 2–80.**

Explores the community structure in the Great Smoky Mountains of Tennessee over several environmental gradients. Discusses the drivers of vegetation distribution and the properties of the local assemblages, as well as the notion of association and classification of communities. Available online for purchase or by subscription.

THE COMPETITIVE EXCLUSION PRINCIPLE

The niche only became an operational concept for understanding community assembly with the formulation of the competitive exclusion principle. Derived from the experiments regarding competitive interactions described in Gauze 1971 (originally published in 1964), the principle proposes that two species competing for the same resources cannot stably coexist together. In Hardin 1960 the concept was rephrased into the famous maxim "complete competitors cannot coexist." The niche theory was later derived from the competitive exclusion principle and now has become the backbone of our current understanding of species coexistence and community assembly, as described in Chesson 2000. It was pioneered in the study of limiting similarity in MacArthur and Levins 1967 (see also Abrams 1983), which asked how similar two species could be to coexist stably together, or alternatively how many species could be packed along an environmental/resource gradient. This influential work gave birth to a wide variety of interpretations of how species could differentiate from each other. One of the most famous is known as the "resource-ratio theory" of species coexistence, proposed in Tilman 1982. For more information, see the *Oxford Bibliographies* in the Ecology article "Niche Versus Neutral Models of Community Organization" by Lindsay A. Turnbull.

Abrams, Peter. 1983. The theory of limiting similarity. *Annual Review of Ecology and Systematics* **14:359–376.**

Reviews the mathematical theory of limiting similarity, from the early studies using the Lotka–Volterra equations to the latest ones based on stochastic calculus. Suggests "limiting similarity is more likely to be useful in explaining differences in species number than variation in the observed resource overlap" (p. 374). Available online for purchase or by subscription.

Chesson, Peter. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31:343–366.**

Review of the coexistence theory. A metamodel of community dynamics is used to define equalizing and stabilizing mechanisms of coexistence, based respectively on aspects of fitness inequality and niche differentiation. The mechanisms are regrouped into four categories: fluctuation-independent, fluctuation-dependent, spatial mechanisms, and non-equilibrium mechanisms. Available online for purchase or by subscription.

Gauze, G. F. 1971. *The struggle for existence.* **New York: Dover.**

Proposition of the competitive exclusion principle based on the study of laboratory competition experiments using the protozoan Paramecium. Discussion of the principle in relation to the Lotka–Volterra equations of competition. Originally published in 1964 (New York: Hafner).

Hardin, Garrett. 1960. The competitive exclusion principle. *Science* **131.3409: 1292–1297.**

Critical review of the competitive exclusion principle. Discussion focuses on its statement and empirical evidence, but also on its circularity, testability, and employability. Available online for purchase or by subscription.

MacArthur, Robert, and Richard Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* **101.921: 377–385.**

First mathematical development of the niche theory, starting from the Competitive Exclusion Principle to define the problem of limiting similarity: how different must two species be to coexist stably together? Available online for purchase or by subscription.

Tilman, David. 1982. *Resource competition and community structur*e. **Princeton, NJ: Princeton Univ. Press.**

Develops a new theory for coexistence of plant species based on the joint limitation by two or several resources, famously known as the resource-ratio hypothesis. Graphical derivation of conditions for coexistence and then proposition of several predictions of the impact of resource availability on community structure.

NEUTRAL THEORY

The niche theory was seriously challenged by the proposition of a neutral theory of coexistence (see Bell 2000, Hubbell 2001, and also the section on Metacommunity Ecology). Although relatively new in ecology, neutral theory deserves a special treatment as an historical landmark given the shift in our interpretation of community assembly processes. It makes the provocative assumption that species are ecologically equivalent. Consequently, only demographic stochasticity and dispersal drive the structure of ecological communities. The debate was stimulated by the remarkable ability of neutral models to fit several well-studied empirical patterns such as species abundance distributions and distance-decay relationships (several reviews have been published on this topic, for example Chave 2004). After more than ten years of debate, reviews such as Rosindell, et al. 2012 find there is now almost a consensus that neutral theory is a well-developed null hypothesis for niche theory and could even be used as an adequate approximation of ecological dynamics in some situations. Some ecologists like Clark (Clark 2012), however, remain strongly critical of the theory and the equivalence assumption, even arguing that neutral models impede progress in community ecology. Coexistence and neutral theories were integrated into a single and coherent framework in Adler, et al. 2007 and a clarification of the link between stochasticity and neutral dynamics was made in Gravel, et al. 2011.

Adler, Peter B., Janneke HilleRisLambers, and Jonathan M. Levine. 2007. A niche for neutrality. *Ecology Letters* **10.2: 95–104.**

This perspective article integrates the neutral theory and coexistence theory. The contribution provides an interesting and accessible introduction to Chesson's framework of stabilizing and equalizing coexistence mechanisms. Available online for purchase or by subscription.

Bell, Graham. 2000. The distribution of abundance in neutral communities. *American Naturalist* **155.5: 606–617.**

Simulation study of a neutral model of biodiversity based on the distinction between local and regional community dynamics. The model is individual-based and differs substantially from Hubbell 2001, although it yields similar predictions. Available online for purchase or by subscription.

Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* **7.3: 241–253.**

Review of the neutral theory of ecology, accessible to a broad range of readers. Covers the neutral models, tests of the theory, critics of the neutrality assumption, and evolutionary aspects of the theory. Available online for purchase or by subscription.

Clark, J. S. 2012. The coherence problem with the unified neutral theory of biodiversity. *Trends in Ecology & Evolution* 27.4: 198–202.

Controversial article where Clark develops the argument that neutral theory created much more confusion than illumination regarding species coexistence. The argument is derived from previous publications where it is said that fundamental knowledge is hidden in the stochasticity of neutral models. Available online for purchase or by subscription.

Gravel, D., F. Guichard, and M. E. Hochberg. 2011. Species coexistence in a variable world. *Ecology Letters* 14.8: 828–839.

Review article focusing on the effects of stochasticity on species coexistence. Emphasizes that understanding the impact of stochasticity requires the integration of the long-term impact of stochasticity into community dynamics and the emerging ecological drift. The article is centered around some mathematical developments but is intended for non-theoreticians.

Hubbell, Stephen P. 2001. *The unified neutral theory of biodiversity and biogeography*. **Princeton, NJ: Princeton Univ. Press.**

Derivation of a neutral model of biodiversity and its several predictions. Considers a local community sustained by immigration from a metacommunity. Speciation is explicitly considered with two different models. Analysis of several predictions, including species abundance distribution, beta diversity, and species-area relationship.

Rosindell, James, Stephen P. Hubbell, Fangliang He, Luke J. Harmon, and Rampal S. Etienne. 2012. The case for ecological neutral theory. *Trends in Ecology & Evolution* 27.4: 203–208.

Reviews the debate stimulated by the neutral theory. Distinguishes between opinions on neutral theory and ecological drift and opinions on testing the theory. Argues that neutral theory cannot be used simultaneously as a null hypothesis and an approximation for community dynamics and structure. Available online for purchase or by subscription.

Community Assembly in Space and Time

Community assembly is a dynamic process occurring over several spatial scales. A first appreciation of the impact of spatial dynamics on community assembly is found in the Island Biogeography theory. While metapopulation ecology has a long tradition in ecology, it has only recently been extended to Metacommunity Ecology. Here are presented models catching the particular aspects of community assembly over space and time.

ISLAND BIOGEOGRAPHY

MacArthur and Wilson 2001 (originally published in 1967) took a different approach to community assembly in their theory of island biogeography. Their work proposed that species richness on islands is the result of a dynamic balance between stochastic immigrations and extinctions. Their thinking thereby radically differs from most of community assembly theory with rejection of a deterministic equilibrium driven by species interactions. The proximity to the mainland, the size of the mainland species pool, and the area of the island are hypothesized to be the three main factors explaining species richness on islands. The theory revolutionized community ecology with at least two important contributions. First, it introduced the idea that a local community could not be understood without reference to its regional context (see Ricklefs 2008 for further discussion on this issue). Second, it proposed that communities are in a permanent dynamic equilibrium, with considerable species turnover, because of colonization and extinction events that constantly modify community composition. This proposition has been subsequently developed in metapopulation ecology in Levins 1969 and greatly summarized in Hanski 1999. Intriguingly, despite MacArthur's contribution to the niche theory, the theory of island biogeography does not account for species interactions. This theory was thus perceived in Hubbell 2001 (cited under Neutral Theory) as a precursor of the Neutral Theory of biodiversity. The theory of island biogeography therefore does not predict species identity in local communities. Elements of food web theory have, however, been introduced into the theory, giving rise to the trophic theory of island biogeography (see Gravel, et al. 2011). This novel approach provides species-specific predictions for occurrence probability on islands as a function of the

generality of their diet and their trophic rank. The theory of island biogeography has been greatly influential in our understanding of the species area relationship and was at the origin of one of the most famous experiments in ecology. Simberloff and Wilson 1969 describes the defaunation of a set of seven mangrove islands of various sizes in the Florida Keys to study the recolonization process by arthropods. They found that colonization occurred rapidly after the disturbance and that the community eventually equilibrated to the initial species richness, although with considerable turnover in species composition. A later reanalysis of the data in Piechnik, et al. 2008 revealed that the generalist species were the first to settle on the islands, in agreement with the trophic theory. A contemporary perspective on island biogeography is also found in the recent book Losos and Ricklefs 2010.

Gravel, D., F. Massol, E. Canard, D. Mouillot, and N. Mouquet. 2011. Trophic theory of island biogeography. *Ecology Letters* **14.10: 1010–1016.**

Extension of the theory of island biogeography presented in MacArthur and Wilson 2001 (originally published in 1967) to include trophic interactions. The predictions are derived and then the model is compared to empirical data. A fundamental result is the derivation of a species-specific incidence function based on diet breadth, which is the first species distribution model accounting for trophic interactions. Available online for purchase or by subscription.

Hanski, Ilkka. 1999. *Metapopulation ecology*. **Oxford: Oxford Univ. Press.**

An accessible overview of thirty years of research in metapopulation ecology. Presents fundamental aspects of metapopulation ecology such as the rescue effect and the Levins model, as well as more applied aspects such as model parameterization and conservation.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15.3: 237–240.**

First formulation and analysis of the metapopulation concept. The fundamental prediction of the model is that a species can be maintained at the regional scale despite regular local extinctions, provided that recolonization from occupied locations is frequent enough. Available online for purchase or by subscription.

Losos, Jonathan B., and Robert E. Ricklefs, eds. 2010. *The theory of island biogeography revisited*. **Princeton, NJ: Princeton Univ. Press.**

Collection with contributions from junior and senior ecologists who had a significant impact on the development of island biogeography. The book covers all aspects of the discipline, including experiments, species-area relationships, trophic interactions, Neutral Theory, adaptive radiation, and ecosystem functioning.

MacArthur, Robert H., and Edward O. Wilson. 2001. *The theory of island biogeography*. **Princeton, NJ: Princeton Univ. Press.**

One of the most influential books in community ecology. It describes in depth the theory that was summarized in the authors' 1963 article entitled "An equilibrium theory of insular zoogeography" (*Evolution* 17, pp. 373–387). It covers the derivation of the species-area relationship, but also other predictions on species turnover and evolution on islands. A chapter is dedicated to community assembly and the niche. Originally published in 1967.

Piechnik, D. A., S. P. Lawler, and N. D. Martinez. 2008. Food-web assembly during a classic biogeographic study: Species' "trophic breadth" corresponds to colonization order. *Oikos* **117.5: 665–674.**

Re-analysis of data contained in Simberloff and Wilson 1969. A metaweb of potential interactions among all species is constructed from expert knowledge (data provided in the supplementary information), asserting that generalist species arrived first on the islands, followed by specialists. Available online for purchase or by subscription.

Ricklefs, Robert E. 2008. Disintegration of the ecological community. *American Naturalist* **172.6: 741–750.**

A provocative essay building the argument that the concept of a local community hindered our understanding of species richness at all spatial scales. Local communities cannot be understood without referring to a broader regional context. Dispersal limitations, historical contingencies, and evolution are all responsible for species biogeography, and ultimately for the biodiversity distribution at all scales. Available online for purchase or by subscription.

Simberloff, D., and E. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50.2: 278–296.**

First experimental test of the theory proposed in MacArthur and Wilson 2001 (originally published in 1967) of island biogeography. The study reports the assembly dynamic of arthropod communities following the entire defaunation of seven mangrove islands from the Florida Keys. The species richness accumulates progressively over time and saturates to a dynamic equilibrium. The original data are provided in the appendix. Available online for purchase or by subscription.

METACOMMUNITY ECOLOGY

Community assembly is concerned with patterns and processes occurring at different spatial scales (Levin 1992). Until the development of metacommunity ecology, studies on community assembly were essentially restricted to models and predictions for local populations. The emphasis on local communities has been vigorously criticized in Ricklefs 2008 (cited under Island Biogeography), whose author has long recognized that local dynamics and community structure are strongly contingent on processes occurring at much larger spatial scales. The metacommunity concept has been proposed in Leibold, et al. 2004 as a novel approach to link different spatial scales in ecology. It emphasizes feedbacks between local scale processes, such as competitive interactions and local adaptation, and regional scale processes such as dispersal, gene flow, and speciation. This influential paper develops the concept and proposes four paradigms for metacommunities (which are often referred to as assembly rules). The patch dynamic view is based on the coexistence mechanism developed in Tilman 1994 and arises from a trade-off between competitive and colonizing abilities. The species-sorting view is the extension at large spatial scales of Hutchinson's niche concept. The mass effect is derived from the source-sink theory advanced in Mouquet and Loreau 2002 and it emphasizes the role of immigration to maintain local coexistence despite a tendency toward competitive exclusion. Finally, the neutral view first proposed in Bell 2000 and Hubbell 2001 (both cited under Neutral Theory) is derived from the assumption that all species are ecologically equivalent and consequently only demographic stochasticity and dispersal limitations are responsible for community structure. This framework has become very influential in the last decade, setting a whole new research agenda for community ecologists, which extends much beyond the scope of this bibliography. It has received considerable empirical and experimental support (see the review in Logue, et al. 2011). As the concept matures there are new themes emerging, such as the investigation of evolution in metacommunities in Urban, et al. 2008, and spatial food webs in Pillai, et al. 2011 and Gravel, et al. 2011 (cited under Island Biogeography). The concept also extends by metaecosystems as proposed in Loreau, et al. 2003. For more information, see the *Oxford Bibliographies* in the Ecology article "Metacommunity Dynamics" by Florian Altermatt.

Leibold, Mathew A., Marcel Holyoak, Nicolas Mouquet, et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* **7.7: 601–613.**

This article sets the foundation of metacommunity ecology. It defines the concept and its domain. Four paradigms are proposed for the interpretation of metacommunity dynamics: species sorting, mass effect, patch dynamics, and neutral dynamics. Several empirical examples are discussed in light of these perspectives. Available online for purchase or by subscription.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73.6: 1943–1967.**

Discusses how the study of most ecological phenomena should be conducted at several scales and how solving the problem of scales could unify population and ecosystem ecology. Envisioning complex sciences and metacommunity ecology, this article emphasizes that mechanisms operating at one scale often generate patterns at other ones. Available online for purchase or by subscription.

Logue, Jürg B., Nicolas Mouquet, Hannes Peter, and Helmut Hillebrand. 2011. Empirical approaches to metacommunities: A review and comparison with theory. *Trends in Ecology & Evolution* **26.9: 482–491.**

Critical review of the empirical support to metacommunity theory. Species sorting, mass effect, and neutral perspectives are the most commonly tested ones. Several perspectives act in combination. A research agenda for future experimental studies is proposed. Available online for purchase or by subscription.

Loreau, Michel, Nicolas Mouquet, and Robert D. Holt. 2003. Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecology Letters* **6.8: 673–679.**

Definition of the metaecosystem concept. A toy model is used to illustrate how mass balance constraints impose global source-sink constraints. The metaecosystem perspective has the power to integrate the perspectives of community and landscape ecology. Available online for purchase or by subscription.

Mouquet, Nicolas, and Michel Loreau. 2002. Coexistence in metacommunities: The regional similarity hypothesis. *American Naturalist* **159.4: 420–426.**

Defines the source-sink and the mass effect perspectives of metacommunity dynamics. A simple model of lottery competition for space in a heterogeneous landscape is analyzed. Predicts that local species richness should peak at an intermediate dispersal rate. Available online for purchase or by subscription.

Pillai, Pradeep, Andrew Gonzalez, and Michel Loreau. 2011. Metacommunity theory explains the emergence of food web complexity. *Proceedings of the National Academy of Sciences of the United States of America* **108.48: 19293–19298.**

Develops a theory explaining the complexity of network structure in trophic metacommunities. Proposes that food web complexity emerges with an increasing spatial scale of investigation. Omnivorousness and generalist feeding links play a structuring role in spatial food webs.

Tilman, David. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75.1: 2–16.**

Definition of the patch dynamics perspective of metacommunity dynamics. The theory is based on a simple model of plant dynamics where coexistence is promoted by a trade-off between competitive and colonization abilities. The theory is discussed in light of extensive data on grasslands. Available online for purchase or by subscription.

Urban, Mark C., Mathew A. Leibold, Priyanga Amarasekare, et al. 2008. The evolutionary ecology of metacommunities. *Trends in Ecology & Evolution* **23.6: 311–317.**

The metacommunity approach is shown to be a promising avenue to the integration of evolutionary and ecological theories. The parallel between species-sorting and local adaptation in the presence of dispersal and gene flow is discussed. Gaps in the theory are highlighted. Available online for purchase or by subscription.

ASSEMBLY DYNAMICS AND HISTORY

Ecological interactions are usually viewed as the main driver of community assembly (but see Island Biogeography). Strong interactions could nonetheless result in either deterministic or historically contingent community structures (Fukami 2010, cited under Definitions). The sequence of vegetation dynamics following a major disturbance is the archetypical deterministic sequence of community assembly (see Ecological Succession). But sometimes interactions are so strong that community structure might diverge among localities because of different sequences of species arrival. In this case, assembly history is the dominant factor explaining community structure. A good

experimental example of the impact of assembly history on final community structure is the study of aquatic microbial communities that is the subject of Drake 1991. It was shown in this study that assembly history and productivity jointly affected final species abundances after thirty generations. Different assembly histories could lead to alternate stable states (also called multiple stable points or multiple stable equilibriums), meaning that two communities may contain different assemblages or structures even if they are found in exactly the same environmental conditions (see Scheffer, et al. 2001). Different assembly histories are caused by priority effects, which have various origins such as preemptive competition, predation, niche construction and other types of indirect interactions (see Fukami 2010, cited under Definitions). Assembly dynamics have been studied theoretically during the 1990s in the work of Law and Morton 1996. Belyea and Lancaster 1999 reviewed the theory with a particular emphasis on three drivers of community assembly: dispersal, environment, and ecological interactions. Post and Pimm 1983 pioneered the theoretical study of community assembly in food webs, with particular attention to stability. Food web assembly in itself has been the subject of several theoretical studies (see also Network Assembly and Disassembly), both in the context of species invasions and food web evolution (e.g., Loeuille and Loreau 2005). The process of community assembly over evolutionary time scales has also been the subject of considerable empirical investigations, with several empirical examples such as the Hawaiian spiders described in Gillespie 2004. Finally, there is now recognition that the assembly history can also lead to alternative long-term transient dynamics even if there is a single endpoint to the course of community assembly (Fukami and Nakajima 2011).

Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86.3: 402–416.

Review of the literature on community assembly with specific attention to historical contingencies. Argues that assembly rules are deterministic within the constraints imposed by the local environment and the assembly history, and that community disassembly may obey different rules than assembly. Available online for purchase or by subscription.

Drake, James A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137.1: 1–26.

Experimental results illustrating the effect of various sequences of species invasions on final community composition. Mechanisms responsible for alternate stable states are discussed; their occurrence prevents finding unifying principles for community assembly. Available online for purchase or by subscription.

Fukami, T., and M. Nakajima. 2011. Community assembly: Alternative stable states or alternative transient states? *Ecology Letters* 14.10: 973–984.

A model of plant community assembly with priority effects is used to show that historical contingencies can affect the transient dynamics in community assembly. The authors argue for a shift from a steady-state perspective of community assembly to a dynamic one focused on alternative transient states. Available online for purchase or by subscription.

Gillespie, Rosemary. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303.5656: 356–359.

The chronological sequence of the formation of the Hawaiian islands is used to analyze the stages of evolutionary history and community assembly. It is concluded that assembly is not random; there is evolutionary convergence of ecomorphs, and the assembly process is highly dynamic. Available online for purchase or by subscription.

Law, Richard, and R. Daniel Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77.3: 762–775.

A new method for the analysis of community assembly in theoretical models is presented. The technique is based on persistence, a global criterion derived from coexistence theory. Several results are derived from the analysis of Lotka–Volterra equations. Available online for purchase or by subscription.

Loeuille, Nicolas, and Michel Loreau. 2005. Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America* **102.16: 5761–5766.**

A model for the evolution of food webs structured with strong body-size constraints is presented. The model reproduces realistic sequences of food web development and statistical aspects of food web structure.

Post, W. M., and S. L. Pimm. 1983. Community assembly and food web stability. *Mathematical Biosciences* **64.2: 169–192.**

Dynamical stability is analyzed through the development of simulated food webs. Species turnover stability, robustness to species extinction, and local stability are compared. Available online for purchase or by subscription.

Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* **413:591–596.**

Review of the concept of the alternate stable state in ecology and its impact on ecosystems' response to environmental change. Theory and empirical examples are discussed. Available online for purchase or by subscription.

ECOLOGICAL SUCCESSION

Ecological succession is the assembly sequence following the initial colonization of a new habitat or a disturbance. The first documentation of an ecological succession is featured in Cowles 1899 in this study of community composition over a chronosequence of sand dunes over the shore of Lake Michigan. Another great example is the documentation of the mechanisms of primary succession following glacier retreat in Alaska in the study Chapin, et al. 1994. These examples illustrate the primary succession occurring in an area that has never been occupied by an ecosystem. Because different ecosystem processes take place along with constraints on the supply of colonists, this type of succession is usually distinguished from secondary succession, which takes place following a disturbance. As cited in the section Definition of the Niche, Clements 2010 proposed a very influential theory of succession based on several developmental phases and culminating with the climax community. His proposition differed considerably from the view in Gleason 1926 (cited under Definition of the Niche) of succession based on the sequential arrival of colonists and differential rate of population growth. The notion of climax is still alive in ecology, at least implicitly through the analysis of equilibrium community structure (e.g., most of the niche theory is based on the analysis of the community invasibility at equilibrium), but the individualistic view of Gleason has consensus. Connell and Slatyer 1977 later proposed three different mechanisms to explain succession. The facilitation model requires that pioneer species modify the environment so that late successional species can eventually establish themselves. The tolerance model is based on a differential rate of population development and tolerance to competition. Finally, the inhibition model is based on the idea that early colonists inhibit the development of late successional species, which can eventually replace them following a period of senescence. These mechanisms were challenged in the theory advanced in Pickett, et al. 1987, based on the following concepts of succession: pathway, cause, mechanism, and model. The work described a set of three causes to succession: availability of open sites, colonization dynamics, and competitive hierarchies. This perspective of succession is often referred as autogenic, i.e., a replacement sequence of species that result from species interactions rather than an external modification of the environment. By contrast, Tilman 1985 proposed a resource-ratio hypothesis for plant succession, in which changes in community composition follow the modification of the ratio of nutrient supply. Succession has also been studied from an ecosystem perspective following the seminal work on ecosystem development in Margalef 1963, Odum 1969, and Bormann and Likens 1979.

Bormann, F. Herbert, and Gene E. Likens. 1979. *Pattern and process in a forested ecosystem.* **New York: Springer-Verlag.**

This book synthesizes the research in community and ecosystem ecology conducted at the Hubbard Brook experimental forest. Provides an extensive overview of the development of northern hardwood forests, from the assembly dynamics of forest communities to nutrient cycling and energy flow.

Chapin, F., L. R. Walker, C. L. Fastie, and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at
Glacier Bay, Alaska. Ecological Monographs 64.3: 149–175.

Documentation of the successional sequence following deglaciation and experimental tests of different mechanisms of succession (dispersal limitations, inhibition, facilitation, competition). Life history traits determine the successional dynamics but there is no single factor to explain primary succession. Available online for purchase or by subscription.

Connell, Joseph, and Ralph Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111.982: 1119–1144.**

This review article presents three different models to explain ecological succession. The models are derived from an extensive review of empirical examples. Available online for purchase or by subscription.

Cowles, Henry C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part 1, Geographical relations of the dune floras. *Botanical Gazette* **27.2: 97–117.**

Foundation article in ecology, reconstructing the sequence of plant associations during the development of sand dunes. Introduces the notion of succession in ecology and the idea that ecological dynamics lead to a stable equilibrium (although not necessarily reached). Article continues in 1899 *Botanical Gazette* 27.3: 167–202.

Margalef, R. 1963. On certain unifying principles in ecology. *American Naturalist* **97.897: 357–374.**

An open discussion of ecosystem dynamics, their organization, complexity, and maturity. The development of an ecosystem is characterized by the amount of information it maintains. The exchanges among ecosystems of different maturities are discussed; the concepts are applied to human social systems. Available online for purchase or by subscription.

Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164.3877: 262–270.**

Presents a theory of the ecological succession and corresponding development of ecosystems. Lists the expected temporal dynamics of several ecosystem properties over the course of succession: productivity, nutrient cycling, diversity, and homeostasis. Ends with a perspective on human ecology. Available online for purchase or by subscription.

Pickett, S., S. Collins, and J. Armesto. 1987. A hierarchical consideration of causes and mechanisms of succession. In *Special Issue: Theory and Models in Vegetative Science.* *Vegetatio* **69.1–3: 109–114.**

A critical review of the models of succession in Connel and Slatyer 1977 and proposition of a new theory based on a hierarchy of causes. Available online for purchase or by subscription.

Tilman, David. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* **125.6: 827–852.**

Interpretation of Tilman's resource ratio theory of coexistence. Based on the assumption that the supply rates of limiting nutrients (e.g., N and P) can change over the course of succession, the theory predicts how several aspects of community structure should change over time. Available online for purchase or by subscription.

The War over Assembly Rules

After more than a decade of research on the community assembly of land birds over fifty islands of the Bismarck Archipelago near New Guinea, Diamond 1975 (cited under Definitions) proposed a set of seven assembly rules manifested by these bird communities. These assembly rules are based on the simple assumption that two species strongly and negatively interacting with each other are expected to have a checkerboard distribution, i.e., they should have a segregated spatial distribution. This quantitative approach to community

structure gave rise to one of the most controversial debates ecology has ever faced. It also stimulated new methodological developments that are now part of the toolbox for the analysis of community assembly.

DIAMOND'S ASSEMBLY RULES

Hostilities were launched by a provocative paper in Connor and Simberloff 1979. The authors first challenged some of the rules, arguing their formulation was either tautological or trivial. But their most influential critique came from the argument that the regular structure observed by Diamond could be expected if species were distributed at random. To demonstrate this, they generated random community structures from Diamond's data by permutating the species distribution in the community presence-absence matrix but maintaining at a constant level regional abundance and island richness (see Methods for the Analysis of Species Co-occurrence). They concluded that the species distributions were no different than if they had been generated randomly. Connor and Simberloff's criticism gave rise first to a series of comments and responses with various randomization designs (e.g., Diamond and Gilpin 1982) and interpretations. The question of whether communities are assembled randomly or not culminated with a meta-analysis of ninety-six data sets in Gotelli and McCabe 2002. Supported by an exhaustive theory of null model analysis, Gotelli and McCabe concluded that these data sets were highly nonrandom and confirmed Diamond's predictions. They found fewer species combinations, more exclusive species pairs, and less co-occurrence than expected by random community assembly. There is however no end to scientific progress: Gotelli and McCabe's conclusions were challenged by the formulation Neutral Theory. Ulrich 2004, followed by Bell 2005, revealed that, surprisingly, we should also expect highly structured species co-occurrence in neutral communities even if those are assembled at random. Ellwood, et al. 2009 tested this idea with tropical arthropod communities and nonetheless found signs of a deterministic community organization. Progress from null model analysis contributed to a significant debate on hypothesis testing in ecology and helped refine the definition of null and alternate hypotheses (an overview of the debates is provided in Weiher and Keddy 1999, while a perspective on neutral theory and null hypotheses is offered in Gotelli and McGill 2006). According to Götzenberger, et al. 2012 (cited under Definitions), the theme of community assembly remains an active area of investigation because the "long history of assembly rules study has failed to reach more definitive conclusions" (p. 125).

Bell, G. 2005. The co-distribution of species in relation to the neutral theory of community ecology. *Ecology* **86.7: 1757–1770.**

Species co-occurrence in neutral and quasi-neutral models is analyzed at different spatial scales. The observed co-occurrences with and without selection are hardly distinguishable from each other. The conclusion is that the analysis of co-occurrence is unlikely to be useful to interpret community dynamics. Available online for purchase or by subscription.

Connor, Edward F., and Daniel Simberloff. 1979. The assembly of species communities: Chance or competition? *Ecology* **60.6: 1132–1140.**

This article challenges the assembly rules proposed in Diamond 1975 (cited under Definitions). Connor and Simberloff first underline some issues with the formulation and testability of several of the seven assembly rules. They then criticize the absence of a null hypothesis and show, with the randomization procedure and related data of Diamond 1975 (cited under Definitions), that there is no evidence of a structured pattern of co-occurrence. Available online for purchase or by subscription.

Diamond, Jared, and Michael E. Gilpin. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. *Oecologia* **52.1: 64–74.**

This paper is a response to Connor and Simberloff 1979. The null model of Connor and Simberloff is first analyzed in depth and is shown to have hidden incorporation of competitive interactions and several other weaknesses. The article is followed by another one in the same journal issue, "Factors contributing to non-randomness in species co-occurrences on islands" (pp. 75–84), where the authors present a new null model, yielding different conclusions in favor of Diamond's hypothesis. Available online for purchase or by subscription.

Ellwood, M. D. Farnon, Andrea Manica, and William A. Foster. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters* **12.4: 277–284.**

Predictions of niche theory are tested using co-occurrence indices and randomization tests on distribution data of arthropod communities living in tropical epiphytes. Conclusions differ among various scales of environmental heterogeneity. Available online for purchase or by subscription.

Gotelli, Nicholas J., and Declan J. McCabe. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology* **83.8: 2091–2096.**

A meta-analysis of ninety-six published presence–absence data sets is conducted with different null models and indices of co-occurrence. The data sets show nonrandom structure and match Diamond's prediction (Diamond 1975, cited under Definitions). There is shown to be less co-occurrence than expected by chance and the pattern is stronger among homeotherms than with poikilotherms. Available online for purchase or by subscription.

Gotelli, Nicholas J., and Brian J. McGill. 2006. Null versus neutral models: What's the difference? *Ecography* **29.5: 793–800.**

A perspective on the definition of null models, with specific attention to neutral models, explaining why the interpretation of neutral models differs from null models. Available online for purchase or by subscription.

Ulrich, W. 2004. Species co-occurrences and neutral models: Reassessing J. M. Diamond's assembly rules. *Oikos* **107.3: 603–609.**

Species co-occurrence in a neutral model is compared to randomly generated species distributions. The pattern is similar to the distribution predicted in Diamond's assembly rules (Diamond 1975, cited under Definitions). Available online for purchase or by subscription.

Weiher, Evan, and Paul A. Keddy, eds. 1999. *Ecological assembly rules: Perspectives, advances, retreats*. **Cambridge, UK: Cambridge Univ. Press.**

Provides an overview of community assembly studies twenty years after publication of Diamond's model (Diamond 1975, cited under Definitions). It covers both theoretical and empirical investigations for a variety of systems.

METHODS FOR THE ANALYSIS OF SPECIES CO-OCCURRENCE

The work of Diamond (Diamond 1975, cited under Definitions) pioneered the analysis of species co-occurrence and together with the controversy provoked in Connor and Simberloff 1979 (cited under Diamond's Assembly Rules) stimulated the development of a new field of research in numerical ecology. An overview of these techniques is provided in the reference textbook Legendre and Legendre 2012. The analysis of species co-occurrence starts with a community presence–absence matrix. The matrix represents the presence (indicated by a 1) and absence (indicated by a 0) of each species (columns) over a set of sites (rows). The row sum yields the local species richness, while the column sum yields the regional abundance (or occupancy) of a species. There are two technical aspects to the analysis of species co-occurrence. The first one is the index used to summarize information on species co-occurrence. The simplest measure of species co-occurrence is the number of species combinations, as defined in Pielou and Pielou 1968. The second index is the count of checkerboards, as proposed in Diamond 1975 (cited under Definitions): "In such a pattern, two or more ecologically similar species have mutually exclusive but interdigitating distributions in an archipelago, each island supporting only one species" (p. 344). A third popular index of co-occurrence is the C-score, proposed in Stone and Roberts 1990. This index is similar to the count of checkerboards; it measures the average association or repulsion between pairs of species. The second aspect of the analysis of species co-occurrence is the formulation of a null model. The controversy generated in Connor and Simberloff 1979 (cited under Diamond's Assembly Rules) was partly (and rightly) based on the absence of a valid null hypothesis in the analysis within Diamond 1975 (cited under Definitions) of community structure. They used a particular null model of community structure and found that when confronted with a null hypothesis, Diamond's patterns were not significantly different from the random expectation. Subsequent debates were mostly concerned with the formulation of the null hypothesis (e.g., Diamond and Gilpin 1982, cited under Diamond's Assembly Rules). Thanks

to the theoretical work of Gotelli and Graves 1996, there is now a clear understanding of the different null models that can be constructed from the community matrix. Götzenberger, et al. 2012 (cited under Definitions) proposed a six-point guideline for best practices, with the top priority being the recognition that there is no unique algorithm to test for a deterministic community assembly. New indices have been proposed in Boulangeat, et al. 2012 to explicitly take into account random expectation and partition the analysis into the attraction and the repulsion components of the C-score. A promising avenue is the one proposed in Araújo, et al. 2011 for the study of the matrix of species co-occurrence with tools borrowed from network theory.

Araújo, Miguel B., Aejandro Rozenfeld, Carsten Rahbek, and Pablo A. Marquet. 2011. Using species co-occurrence networks to assess the impacts of climate change. *Ecography* **34.6: 897–908.**

This article presents a novel method for analyzing co-occurrence structure. Instead of focusing on checkerboard distributions, the authors use network metrics to characterize the community structure. The method goes beyond co-occurrence of species pairs with a characterization of multi-species assemblages. Several data sets are used as examples. Available online for purchase or by subscription.

Boulangeat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* **15.6: 584–593.**

This article proposes a framework for the analysis of species abundance distribution. New indices are proposed to account for dispersal limitations and source-sink dynamics, as well as new co-occurrence indices to account for biotic interactions. Available online for purchase or by subscription.

Gotelli, Nicholas J., and Gary R. Graves. 1996. *Null models in ecology.* **Washington, DC: Smithsonian Institution.**

This book covers the history of null models in ecology, the philosophy of hypothesis-testing, and several methods to develop null models for the analysis of community data (e.g., species diversity, co-occurrence, relative abundance, size ratios, species-area relationships, biogeography, food web structure).

Legendre, P., and L. Legendre. 2012. *Numerical ecology.* **3d English ed. Amsterdam: Elsevier Science.**

Essential reference resource for graduate students on numerical methods for the analysis of community data. Covers hypothesis-testing, randomization tests, covariance structure, single and multiple regression, measures of similarity, ordinations, and temporal and spatial structure. Emphasis on multivariate analysis.

Pielou, D. P., and E. C. Pielou. 1968. Association among species of infrequent occurrence: The insect and spider fauna of *Polyporus betulinus* **(Bulliard) Fries.** *Journal of Theoretical Biology* **21.2: 202–216.**

Analysis of the diversity of assemblages of fungus-dwelling insects and spiders. Introduction of the idea of nonsegregative and segregative assemblages. Comparison between the observed and expected numbers of associations. Available online for purchase or by subscription.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. *Oecologia* **85.1: 74–79.**

Introduction of the C-score, an index determining the "checkerboardness" of a community. The performance of the index is compared with other indices and the null model proposed in Connor and Simberloff 1979 (cited under Diamond's Assembly Rules). The index is applied to Antillean bat communities. Available online for purchase or by subscription.

Outlook

The theme of community assembly is so vast that each of the topics in this article could cover one if not several chapters in a dedicated textbook. Here are presented three new directions in which the field has grown substantially over the recent years and that are likely to be influential over the next decade.

ECOPHYLOGENETICS

Ecophylogenetics (also called community phylogenetics) is an emerging field at the crossroads of community ecology, biogeography, and macroevolution. Fussmann, et al. 2007 recently proposed that predicting the response of biodiversity to global changes requires a joint understanding of evolutionary dynamics and community ecology. Ecophylogenetics thus aims at incorporating aspects of evolution and historical contingencies into the ecological research agenda, for a better understanding of community assembly and ecosystem functioning. Webb, et al. 2002 were the first to propose that community assembly could be investigated using the phylogenetic structure of a community, based on the hypothesis that the phylogeny could be used as a proxy for ecological similarity. The field bloomed with publication of phylogenies for important taxonomic groups and now they are commonly used to study community assembly. The methodology has some proximity to the classical study of assembly rules with null models (note here the distinction to neutral models). In these studies, the phylogenetic structure of local communities is compared to the one of a random subset of species from the regional pool in order to evaluate if competition, environmental filtering, and facilitation are responsible for the observed community structure (see Cavender-Bares, et al. 2004). A first prediction is that if competitive interactions are structuring the community, if traits are conserved in the phylogeny and are responsible for the intensity of competition, then co-occurring species should be less closely related than expected by chance (phylogenetic over-dispersion). On the other hand, if environmental filtering is structuring the community and traits influencing species' response to the environment are conserved, then co-occurring species should be more closely related than expected by chance (phylogenetic clustering). Even though these two processes have opposite effects on community phylogenetic structure, Cavender-Bares, et al. 2009 hypothesized that they are expected to have distinct signatures at different spatial scales, allowing ecologists to disentangle them. It is important to emphasize that the success of this approach is derived from two fundamental assumptions: (a) traits have a phylogenetic signal (conserved or not, but not random) and (b) these traits are influencing community assembly. The approach is still in its infancy and consequently subject to regular criticisms. For instance, Mayfield and Levine 2010 refined the predictions about phylogenetic structure and community structure, while Wiens, et al. 2010 and Mouquet, et al. 2012 critically revisited methods and evidence for niche conservatism (i.e., that closely related species are more similar than distant species). Ecophylogenetics therefore promises to shed some light on species co-occurrence and community assembly, and most of all, to help ecology become a more predictive science.

Cavender-Bares, Jeannine, David D. Ackerly, David A. Baum, and Fakhri A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* **163.6: 823–843.**

Tests the hypothesis that environmental filtering and competitive interactions should impact the phylogenetic structure of communities if traits are conserved in the phylogeny. Oak species in north central Florida are found to be phylogenetically overdispersed because of the segregation of closely related species. Available online for purchase or by subscription.

Cavender-Bares, Jeannine, Kenneth H. Kozak, Paul V. A. Fine, and Steven Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* **12.7: 693–715.**

Review article developing predictions of community phylogenetic structure under different community assembly dynamics (competition, environmental filtering, neutral, mutualism, and facilitation). Considers the issue of temporal and spatial scales. Available online for purchase or by subscription.

Fussmann, G. F., M. Loreau, and P. A. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* **21.3: 465–477.**

Theoretical and empirical studies on the interaction between evolutionary and ecological dynamics are reviewed. Special attention is given to multispecies evolution and the emergence of ecosystem functioning. Available online for purchase or by subscription.

Mayfield, Margaret M., and Jonathan M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* **13.9: 1085–1093.**

A counterargument to the hypothesis that competitive exclusion will segregate closely related species. The argument is derived from contemporary coexistence theory based on fitness equalizing and stabilizing mechanisms. Two types of species differences may determine the outcome of competitive interactions and thus lead to opposing phylogenetic structures. Available online for purchase or by subscription.

Mouquet, Nicolas, Vincent Devictor, Christine N. Meynard, et al. 2012. Ecophylogenetics: Advances and perspectives. *Biological Reviews of the Cambridge Philosophical Society* **87.4: 769–785.**

Review of how phylogenetic information has been used to better understand community assembly and structure. The review covers phylogenetic structure of communities and assembly rules, network organization, ecosystem functioning, and conservation. Argues that a "consistent unified framework is still missing to link ecological dynamics to macroevolution" (p. 770). Available online for purchase or by subscription.

Webb, Campbell O., David D. Ackerly, Mark A. McPeek, and Michael J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33:475–505.**

Review article discussing how information about the evolutionary history of coexisting species could be used to better understand community assembly and evolutionary processes. The "phylogeny-as-a-proxy" hypothesis is proposed and predictions are derived. Biogeographic history is also explored. Available online for purchase or by subscription.

Wiens, John J., David Ackerly, Andrew P. Allen, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13.10: 1310–1324.**

Niche conservatism is the central assumption of the ecophylogenetic approach to community assembly. Its importance for several themes in ecology is reviewed and methodologies to quantify it are detailed. Available online for purchase or by subscription.

TRAIT-BASED APPROACH TO COMMUNITY ASSEMBLY

There is a general agreement that community ecology needs more accurate and predictive models to solve the current threats to biodiversity. There is no doubt that these models will require knowledge of the ecological interactions driving community assembly. The challenge of quantifying all pairwise interactions is, however, considerable, if not insurmountable. Several eminent ecologists have suggested that "community ecology is a mess" and doubted the existence of any general rules. Some community ecologists nonetheless have proposed there is hope for general rules albeit requiring a change of approach. McGill, et al. 2006 proposes to get rid of the study of pairwise interactions (the number of potential direct interactions in a community increases with the square of species richness!) in favor of a more general approach to community assembly derived from functional traits. A trait is defined in Violle, et al. 2007 (p. 884) as "any morphological, physiological or phenological feature measurable at the individual level." Traits of an organism are acquired by selection and thereby should have (or have had) an effect on its performance via their effect on various demographic parameters. Keddy 1992 (cited under Definitions) proposed that traits could be used to develop both assembly and response rules. The proximity of two species in the multidimensional trait space should allow ecologists to infer the interaction strength among pairs of species, even without a detailed knowledge of the autecology of these species. The community functional structure has been studied with methods similar to the study of phylogenetic structure, with the comparison of the functional trait structure to random expectations (e.g., Cornwell and Ackerly 2009). The relationship between trait distribution and environmental conditions could also be used to infer community composition over environmental gradients, as exemplified in Shipley, et al. 2006. The combination of information on species and trait distribution and phylogenetic structure was also shown in Kraft, et al. 2007 and Münkemüller, et al. 2012 to be the best way to reveal the underlying mechanisms driving community structure.

Cornwell, William K., and David D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* **79.1: 109–126.**

The functional structure of plant communities across coastal California is studied. Traits were nonrandomly distributed, consistent with the hypothesis that community assembly could be understood from functional traits. Available online for purchase or by subscription.

Kraft, Nathan J. B., William K. Cornwell, Campbell O. Webb, and David D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* **170.2: 271–283.**

A simulation framework is proposed to study the functional and phylogenetic structure of communities. Environmental filtering and competitive interactions are compared under different scenarios of niche conservatism. The results provide a critical assessment of using phylogenetic structure to infer community assembly. Available online for purchase or by subscription.

McGill, Brian, Brian Enquist, Evan Weiher, and Mark Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21.4: 178–185.**

Proposition that generalities in community ecology can be achieved when given a shift in focus from pairwise interactions to functional traits. The framework is based on four related themes: traits, environmental gradients, interaction milieu (or biotic background), and performance currency. This approach, if proven right, could help to develop quantitative and general predictions for response of communities to global changes. Available online for purchase or by subscription.

Münkemüller, T., F. de Bello, C. N. Meynard, et al. 2012. From diversity indices to community assembly processes: A test with simulated data. *Ecography* **35.5: 468–480.**

Comparative analysis of the performance of different diversity indices—including taxonomic, functional, and phylogenetic information—to infer community assembly mechanisms. Simulations are conducted with known underlying coexistence mechanisms to evaluate the performance of several indices and different null models. It is concluded that only a combination of various indices could be used to infer processes. Available online for purchase or by subscription.

Shipley, Bill, Denis Vile, and Éric Garnier. 2006. From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science* **314.5800: 812–814.**

Development of a method, inspired by statistical mechanics, to link trait variation along with environmental gradient and community assembly. The method considers how the environment filters species by their traits, and consequently influences community composition. Predicts shifts in community composition over environmental gradients without specific knowledge of pairwise interactions. Available online for purchase or by subscription.

Violle, Cyrille, Marie-Laure Navas, Denis Vile, et al. 2007. Let the concept of trait be functional! *Oikos* **116.5: 882–892.**

Review of the different definitions of the term "trait" and its underlying usage. A formal definition is proposed, with special attention to functional traits, and the definition is related to the fitness of the plant. There is also formulation of a framework linking traits, fitness, and environmental variation. Available online for purchase or by subscription.

NETWORK ASSEMBLY AND DISASSEMBLY

Solé and Bascompte 2006 revealed in its synthesis how community reassembly following specific responses to environmental changes is one of the most fundamental challenges community ecology is facing today. A fundamental goal of network ecology is to better understand how the structure of ecological interactions develops. This question has been explored in Bascompte and Stouffer 2009 in its

synthesis of the assembly and the disassembly dynamics of ecological networks. As a first step, static models such as the cascade and the niche models in Williams and Martinez 2000 have been proposed to reproduce nonrandom and consistent features of ecological networks. These models are not designed, however, to provide insights onto community assembly. The simplest model of network assembly has been proposed in Barabási and Albert 1999 to explain the skewed distribution linking density. In this model, these two physicists show that newly introduced nodes are preferentially attached to the most connected ones (a "rich gets richer" process of network build-up). Most existing models of ecological network assembly focus on food webs (e.g., Gravel, et al. 2011, cited under Island Biogeography, and Loeuille and Loreau 2005, cited under Assembly Dynamics and History) but a recent model was also proposed for plant-pollinator community assembly in the work of Campbell, et al. 2011. Stouffer, et al. 2007 analyzed how some fundamental trophic modules in large networks are represented relative to the expectation of null models, in order to detect possible mechanisms of network assembly. There are motifs, such as linear food chains, apparent competition, and intraguild predation that are overrepresented in empirical food webs, while other ones such as exploitative competition are underrepresented. The study of the flip side of network assembly, i.e., its disassembly, also provided some fundamental insights about the factors structuring ecological networks. Inspired by previous studies in physics on network resistance to node deletion, Dunne, et al. 2002 studied the robustness of ecological networks to species extinctions. A main result is that ecological networks are quite robust to random species extinction because of the few generalized species that keep the network glued together. The preferential extinction of the most connected species was, however, followed by severe secondary extinctions. Another major finding about network disassembly is that secondary coextinction cascades are not random with respect to past evolutionary history. Rezende, et al. 2007 first showed that in several communities closely related species often share several ecological interactions, meaning that niche conservatism extends to network structure (see the review in Mouquet, et al. 2012, cited under Ecophylogenetics). These results imply that the mechanisms responsible for the emergence of network structure are tightly related to the past evolutionary history of the species found in the network.

Barabási, A., and R. Albert. 1999. Emergence of scaling in random networks. *Science* **286.5439: 509–512.**

This paper presents a very simple and general model of network assembly. It aims at predicting the power law shape of the degree distribution. The model is based on preferential attachment of new nodes to the most connected nodes. Available online for purchase or by subscription.

Bascompte, Jordi, and Daniel B. Stouffer. 2009. The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364.1524: 1781–1787.**

Very little is known about network assembly but there is considerable work on the coextinction cascades following species loss. This review presents the link between network structure, assembly, and disassembly. Aspects of network structure such as degree distribution and motif distribution are used to interpret network assembly. We do not know yet how network assembly is related to network collapse.

Campbell, Colin, Suann Yang, Réka Albert, and Katriona Shea. 2011. A network model for plant-pollinator community assembly. *Proceedings of the National Academy of Sciences of the United States of America* **108.1: 197–202.**

This model simulates the colonization and extinction process occurring over the course of the assembly of mutualistic communities using novel techniques brought from physics.

Dunne, Jennifer, Richard Williams, and Neo Martinez. 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters* **5.4: 558–567.**

Analysis with simulations of network disassembly following species loss. Different deletion sequences are compared. Networks are found extremely robust to random species loss but vulnerable to a targeted loss of the most connected species. Available online for purchase or by subscription.

Rezende, Enrico L., Jessica E. Lavabre, Paulo R. Guimarães Jr., Pedro Jordano, and Jordi Bascompte. 2007. Non-random

coextinctions in phylogenetically structured mutualistic networks. *Nature* **448:925–928.**

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BACK TO TOP