# HOW ECOLOGICAL COMMUNITIES ARE STRUCTURED: A REVIEW ON ECOLOGICAL ASSEMBLY RULES

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## ABSTRACT

Whether biological communities are deterministic or stochastic assemblages of species has long been a central topic of ecology. The widely demonstrated presence of structural patterns in nature may imply the existence of rules that regulate the organization of ecological communities. In this review, I present a compilation of major assembly rules that fundament, in a great proportion, the community assembly theory. Initially, I present a general overview of key concepts associated to the assembly of communities, in particular the origin of assembly rules, definition, the problem of scale and underlying mechanisms in the structure of ecological communities. Subsequently, two major approaches or paradigms (i.e. species-based and trait-based) for the assembly of communities are discussed. Finally, major tested assembly rules are explored and discussed under the light of available published literature.

KEYWORDS: Community Assembly Theory; Assembly Rules; Community Structure; Species Patterns; Traits Patterns.

## CÓMO SE ESTRUCTURAN LAS COMUNIDADES ECOLÓGICAS: UNA REVISIÓN SOBRE REGLAS ECOLÓGICAS DE ENSAMBLE

## RESUMEN

Una punto central de la ecología es la idea de si las comunidades ecológicas son estructuras determinísticas organizadas o si son colecciones idiosincráticas de especies al azar. La demostrada presencia de patrones estructurales en la naturaleza puede implicar la existencia de reglas que regulan la organización de comunidades ecológicas. En esta revisión presento una compilación de las principales reglas de ensamble que fundamentan, en una gran proporción, la teoría de ensamble de comunidades. Inicialmente, presento una visión general de conceptos clave asociados al ensamble de comunidades, en particular el origen de las reglas de ensamble, su definición, el problema de la escala y mecanismos que actúan en el estructuramiento de comunidades ecológicas. Posteriormente, discuto dos aproximaciones o paradigmas (*i.e.* basados en especies y en rasgos) para el ensamble de comunidades. Finalmente, presento las reglas de ensamble más conocidas a la luz de la literatura publicada disponible.

PALABRAS CLAVE: teoría de ensamble de comunidades; reglas de ensamble; estructura de comunidades; patrones de especies; patrones de rasgos.

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# COMO SÃO ESTRUTURADAS AS COMUNIDADES ECOLÓGICAS: UMA REVISÃO DAS REGRAS DE MONTAGEM ECOLÓGICAS

## RESUMO

Um ponto central da ecologia é a idéia de se as comunidades ecológicas determinísticos são estruturas e organizadas ou são coleções idiossincráticas de espécies de forma aleatória. A presença comprovada de padrões estruturais na natureza pode indicar a existência de regras que regem a organização das comunidades ecológicas. Nesta revisão eu apresento uma compilação das principais regras de montagem que fundamentam, em grande medida, a teoria de montagem de comunidades. Inicialmente, eu apresento uma visão geral dos conceitos-chave associados a montagem de comunidades, em particular a origem das regras de montagem, sua definição, o problema da dimensão e dos mecanismos envolvidos na estruturação de comunidades ecológicas. Posteriormente, discuto duas abordagens ou paradigmas (i.e. baseados em espécies e traços) para a montagem das comunidades. Finalmente, apresento as regras de montagem mais conhecidas à luz da literatura publicada disponível.

**PALAVRAS-CHAVE:** teoria da montagem da comunidade; regras de montagem; estrutura da comunidade; os padrões de espécies; os padrões de traços.

## 1. INTRODUCTION

Whether biological communities are deterministic or stochastic assemblages of species has long been a central topic of ecology (Clements, 1916; Gleason, 1926; Connor and Simberloff 1979; Grant and Abbott, 1980; Simberloff, 1981 and Drake, 1990). This is highlighted by the interaction between a contingent ecology, where community assembly is dependent on uncertain local and historical effects, and a deterministic ecology, where community assembly conforms to general principles (Belyea and Lancaster, 1999). Because of its complexity, understanding organization at the community level has been a difficult and many times frustrating enterprise (Weiher and Keddy, 1999). Extensive descriptions of organisms and where they are found is not the central subject of study of community assembly. The examination of whether there are mechanics to the assembly process of the community that provide the foundation for a general theoretical approach of organization at the community level is what raised the need of the development of community assembly theory as a major branch of study of community ecology (Drake, 1990; Meyer and Kalko, 2008).

Assembly theory deals with one major priority for ecological research, and it is how ecological processes shape the earth's biological diversity and how complex communities are formed or assembled over time from a regional species pool (Booth and Swanton, 2002). Community assembly theory is relatively new, and it is an ongoing developing field within community ecology and theoretical ecology (Weiher and Keddy ,1999; Meyer and Kalko 2008). It stresses process and history, and seeks explanation for community patterns (e.g. composition) in the context of dynamic rather than static (equilibrium) community structure (Moyle and Light, 1996; Booth and Swanton, 2002).

Community assembly has been explored through the examination of natural patterns (e.g. Diamond, 1975), laboratory and field experimentation (Wilbur and Alford, 1985; Robinson and Dickerson, 1987; Robinson and Edgemon, 1988 and Drake, 1991) and computer simulation (Post and Pimm, 1983; Drake, 1990b and Strange, 1995). The National Science Foundation has recognized the importance of an assembly perspective to fields of ecological restoration, bioremediation, species invasions and extinctions, and biological control (Thompson

*et al.*, 2001). Community assembly theory has been broadly used in the invasion ecology; as the integrity of many terrestrial and aquatic ecosystems is being challenge worldwide by invading species, there is a growing need to understand the invasion process and, moreover, to predict the success and effects of invading species (Townsend, 199; Moyle and Light, 1996). This theory provides a framework to understanding why and how species invade or become extinct, how communities respond to perturbations and why their response will differ over time and, finally, why attempts at community restoration may fail (Booth and Swanton, 2002).

## 1.1. Assembly Rules

One interesting challenge in reviewing the community assembly literature is to define the term "assembly rule". Most of this difficulty is related to the wide range of phenomena proposed as rules which has led to the problem of finding just a handful of studies (e.g. Fox, 1987; Weiher and Keddy, 1995b) that explicitly state hypothesized rules, and even fewer propose underlying mechanisms (e.g. Morris and Knight, 1996). Belyea and Lancaster (1999) identified two essential elements for the definition of a rule. Firstly, a rule is a fundamental principle that applies across many different situations. Secondly, a rule constrains the behavior of an "action or procedure" (i.e. a process). Within the context of community assembly, rules should therefore arise from processes occurring within the community, rather than describe patterns arising in particular circumstances for particular taxa. The same rule may apply to communities that differ historically, leading to similar or divergent trajectories (Belyea and Lancaster, 1999). Hence, according to these authors, assembly rules are general and mechanistic, and operate within the case-specific constraints imposed by colonisation sequence and environment. They are used to describe general principles arising from mechanisms operating within the community and to which the assembly of a community conforms (Belyea and Lancaster, 1999).

While the ideas of community assembly, and particularly whether plant communities are discrete communities or random assemblages, date back to Clements, Tansley, Gleason, Ellenberg and Whittaker in the early 1900s (Weiher and Keddy, 1995b; Booth and Larson, 1999), the term "assembly rule" was first introduced by Diamond (1975) to explain the patterns of bird assemblages observed in New Guinea islands. There are differences in the way community assembly is viewed, and there have been strong debates on how assembly theory should be approached. Some authors (e.g. Diamond, 1975; Wilson and Whittaker, 1995) argue that it should focus on constraints on biotic interactions, whereas others (e.g. Drake, 1990; Roughgarden, 1989) include both biotic and abiotic constraints (Booth and Larson, 1999).

Belyea and Lancaster (1999) proposed a terminology that groups the agents and factors of community assembly into three principal determinants: (1) dispersal constraints, (2) environmental constraints, and (3) internal dynamics. Factors external to the community (dispersal and environmental contraints) are separated from internal processes (internal dynamics) and all three determinants define which subset of the total possible species pool actually occurs at a site. Dispersal and environmental constraints determine the boundary conditions within which internal dynamics operate (Booth and Swanton, 2002). Other authors (e.g. Diaz *et al.*, 1999; Keddy, 1992) have suggested that filtering or constraints are produced by climatic conditions, disturbance regime, and biotic interactions, which represent a different terminology, but the groupings are similar.

## 1.2. Influence of Scale on Assembly Rules

Several studies have shown that many assembly rules might be both temporally dependent and spatially contingent (Drake, 1990; Chase, 2003; Connolly *et al.*, 2005; Sanders *et al.*, 2007). Relatively little is known about how assembly rules change through time and the way they vary with habitat type disturbance history and spatial scale. Most of

the studies have assumed that communities are in an equilibrium state, and there has been little consideration of whether co-occurrence or body-size overlap patterns are stable in time or vary in space (Sanders *et al.* 2007). Species co-occurrence and body-size distributions can depend of the spatial scale of analysis (Gotelli and Ellison, 2002; Jenkins, 2006). For example, at regional (e.g. across communities) spatial scales, body-size distributions and species co-occurrence patterns might be aggregated if climate acts as a filter to limit the pool of potentially colonizing species (Sanders *et al.*, 2007). At local scales, however, behavioral modifications and fine-scale resource partitioning might act to promote coexistence among species (Albrecht and Gotelli, 2001). Gotelli and Ellison (2002) studying ant assemblages in New England, found at the regional scales that species co-occurrence of ants in forests, but no bogs, was less than expected by chance, whereas, at the local scale, co-occurrence in both forests and bogs was not different from random.

Sanders *et al.* (2007) in a comprehensive analysis for ground-foraging ant assemblages concluded that the operation of assembly rules depends on spatial scale, and obtained little consistency in the modification of assembly rules by disturbance history or habitat type. Dayan and Simberloff (2004) argue that the pattern of evenly spaced body-distributions at regional but not at local scales might be related to coevolutionary mechanisms among competing species that act more likely at regional than at local scales. Thus, at local scales, species might not coevolve in response to one another; instead, they may simply partition time or resources. That is, the evolutionary pressure is not substantial enough to lead to morphological change at local scales, especially when individuals could just modify their foraging behavior or activity cycles in response to competition (Sanders and Gordon, 2004).

## 2. UNDERLYING MECHANISMS IN THE ASSEMBLY OF COMMUNITIES

The community assembly approach considers communities to be assembled entities and asks how particular species assemblages came about. Over time and space, communities follow a trajectory that is controlled by various processes (e.g. competition) and constraints (e.g. environmental conditions) that act at multiple scales. From a total species pool, environmental and dispersal constraints control which species enter an ecological species pool. Within this pool, internal dynamics determine which of these species become part of the extant community. Environmental constraints or filters act by removing species that lack specific traits. Thus, traits are filtered and, with them, species (Booth and Swanton 2002).

Drake (1990) suggests that the consequence of the mechanism (coexistence, extinction, variation in ensemble properties and configurations) appears to be strongly dependent on historical context. While specific events during community assembly may have a stochastic element (e.g. which species colonizes when), the result of assembly history can define which rules operate and which do not. For example, several experimental studies have shown that communities assembled with different sequences of invasion produced communities that contained different species (Cole, 1983, Wilbur and Alford, 1985; Robinson and Dickerson, 1987; Robinson and Edgemon, 1988; Drake 1991). Therefore, assembly rules may have a strong historical component (Drake, 1990).

The three principal determinants or factors of community assembly define which subset of the total possible species pool actually occurs at a site (Belyea and Lancaster, 1999). The total species pool of a focal site is determined by evolutionary and large-scale biogeographical processes (Kelt *et al.*, 1995). Belyea and Lancaster (1999) provide a schematic illustration of various types of species pools, the relationships among them and the processes that determine membership of each pool. A subset of the total species pool, the geographic species pool (1), contains all species that are able to arrive at a site, and hence are available to colonize, and it is determined by dispersal constraints. The habitat species

pool (2) contains species that are able to persist under the abiotic conditions, and thus are determined by environmental constraints. They are subjet to be established and developed under the enviromental conditions at the focal site. The ecological species pool (3), is the overlaping portion of these. At this level, internal dynamics (species interactions such as competition, predation and mutualism) acting over the ecological species pool will determine which species become part of the community, creating the actual species pool (4) (Belyea and Lancaster, 1999). Species found alive at the focal site must belong to all species pools, and constitute the observable community (Belyea and Lancaster, 1999; Booth and Swanton, 2002). The three principal determinants of community assembly act on each species pool. Thus, dispersal constraints determine the geographic species pool, environmental constraints determine the habitat species pool, and internal dynamics act on the ecological species pool to finally determine the actual species pool (Booth and Swanton, 2002).

## 2.1. Internal Dynamics

After a group of species has accomplished to disperse into a community (geographic species pool), and the environmental conditions are suitable (habitat species pool) a third filter or constraint –Internal dynamics– acts on the ecological species pool (the overlap of the geographic and habitat species pool) to determine the community structure (Booth and Swanton, 2002). Not all the species will pass through the filters determined by internal dynamics, and the ecological species pool is further reduced to constitute the actual species pool (Belyea and Lancaster, 1999). Understanding the internal dynamics of a community is, perhaps, the most difficult aspect of community assembly (Booth and Swanton, 2002). Processes such as competition (Grace and Tilman, 1990), predation (Olff *et al.*, 1999) and mutualism (Withgott, 2000) are well described, but their role and how they interact to determine the composition of a particular community is poorly understood (Booth and Swanton, 2002).

As shown, a series of interacting controls acting at many scales determine which species persist in a community. Environmental and dispersal constraints usually set the scene for internal dynamics (Weiher and Keddy, 1995); for example, invasion sequence (mediated by dispersal constraints) can determine which species has the competitive advantage (internal dynamics). Alternatively, changes in the biotic structure might alter the effect of dispersal or environmental constraints (Booth and Swanton, 2002). Whereas it is possible to predict the outcome of some interactions, others will not be predictable, either because they are too complex or they are not fully understood. Likewise, it is not possible to predict the outcome of every possible species interaction under every set of dispersal or environmental constraints (Booth and Swanton, 2002).

Due to this, one way to deal with the complexity of the interactions and, therefore, improve our capacity of predictability, is the use of traits rather than species in the framework of the community assembly theory (Booth and Swanton, 2002).

## 2.2. Environmental Constraints

The environment can exert persistent effects on the community structure, controlling and even removing unsuitable species. Species that more easily pass through the environmental filter are more likely to occur in the habitat species pool (Strange and Foin, 1999).

The abiotic environment influences community assembly by restricting which species can be established at the site (i.e. membership of the habitat species pool), and by constraining the function of successful colonists (Belyea and Lancaster, 1999; Booth and Swanton, 2002). Change in environmental constraints may be directional (e.g. the exposure of land surfaces with marine regression) or locally catastrophic (e.g. landslides). Either of these types of change may lead to local extinctions and range contractions of previously successful colonists, or invasions and range expansions of species excluded previously (Law and Morton, 1996). In the case of

locally catastrophic change, extinctions are non-selective in the sense that species remaining do not necessarily conform any more closely to the assembly rules than those species that have gone extinct. Even if the same set of rules apply, whether the original community trajectory will be repeated may depend on whether all original species are available for reinvasion (Law and Morton, 1996).

On the other hand, environmental constraints are assumed to remain constant for long enough that communities approach equilibrium and the outcome of many assembly rules that are resource-based is more likely to be detected. Hence, environmental constraints influence species interactions and the expression of assembly rules through the availability of space, energy and nutrients and the consistency of this supply (Belyea and Lancaster, 1999).

Community composition does not always conform to our expectations because we often consider only averages conditions rather than environmental extremes; occasional or rare events might have a greater effect on long-term community structure than average environmental conditions (Booth and Swanton, 2002). Due to this, the greatest changes in community composition may occur during occasional stressful periods or during environmental fluctuations because assembly dynamics during this time may be more influential in determining species composition (Booth and Swanton, 2002). For some fish communities, for example, Strange and Foin (1999) found that the timing of floods and drought determines subsequent community composition, and multiple stable states are possible from the same species pool when the environment fluctuates. Thus, the success of an invader or colonizer can be dependent on environmental perturbations and extremes, as well as on average environmental conditions (Booth and Swanton, 2002).

## 2.3. Interaction of environmental constraints with internal dynamics

In harsh or variable environments, deterministic processes such as predation and competition traditionally have been considered weak or dynamically trivial compared with abiotic or non-equilibrial processes (Belyea and Lancaster, 1999). In highly disturbed habitats, temporal variation is a characteristic feature of the abiotic environment (e.g. streams subject to frequent spates or annual droughts, or grasslands subject to periodic fire), and magnitude and periodicity of change are as important as the average in defining the environmental constraints. The constraints are stable in that only those species which can persist in the variable environment are members of the habitat species pool (Belyea and Lancaster, 1999). Assembly rules with an underlying competitive mechanism (e.g. the co-occurrence rule, explained below) may be dynamically trivial in variable environments or the nature of competition may change, e.g., from competition for nutritional resources to competition for space in disturbance-free refugia (Belyea and Lancaster, 1999). Hence, stochastic events may interrupt or weaken species interactions, but need not preclude or diminish the importance of deterministic processes in community structure (Chesson and Huntly, 1997). Therefore, environmental constraints may influence the relative importance and interactive effects of assembly rules, but do not necessarily eliminate their role in structuring communities (Belyea and Lancaster, 1999).

Finally, autogenic alteration of the local environment is another way in which environmental constraints interact with assembly rules: changes to environmental constraints are induced by the organisms themselves, not imposed by external forces (Belyea and Lancaster, 1999). For example, dense beds of riverine macrophytes can reduce the magnitude of flow variations and increase sedimentation (San-Jensen and Mebus, 1996). In other cases, the habitat may become increasingly harsh, excluding species which would otherwise compete with the instigator of the change. *Sphagnum* mosses, for example, alter soil chemistry and hydrology to such an extent that many previously extant species are excluded (van Breemen, 1995). Consequently, the autogenic alteration of environmental constraints

may help to induce a directional change in the community (Belyea and Lancaster, 1999).

## 2.4. Dispersal Constraints

Dispersal constraints determine what species arrive at a site (Booth and Swanton, 2002). Whereas it is sometimes assumed that there is an unlimited and continuous supply of species invading, this is not generally the case. In reality, the supply of hopeful invaders (the geographic species pool) is only a subset of the total species pool and is not static over time (Belyea and Lancaster, 1999). Many assembly rules assume implicitly that species invasions are independent and are separated by a sufficiently long period of time for the community to reach equilibrium before the next invasion (Weiher and Keddy, 1999).

Determining membership of the geographic species pool for empirical studies of community assembly is difficult, because regional species checklists (i.e. a sum of actual species pools) may over- or under- estimate the true geographic species pool (Srivastava, 1999). In addition to the problems of enumeration, there are more subtle difficulties in defining the timing and sequence of species arrival at a site (Belyea and Lancaster, 1999). Different communities might result simply by altering the sequence, frequency, and rate of species introductions into the community. Of these, the effect of the invasion sequence is typically the most understood (Booth and Swanton, 2002). In fact, many studies at the microcosm level (Robinson and Dickerson, 1987; Drake 1991; Drake *et al.*, 1993) and in natural ecosystems (Cole 1983, Abrams *et al.*, 1985, McCune and Allen, 1985) have shown evidences that the order of arrival can influence the ultimate community composition. For example, Drake (1991) introduced species into freshwater microcoms in varied sequence. Succesful primary producers tended to be those introduced first, meanwhile success of the consumer species was much more variable. Similarly, Cole (1983) found that two species of ants never co-occurred on small mangrove islands because whichever was first

was able to outcompete the other. However, early invaders are not always more successful (Booth and Swanton, 2002).

In addition to sequence effects, the rate (i.e. how quickly invasions are repeated) and frequency (i.e. number of times a species' invasion is repeated) of invasions can also determine trajectory direction. These effects, however, are less studied than sequence effects (Booth and Swanton, 2002). In general, increasing the rate or frequency of species introductions will increase the number of species able to persist in the community, and it will also decrease the likelihood of reaching a single trajectory because different species will be favored over time (Hraber and Milne, 1997; Lockwood *et al.*, 1997). Both rate and frequency effects appear to act by minimizing the influence that past historical events have had on composition (Lockwood *et al.*, 1997). Therefore, communities with low invasion rates will be more persistent because high invasion rates disrupt the assembly process, and the community never reaches an invasion-resistant state (Booth and Swanton, 2002).

Finally, dispersal is also contingent upon space (Lockwood *et al.*, 1997). Nevertheless, the constraints of dispersal across space may be avoided, for example, by producing banks of dormant propagules that can remain viable for hundreds of years (Thompson, 1987). Species with such long-lived propagules may remain part of the geographic species pool for long periods in which they have excluded from the habitat species pool, but a change in environmental constraints may allow rapid establishment (Thompson, 1987).

## 2.5. Interaction of Dispersal Constraints with Internal Dynamics

As mentioned in the previous section, variations in the order of species' arrivals, through temporal variations in the membership of geographic species pool or chance events during dispersal, can strongly influence community assembly, as demonstrated in several empirical and theoretical studies (Blaustein and Margalit, 1996;

Drake *et al.*, 1993; Law and Morton, 1996; Grover, 1994; Wilbur, 1997). Historical contingencies result from interactions between the order of species invasions (i.e. dispersal constraints) and assembly rules (Belyea and Lancaster, 1999). For example, larval mosquitoes and toads compete for prey in temporary pools, and both species may dominate different pools in the same complex (Blaustein and Margalit, 1996). The order of arrival of the competitors in a particular pool may depend on chance, but alternative communities arise because the first colonist prevents the subsequent establishment of its competitor. Hence, alternative community structures arise only if more than one invasion sequence is possible, and if early invaders are involved in interactions that promote or prevent the subsequent establishment of another species (Belyea and Lancaster, 1999).

Modeling studies suggest that rates of species invasions so high that the system never reaches equilibrium may disrupt the operation of assembly rules; simulated assembly of communities with a slow invasion rate (one species per 100 years) produced several alternative communities states dominated by those species which arrived early in the sequence (Lockwood *et al.*, 1997).

Dispersal constraints may restrict the rate at which conspecifics arrive in a community and this may also influence the expression of assembly rules (Roughgarden *et al.*, 1987). In marine intertidal systems, for example, settlement rates of barnacle larvae are determined by the effect of oceanic circulation patterns on onshore transport and the density of kelp beds that harbour predators of zooplankton (Roughgarden *et al.*, 1987). Communities with very high settlement rates of barnacles may be structured by predators, whereas low settlement rates themselves can limit community structure and dynamics in other habitats (Roughgarden *et al.*, 1987). The idea that communities are continously invaded by potential colonists and that this invasion rate itself might influence community assembly has not been explored in detail (Belyea and Lancaster, 1999).

## 3. APPROACHES TO COMMUNITY PATTERN DETECTION: THE SPECIES-BASED AND THE TRAIT-BASED APPROACH TO COMMUNITY ASSEMBLY

Weiher and Keddy (1995b) identified two developing paradigms or approaches for the assembly of communities: species-based and trait based approaches. The first, sometimes called the island paradigm, deals with islands or fragmented systems, inmigration and coexistence. The rules or models generated through this approach are usually built upon the raw data lists of species (Weiher and Keddy, 1995b). A good example of this sort of study comes from Diamond's (1975) work on the avifauna of New Guinea (see co-occurrence rule in next section). Main limitation of this approach is that despite the historical success in finding patterns, few attempts have been done to both explain the pattern's mechanisms and to state the explicit rule that generate those patterns of community assembly (Weiher and Keddy, 1995b).

In contrast, the trait-based and functional group approach, instead of using lists of organisms, focuses upon their traits (Weiher *et al.*, 1999). Many researchers have suggested using traits, rather than species, as the unit to examine constraints on community assembly (Keddy, 1992b; McIntyre *et al.*, 1999; Weiher and Keddy, 1995b; Weiher *et al.*, 1999; Thompson *et al.*, 2001). This approach facilitates generalisations and finds clues to the mechanisms that underlie rules (Belyea and Lancaster, 1999). Dispersal and enviromental filters as well as internal dynamics remove species that lack specific traits. Thus, traits, rather than species, are filtered. The most important advantage of using traits is that they are more likely to lead to general principles that can be applied to other situations because the results are not species-specific (Weiher and Keddy, 1995b). Due to this, it is a simplified way to approach community assembly (Booth and Swanton, 2002). Only those species possessing the set of traits suited to that environment will enter the assembly process

(Keddy, 1992b; Weiher and Keddy, 1999b). The process of species filtering occurs through a series of filters that remove species that do not possess the required trait complex. Keddy (1992b) compares the assembly process to natural selection. However, rather than acting on individual genotypes (as selection does during evolution), assembly selection acts against specific traits. In this way, species holding disadvantageous traits will be filtered from the community (Booth and Swanton, 2002). Moreover, a species does not have to surpass in passing through any one filter, but it has to pass through all the filters; likewise, the ability of a species to pass through one filter may have no effect on its ability to pass through all the other filters (Booth and Larson, 1999).

One of the major difficulties in using this approach is determining what traits are biologically meaningful and should be measured. Diaz *et al*. (1999), suggested that for plants, both vegetative (e.g. size, logevity) and reproductive (seed production, dispersal mode) traits should be included: the former influences the acquisition and storage of resources, and the latter influences recolonization after disturbance and migration ability. They also suggested that short-term physiological traits (growth rate) morphogenic traits (reproduction and dispersal in space), and trophic relationships (herbivores, root symbionts), are also important. Bellwood *et al*. (2002), for example, linked fin morphology and swimming performance to estimate functional abilities of reef fishes assemblages in three biogeographic regions to study to what extent labrid assemblages were similar among habitats and regions. They found that all three regions displayed highly congruent patterns of habitat use, in terms of assemblage structure and functional characteristics, despite a significant difference in species richness, limited to no species overlap and different histories of isolation among regions. The relationship between swimming ability and habitat use revealed underlying assembly rules at a functional level, emphasizing the utility of functional attributes as a metric for

comparing system-level properties in taxonomically distinct faunas (Bellwood *et al*., 2002).

One way to further simplify the trait-based approach is to group species with a similar set of traits into functional groups (guilds, syndromes, or functional types). Functional groups contain species with a similar set of traits, and are therefore filtered from a regional species pool in a similar fashion (Booth and Swanton, 2002).

A number of attempts have been made to characterize species based on their functional groups. Box (1981) divided the world flora into 90 plant functional groups based on eight bioclimatic indices (e.g. mean temperature of the warmest or coldest month and mean total precipitation for the year or for the warmest or the coldest month) mediated by environmental constraints. Nobel and Slatyer (1980) identified functional groups based on three sets of traits: (1) arrival and persistence following disturbance, (2) ability to establish and grow after disturbance, and (3) the time to reach important life stages. They found 15 functional groups (attribute groups) that were evident in two forest communities and were able to predict changes following various disturbances. The creation of functional groups can be done either by selecting important traits based on ecological knowledge and experience or by creating data sets of species traits and applying clustering techniques which detect correlations among traits across species (Smith *et al*., 1997).

The trait-based approach may create a huge list of traits to consider (e.g. Booth and Swanton, 2002; Diaz *et al*., 1999), but it is still simpler than quantifying each species individually. The use of traits and functional groups may simplify the modeling process; models based on traits or functional groups can be more widely applicable than species-based models because their subprograms will be based on traits or functional rather than specific species (Booth and Swanton, 2002).

Weiher and Keddy (1995b) proposed a qualitative model for trait patterns, in which traits related to interspecific competition for space or resources

(internal dynamics) become overdispersed during assembly (i.e. become less similar than expected by chance), while traits subject to environmental constraints become overdispersed (i.e. become more similar than expected by change). Their model suggests also that the prevalence of trait overdispersion decreases as the spatial scale of the investigation increases. However, Silvertown and Dodd (1996) suggest that analyses of trait patterns should control for phylogeny, which may influence trait dispersion independently of any functional community explanation.

## 4. MOST PROMINENT ASSEMBLY RULES

### 4.1. Diamond's Assembly Rules

The most influential model remains Diamond's (1975) original treatment of community assembly rules (Gotelli N. J., 1999). Jared M. Diamond's (1975) seminal paper "Assembly of Species Communities" forms the basis for modern ideas about community assembly rules (Gotelli N. J., 2004). It was highly influenced by the theory of island biogeography that MacArthur developed with E. O. Wilson in 1967. In this study, Diamond summarized decades of study of the distribution of 513 bird species on New Guinea and the satellite Bismarck Islands, and emphasized that islands with similar habitats do not always support the same species. Even when the same species occurred on different islands, they did not always use the same microhabitats or resources (Fox, 1999).

Diamond (1975) proposed that interspecific competition is the principal factor determining the structure of faunal communities. He posited a series of rules by which communities are assembled and maintained and describes how biotic interactions constrain community assembly. Diamond's assembly rules could be analogous to other biogeographical 'rules', such as Bergmann's rule, but the assembly rules describe generalized restrictions on species presence or abundance that are based on the presence or abundance of one or several other species (Wilson and Whittaker, 1995).

Diamond's (1975) rules may be summarized as follow:

1. "If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature".

2. "Permissible combinations resist invaders that would transform them into forbidden combinations".

3. "A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island".

4. "On a small or species-poor island, a combination may resist invaders that would be incorporated on a large or more species-rich island".

5. "Some pairs of species never coexist, either by themselves or as part of a larger combination".

6. "Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination".

7. "Conversely, some combinations that are composed entirely of stable sub-combinations are themselves unstable".

Over the last few decades Diamond's Assembly Rules have been the focus of multiple researches and have been at the center of intense theoretical and statistical debates (Connor and Simberloff 1979, Gotelli and MacCabe, 2002). As a result of these debates, many tests have been performed to explicitly test Diamond's model against randomized null communities (Feeley, 2003; Sanderson *et al.*, 1998; Manly, 1995; Stone and Roberts, 1990), in particular rules 1, 2 and 5. The strongest critic to this work came from Connor and Simberloff (1979), who used a Monte Carlo null model analysis to demonstrate that many of the patterns attributed by Diamond (1975) to interspecific competition could also arise in communities that were assembled by random colonization and were competition-free. Following studies (Sanderson *et al.*, 1998; Manly, 1995; Stone and Roberts, 1990) clarified many statistical issues surrounding null models and potential flaws in the analysis of Connor and Simberloff (1979), but it was not until the work published by Gotelli and McCabe in 2002 that

the debate settled down significantly (but see Ulrich, 2004). Gotelli and McCabe's (2002) research is perhaps the most representative study conducted to test the predictions of Diamond's rules, where they carried out a comprehensive meta-analysis of 96 published presence-absence matrices of species composition. They demonstrated that species co-occurrence, measured for a variety of taxa at many different spatial scales, is usually less than expected by chance, in accordance with the predictions of Diamond's (1975) assembly rules model. Thefore, this study found that the majority of the studied communities adhere to Diamond's rules and that, in general, communities appear to be structured by intespecific competition.

In accordance with Diamond's first and second assembly rules (known together as the co-occurrence assembly rule), the number of species combinations found among a set of communities or sites is predicted to be less than expected by chance (Burns, 2007; Feeley, 2003; Gotelli and MacCabe, 2002). This is perhaps the most frequently cited and tested assembly rule (Burns, 2007; Chase and Leibold, 2003). Diamond (1975) found in his study in New Guinea that similar species were unlikely to occur on the same island. He concluded that local assemblages are composed of a set of species with co-adjusted niches that partition limited resources and, therefore, it could be predicted that among assemblages competing species should co-occur less than expected by change.

The reasoning behind this rule is that competitive exclusion prohibits the coexistence of similar species on small spatial scales (Gotelli and McCabe, 2002). They found general support for non-random co-occurrence patterns. Earlier reviews found only weak evidence for segregated patterns of co-occurrence among birds (Schluter and Grant, 1984), and suggested that competition may not structure avian assemblages. However, the meta-analysis conducted by Gotelli and McCabe (2002) found evidence for species segregation that is consistent with the hypothesis that competition and niche-partitioning structure species assemblages. Moreover, non-random species segregation has been further described for other animal groups, in spe-

cial ants assemblages (Cole, 1983; Gotelli and Ellison, 2002; Sanders *et al.*, 2003). Meyer and Kalko (2008), using distribution data of 20 bat species collected on 11 islands in Gatun Lake, Panama, tested for non-randomness of species co-occurrence. Different results emerged depending on whether the whole assemblage or particular species subsets were considered and the weighting factors used. Moreover, the outcome of analyses was sensitive to weighting factors such as island isolation. For example, weighting analyses by island isolation retained a non-random pattern for the whole species. Meyer and Kalko's (2008) results indicate that bat assemblages on those islands were most strongly shaped by isolation effects and species' differential movement and colonization ability, and limited evidences of competitive interspecific interactions.

On the other hand, if Diamond's fifth assembly rule is valid, there should be significantly more species pairs (referred to as checkerboard pairs) in a matrix forming checkerboards than expected by chance (i.e. the number of species combinations that never co-occur should be greater than expected by chance; Feeley, 2003).

Diamond's (1975) other assembly rules (number 3, 4, 6, and 7) are more difficult to test with simple null models because they involve complex comparisons of patterns in species-rich and species-poor communities (Gotelli and MacCabe, 2002). Thus, if Diamond's assembly rules are in operation, real communities should contain fewer species combinations and more checkerboard pairs than randomly assembled communities that are not structured by species interactions (Gotelli and MacCabe 2002).

### 4.2. Incidence Assembly Rule

The incidence and abundance of some species are inversely related to the abundance of other species. Because species richness and total population sizes increase with island or fragment size, the rationale behind the incidence assembly rule is that diffuse competition restricts the incidence of occurrence of poor competitors to areas devoid of other species (e.g. smaller islands), which house smaller

number of potential competitors (Horn and MacArthur, 1972; Burns, 2007). For example, Burns (2007) found that the incidence and abundance patterns of most woody angiosperm species on islands off the west coast of Vancouver Island, British Columbia, were consistent with randomized patterns. However, the incidence and abundance of one plant species (*Sambucus racemosa*) declined with the abundance of other plant species, a pattern consistent with the hypothesis that competition limits the assembly of natural communities (Burns, 2007).

## 4.3. Core-Satellite Hypothesis

The core-satellite hypothesis (Hanski, 1982) predicts the regional distribution of species from local population processes of extinction and inmigration. This hypothesis is derived from the observation that local species abundance is strongly and positively correlated with regional distribution (Gaston and Lawton, 1989). This correlation has been demonstrated for a number of taxa, including insects (Hanski, 1982b), birds and terrestrial plants (Gaston and Lawton 1989). The processes of colonization and extinction in the model are stochastic, creating local extinctions of populations and the founding or reestablishment of others. For appropriate parameter values, it then predicts bimodality in the pattern of regional distribution of a group of taxonomically closely related species (Hanski, 1982a).

One group of species, the 'core' species, should occur at a great many sites and have high levels of abundance within sites; they are the core members of the community. These are typically species which are widely distributed and often abundant within local patches (Ulrich and Zalewski, 2006). The other group of species, the 'satellite' species, should have low abundances (i.e. rare species) and occur at a limited number of sites (Ulrich and Zalewski, 2006). An important subsidiary prediction of the model is that within communities over ecological time, because colonization and extinction are stochastic, species switch from core to satellite status and vice versa, referred as core-satellite switching (Gaston

and Lawton, 1989). Hanski (1982a) described three ways in which, given a large number of ecologically similar sites, the core-satellite hypothesis may be tested. The first is to seek evidence for bimodality in the frequency of site occupancy by the species. The second is to use long-term population data to document the occurrence of core-satellite switching. The final test is to use detailed knowledge of colonization and extinction rates to measure directly these parameters of the model (Hanski, 1982a).

The first test, seeking bimodality in regional species distributions, has received significant evidence for mangrove-island insects and scarab beetles (Hanski, 1982b), anthropochorous plants (Hanski, 1982c), bumblebees (Hanski, 1982a) and prairie grasses (Gotelli and Simberloff, 1987). Nevertheless, the core-satellite hypothesis is not the only model that might predict bimodality and those investigations have failed to demonstrate either that its assumptions are adequately met or that there is agreement with other predictions of the hypothesis (Gotelli and Simberloff, 1987; Gaston and Lawton, 1989). Gaston and Lawton (1989) tested data on the insects feeding on bracken (*Pteridium aquilinum*) for agreement with the model's assumptions and with its predictions. However, their analysis showed no consistent evidence for bimodality or for further predictions of the hypothesis. In particular, population data from two well-studied sites provided no evidence of core-satellite switching. Therefore, the insect herbivores of bracken did not support the core-satellite hypothesis of community organization.

Ulrich and Zalewski (2006) used data of ground beetle assemblages of 15 lake islands and two mainland sites in northern Poland to study the species' abundance distribution of core and satellite species. They showed that ground beetle assemblages can be divided into core and satellite species and that that division was not only manifested in patterns of relative abundance and co-occurrence, but can also be seen in the distribution of body sizes and the relation between site abundance and occupancy. From those findings, they inferred that

the regional distribution of core species might be shaped by species interactions and processes of niche division, whereas the spatial distribution of satellite species are best interpreted as stemming from random dispersal (Ulrich and Zalewski, 2006). These findings showed that core and satellite species differed in patterns of spatial distribution and body size ratios, away from simple random draws from the overall species pools.

## 4.4. Constant Predator-Prey Ratios

Studies in which species are classified either as predators or as prey report that the ratio of predators to prey is roughly constant across communities (Briand and Cohen, 1984; Jeffries and Lawton, 1984, 1985). If predator richness is determined by prey richness, the result will be a broadly constant ratio of predators to prey. Invasion and stable coexistence of prey are favored if species differ in traits such as body size, feeding habits, movement patterns, and anti-predator defenses (Belyea and Lancaster, 1999). A computer simulation model of food web development (Mithen and Lawton, 1986) based on apparent competition produced webs that converged on an approximately constant ratio of predator to prey species and the frequency distribution of particular values was similar to that reported for real food webs. Belyea and Lancaster (1999) suggest that the underlying mechanism may involve a balance between increased resource use by predators and reduced predation risk to prey via competition among prey for predator refuges.

For this rule to work in nature, the whole prey trophic level must be predator-limited (Holt, 1984; Mithen and Lawton, 1986), so patterns in communities that deviate from the expected do not necessarily refute the rule (Belyea and Lancaster, 1999).

The veracity of constant predator-prey ratios has been challenged on the basis that lumping of species into such broad categories is inappropriate (Pimm *et al.*, 1991), and that appropriate null models are difficult or impossible to construct when

only part of the ecological species pool is known (Wilson, 1996).

## 4.5. Constant Body-Size Ratios Rule

A particular way by which interspecific competition may structure community composition is by limiting the degree of similarity that is "allowed" between co-occurring species (Hutchinson, 1959). Within assemblages, species should differ in body size to reduce overlap in resource use and allow for species coexistence (MacArthur and Levins, 1967; Dayan and Simberloff, 2005). Hutchinson (1959) observed that sympatric species tend to have body lengths that differ by a factor of approximately 1.3. It was proposed that if species exhibit a size difference ratio of less than 1.3, they will compete heavily for resources and that this intense competition will eventually drive one of the species to local extinction. On the other hand, if the size ratio between species is greater than 1.3, the community will be susceptible to invasion (Hutchinson, 1959; Feeley, 2003). The "1.3 rule" has been challenged in several occasions (e.g. Roth, 1981; Simberloff and Boecklen, 1981), but several communities have been observed to exhibit larger average size differences, larger minimum size differences, and smaller variation of within-community size differences than would occur if the communities had been assembled at random (Case *et al.*, 1983; Diamond, 1975; Faaborg, 1982; Hutchinson, 1959).

Early meta-analyses found weak evidence for regular spacing of body sizes within assemblages (Simberloff and Boecklen, 1981), but a recent review of more than a dozen of studies found that the body sizes of close competitors often differ in such a way as to reduce competition (Dayan and Simberloff, 2005). Bowers and Brown (1982) found for desert rodent communities that species of similar size in the granivore guild coexist less frequently in local communities and overlap less in their geographic distributions than expected on the basis of change, suggesting that their co-occurrence is precluded by interspecific competition. When granivores species and members

of other guilds (i.e. herbivores, insectivores and omnivores) are combined in the same analysis, the patterns apparent in granivores diminish or dissapear, indicating that the ability to detect community structure depends to a large extent on thorough knowledge of the organisms and choice of appropriate statistica tests (Bowers and Brown, 1982).

Sanders *et al.* (2007) did not find evidence for competition among species of ground-foraging ant assemblages in body-size distributions at local scales in Southern Oregon and Northern California, but at regional scale they found segregated body-size patterns (i.e. constant body-size ratios) in assemblages of forest ants, suggesting the working of competition-based assembly rules in this habitat. Similar results have been obtained for European bumblebees (Ranta, 1982) and desert rodents (Dayan and Simberloff, 1994), indicating that species were overdispersed at regional but not at local scales.

On the other hand, Gotelli and Ellison (2002) found for ant assemblages in New England in two types of habitats (forests and bogs) some support for the notion that co-existing species exhibit regular spacing of body sizes, but their results depended on the spatial scale of the analysis. In particular, at the local scale, body size ratios of co-existing species in bogs tended toward constancy, accompanied by greater generic diversity than expected.

## 4.6. Guild proportionality Rule

The guild proportionality model relies on the importance of analyzing the way competition structures communities at the level of functional groups or guilds (e.g. insectivore, omnivore and herbivore) rather than at the individual species level (Wilson, 1989). If competition is important at these higher levels, the relative proportion of species within each guild is expected to remain stable among communities of varying species diversity and composition (Wilson, 1989; Wilson and Whittaker, 1995). Competitive exclusion would occur mainly within guilds rather than between guilds (Wilson and Gitay, 1995). This would result in a limit to the number

of species representing each guild, and in a relative constancy in the *proportion* of species from each guild (Fox, 1989; Wilson, 1989; Wilson and Roxburgh, 1994).The guild proportionality rule focus on determining the distribution of species between guilds or functional groups in an assemblage, rather than determining the identity of each individual species in an assemblage (Fox, 1989; Wilson, 1989). These subsets of the species present (guilds) can be defined *a priori* on the basis of ecological similarity (e.g. Fox, 1987; Wilson and Whittaker, 1995).

The rule is based on the assumption that interspecific competition and competitive exclusion are most likely to occur within functional groups of morphologically and ecologically similar species (guilds). If this were so, a species dispersing into a community patch would have a lower chance of establishing if it were in the same guild as the majority of the resident species. If a new species did establish, it would be more likely that a species of the same guild would disappear. The net result would be that species representation from different guilds would be relatively constant (Fox, 1989; Wilson, 1989). Therefore, it predicts that communities are assembled to best match the distribution of species among such functional groups to the availability of resources for each functional group, rather than that expected by chance (Fox, 1987). Several studies of different island and fragment systems have found that certain guilds are more prone to local extinction than other guilds and this guild proportionality often changes in response to changes in species diversity or patch area (Terborgh, 1974; Faaborg, 1982; Simberloff and Dayan, 1991; Stouffer and Bierregard, 1995).

Empirical evidences for plant communities include grassland communities (Wilson and Roxburgh, 1994; Holdaway and Sparrow, 2006) and salt-marshes (Wilson and Whittaker, 1995). The latter authors, for example, found highly significant guild proportionality for two *a priori* guild classifications, narrow vs. broad leaves and monocots vs. dicots, suggesting a regularity in

community structure and evidences of assembly rules. Wilson and Gitay (1995) studied the proportional representation of functional guilds in four dune slacks in West Wales, in guilds based on morphology and life history (five morphological/life form guilds: creeping, rhizomatous, tuberous, bryophyte and annual) and they found significant constancy of guild proportion for one of the five guilds (annual). Wilson (1989) investigated guild proportionality using stratum/synusial guilds in a forest, finding also significant constancy or guild proportion. Holdaway and Sparrow (2006) found that the guild proportionality increased with increasing ecological age in plant communities along two successional river terrace sequences in New Zealand, which indicated an increase in the relative importance of competitive structuring at later stages of succession, providing empirical support to the existence of assembly rules. More recently, Colorado and Rodewald (2015) found that the proportion of avian species within foraging guilds remained stable among mixed-species Andean flocks in a continental-wide study, supporting the guild proportionality hypothesis. They suggested that antagonistic interactions could be a central mechanism behind this assembly rule.

## 4.7. Favored States Rule

A stricter form of the Guild proportionality model is the Favored States model, initially stated by Fox (1987). Whereas both rules are similar in most of their theoretical development (the use of functional groups or guilds instead of individual species), Fox's rule is based on numbers of species, meanwhile Wilson's is based on proportions. According to the favored states model (also refered in the literature as the guild assembly rule; Fox, 1999), the number of species within guilds is not just homogenous among communities but also within communities, such that each guild or functional group is as equally represented as possible given the number of species present. Species assemblages that obey the rule have a high probability of coexist-

ing, whereas those that do not will have a low probability of coexisting (Fox and Fox, 2000).

Fox (1987) stated the guild assembly rule as: 'There is a much higher probability that each species entering a community will be drawn from a different functional group (or other taxonomically related group of species with similar diets) until each group is represented, before the cycle repeats'. The only input required was an *a priori* knowledge of how the species in the pool are divided into functional or taxonomic groups (Fox, 1989). Functional groups should be equally represented in local communities derived from a larger regional pool. The rule is based on interspecific competition, primarily for food (Fox and Brown 1995); if some functional group becomes disproportionately represented in a local community, competition lowers the probability that the next species to colonize will belong to that group and raises the probability that it will belong to one of the other group (Simberloff *et al.*, 1999). Resource availability and resource partitioning have also been proposed as the major factors in the operation of the favored state rule (Fox, 1987, 1999; Kelt *et al.*, 1995).

Assemblages in which guilds are as equally represented as possible are considered to be in a "favored state" (Fox, 1987; Fox and Brown, 1993). Assemblages for which the rule was not followed were termed 'unfavored'. For example, in a community composed of three guilds, species compositions of (1,1,1), (1,1,2), or (2,2,1) would all be considered favored states since functional groups are evenly represented (i.e. all pairs of functional groups have the same number of species or differ by at most one). By contrast, (1,3,1), (0,1,2), or (2,2,0) would all be classified as "unfavored states" since the number of species in any pair of functional groups differs by more than one (Feeley, 2003; Fox and Brown ,1993, Simberloff *et al.*, 1999). Stated mathematically: (a) 'favored' states are those for which differences between the number of species from each functional group are never more than one; or (b) 'unfavored' states are those with a difference of more than one

between the number of species from each functional group (Fox, 1999).

Fox and Brown (1993) looked at communities of small rodents in a North American desert and found more communities in favored states than would be expected at random. These results and, therefore, the underlying model, have been critized for relying upon the assumption that species abundances are equal at all sites within their respective geographic ranges (Wilson, 1995). In addition, Stone *et al*. (1996) suggested that it is needed to incorporate information about species' geographic ranges in order to correctly analyze this favored states model. While this rule was developed from Australian communities (Fox, 1987, 1999), it has shown now to operate for a variety of taxonomic groups, habitats and biogeographic areas, from deserts to forests and coasts to mountains. The favored states assembly rule has been tested for data sets from four continents, and has examined a wide range of mammalian taxa and guilds based on taxonomic relatedeness, body size, diet, and foraging behavior (Fox, 1999). Also, the analyses have been between diet guilds (insectivore, granivore and herbivore), within a diet guild (insectivores, granivores) and finally for a combination of between and within guild analysis (Fox, 1999). In North America, Fox and Kirkland (1992) demonstrated significant departure from random assembly for the soricid communities in the New England area, dividing shrews into three guilds based on body size. Fox and Brown (1993) found significantly more favored states than expected by 10.000 Monte-Carlo simulations for granivorous desert rodents in southwestern deserts of USA. Morris and Knight (1996) found the same pattern for voles and chipmunks in boreal forests in Ontario, Canada. Finally, Brown *et al*. (2000) in a comprehensive analysis of data for desert rodent communities for USA concluded that North American desert rodent assemblages exhibit highly nonrandom structure on two contrasting spatial scales, geographic and local. Similarly, Kelt *et al*. (1995) identified functional groups from four trophic categories of species of rodents in southern Chile at the Valdivian rainforest, and their analysis enabled them to reject the null hypothesis for random assembly. In Madagascar, Ganzhorn (1997) demonstrated that communities of arboreal lemurs from evergreen rainforest habitats obeyed the guild assembly rule when compared to 10 000 Monte-Carlo simulations for neutral models.

## 4.8. Species Nestedness Rule

The nestedness model states that communities within archipelagos or fragmented systems are expected to exhibit nested structures such that the species comprising a small fauna or flora represent a proper or included subset of those on larger, richer islands, rather than a random draw of those found in the entire species pool (Patterson and Atmar 1986, Atmar and Patterson 1993). In accordance with this, if the species composition of small communities are subsets of the larger communities, the assemblage is said to be "nested" in its distribution, and the species present on less diverse island will tend to occur on progressively more diverse islands (Patterson and Atmar, 1986; Atmar and Patterson, 1993). Species that coexist in local habitat patches tend to be more different in body size, more distantly related taxonomically, and more likely to be in different functional groups (e.g. guilds) than expected on the basis of chance (Bowers and Brown, 1982; Hopf and Brown, 1986; Simberloff and Boecklen, 1981).

The nestedness model of community assembly is a system that does not rely on competition, either interspecific or interguild (Blake, 1991; Bolger *et al*., 1991; Patterson, 1987). In fact, insular assemblages that are highly nested often contain species of such different ecology (including predators and their prey) that competition between them is unlikely (Patterson and Atmar, 1986). Nestedness implies that certain combinations of species occur together frequently and predictably. These patterns of joint occurrence exhibit a hierarchical relationship: each species coexisted frequently with certain species and infrequently with others (Patterson and Brown, 1991).

Nestedness is one of the most pervasive biogeographical patterns and it has been observed in a wide variety of organisms and localities (Wright *et al.*, 1998). Nested community structure has been found most commonly in systems that are influenced primarily by local extinction forces (i.e. in land-bridge islands or fragment systems) but nestedness has also been observed in several oceanic island archipelagos that are clearly driven by colonization processes (Patterson, 1987, 1990; Patterson and Brown, 1991; Feeley, 2003; Burns, 2007). Other nestedness' cited explanations involve interactions between life-history traits and site characteristics, such as dispersal ability and island isolation (Lomolino, 1996), area requirements and island size (Kodric-Brown and Brown, 1993; Gotelli, 2004), habitat requirements and habitat availability (Wright *et al.*, 1998; Calmé and Desrochers, 1999; Gotelli, 2004), and stress tolerance and disturbance regimes (Worthen *et al.*, 1998). On the other hand, processes believed to inhibit nestedness include evolutionary divergence between sites, historical events, and environmental heterogeneity (Wright *et al.*, 1998).

Nested subset structure is not limited to higher vertebrate communities on islands, but also characterizes insular assemblages of other organisms, including plants, insects, amphibians and reptiles (Patterson, 1990). Nestedness was initially thought to be a strictly insular phenomenon, but it has shown to be prevalent not only among different taxonomic groups and across differente geographic regions, but also on terrestrial communities (Patterson, 1990; Feeley, 2003).

Feeley (2003) found a highly nested structure in community islands in Lake Guri, Venezuela, and he suggested that the assemblages were more strongly determined by differential extinction vulnerability and selective species loss than by intespecific or inter-guild competition. Meserve and Glanz (1978) described a perfectly nested assemblage of eight mammal species in nine non-isolated sites in the semi-arid zone of Chile. In the same way, Patterson and Brown (1991) examined collectively the com-position of continental communities of granivorous rodent assemblages at 202 sites in four major western North American deserts and nested patterns of species composition were found to characterize the entire assemblage of all the sites. Their results suggest that three conditions, common biogeographic history, generally similar contemporary environments and hierarchical organization of niche relationships, may be necessary for the development of nested structure. The presence of this structure in diverse continental communities indicates that it is not solely an attribute of island communities but is a more general ecological property. Meyer and Kalko (2008) found that Phyllostomid bat assemblages on Gatun Lake Islands, Panama, were highly significantly nested when all species were considered. The bat distribution across islands remained more significantly nested than expected by chance: species that occurred on depauperate islands were also found on larger, more species-rich islands.

On the other hand, Patterson and Atmar (2000) determined that latitude and forest area were the strongest determinants of nested structure in montane mammals in the southeastern Rocky Mountains, while elevation was the strongest determinant of nestedness in bat communities of the Peruvian Andes. Burns (2007) studying the assembly of an island plant community of woody angiosperm species found weak and variable support for nestedness of the total plant community. However, he obtained stronger and consistent support for this rule after removing one plant species (*Sambucus racemosa*) from the matrix prior to analyses.

Finally, nested subset theory has also received considerable attention regarding its relevance to biodiversity management and conservation, concerning its potential to identify fragmentation-sensitive species, but particularly as it relates to the 'Single large or several small' debate regarding reserve design where its utility, however, appears to be limited (Fischer and Lindenmayer, 2005; Martinez -Morales, 2005).

## 4.9. Variance in Richness Rule

The simplest type of presence/absence assembly rule is one in terms of species richness. The general idea is based on the assumption that species too similar in niche cannot coexist (Pacala and Tilman, 1994). If this is true, the number of species that can coexist locally should be limited because there is a limited number of niches (Ricklefs, 1987). Deterministic theory suggests that competition between species, particularly those with similar niche, limits how closely species can be packed along a niche/resource gradient, thereby limiting how many species can coexist in a small area (MacArthur and Levins 1967; Tilman, 1982; Abrams, 1984). Such a limitation to species coexistence would result in a relative spatial constancy in local species richness (i.e. low variance in species richness), compared to a null model in which species associate at random (Wilson and Gitay, 1995a; Wilson, 1999). This effect has proved surprisingly difficult to find, but it can be found, at least at small scale (Wilson, 1999). Limitations include that this effect should be sought in a stable community since disturbance might allow release from niche limitation. It also should be sought over a narrow habitat range to avoid variation in the number of niches between environments (Pielou 1975; Armesto and Pickett ,1985).

Watkins and Wilson (1992) sampled a number of lawns, examining richness; the observed frequency histogram of species richness was narrower than expected on a random basis, i.e., species richness was more constant. It is possible, however, that some of this effect was due to physical constraints on individual module packing (Palmer and van der Maarel, 1995; Watkins and Wilson, 1992).

Spatial heterogeneity in environment may be a confounding factor also. One way to overcome this is to record the same quadrat thorough time; Wilson *et al.* (1995) did this on limestone grassland in Sweden. Variance in richness, when adjusted for overall year-to-year variance in richness, was significantly less than null-model expectation at two sites (Wilson *et al.*, 1995).

## 4.10. Biomass Constancy Rule

Assembly rules have usually been considered in terms of species presence/absence. However, differences in species abundance are often marked, and might better reflect limitation to species coexistence (Wilson and Gitay, 1995a). One abundance-based rule would be constancy (between patches of a community) of total biomass because of competition: when the abundance of one species is higher, that of another or others is lower (Wilson, 1999). Biomass constancy is a rule that offers the opportunity to find repeated structural patterns among communities, and that is independent of species composition (Wilson *et al.*, 1996). Wilson and Gitay (1995b), in a Welsh dune slack, examined variance in total biomass between quadrats, and compared it with that expected under a null model in which the biomasses of the species were allocated at random. In spite of habitat heterogeneity, they found evidences for this rule using a patch model (but see Wilson and Gitay 1995a for an initial stage of the analysis where biomass analyses gave no evidence that competition affected plant performance).

## 4.11. Texture Convergence Rule

Texture refers to the range of plant characters in a community, irrespective of taxon. The characters considered are generally those believed to be indicative of niche, e.g. leaf thickness, leaf angle, NPK content, chlorophyll content, respiration rate, rooting pattern, etc. (Wilson, 1999). For example, a grassland has a different texture from a shrubland, because of differences in leaf shape, woodiness, etc. An assembly rule in this context is observed when biotic interactions cause convergence: similar texture in different sites, even those on different continents (Wilson, 1999).

Many authors have assumed that community convergence would have to be the result of evolution (e.g. Orians and Paine, 1983; Schluter, 1986; Wiens, 1991). Weiher and Keddy (1995b) assumed that all 'trait overdispersion' was caused immediately by competition, i.e. by ecological sorting. If

ecological sorting is occurring, then when two species that are too similar are present, one of them will suffer competitive exclusion. It will continue to operate as species from the regional species pool continue to invade, either failing to establish due to suppression by superior competitors struggling for the same niche space, or causing functionally similar species already present to succumb to competitive exclusion (Wilson, 1999). If there are niches in a community for a range of functional types, with more or less one species per niche, the result would be expected to be convergence between comparable communities in different areas. The same pressures will act via selection in evolutionary time to cause evolutionary convergence between regions (Orians and Paune, 1983).

Thus, convergence, in the sense of communities with a more similar distribution of species in niche space than expected on the basis of random assortment from species pools (Wilson *et al.*, 1994), can be produced by either ecological or evolutionary processes (Wilson, 1999). However, at the community level, evolutionary convergence might be expected to be rare, because most species occur in several different associations, and can not coevolve simultaneously to fit in with each set of associates (Orians and Paune, 1983; Schluter, 1986; Wilson, 1999).

Most studies of texture convergence have compared Mediterranean shrublands (Wilson, 1999). The problem has been the absence of null models. However, Wilson *et al.* (1994) developed a suitable null model and used it to look for convergence in carrs (i.e. wooded ferns) in Britain and New Zealand. They measured five functional characters related to light capture, but species presence/absence data revealed no convergence. Nevertheless, when species were weighted by their abundance, convergence was seen in some variates (Wilson *et al.*, 1994).

Studies with animals have also failed to find texture convergence (Wiens, 1991b). With texture convergence, there is the additional problem of historical noise, i.e. the different evolutionary and biogeographic history of different continents may have

resulted in species pools that are too different for convergence to have been completed (Wilson, 1999).

## 4.12. Final Remarks on Community Assembly Theory

The debate on the importance of chance and determinism in structuring ecological communities is been running for nearly a century, and it seems that controversy will continue. Nevertheless, a growing body of theoretical and empirical studies briefly presented in this review seems to provide evidences to support the idea that assembly rules can govern certain communities. Admittedly, assembly rules are difficult to uncover in natural communities, and a big part of this is due to our inability to view past events (Drake, 1990); patterns may not be the result of contemporary ecological processes but of events that occurred sometime during community assembly.

Weiher *et al.* (1998) suggest that two paths of inquire have predominated in the study of how different communities come into existence given a common pool of species, both of which have relied on null o neutral models of community assembly. The first path comprised the development of models that tested for patterns of species co-occurrence that differed from the null hypothesis that species are independent of each other (Connor and Simberloff, 1979).The second path of inquiry involves ecomorphological analyses, and considers the role of competition, the importance of limiting similarity, and the patterns consistent with them (Weiher *et al.*, 1998). There are numerous examples where these types of patterns have been found. For example, body size ratios are larger than expected by chance in desert rodents (Hopf and Brown, 1986), and birds introduced to oceanic island show morphological overdispersion (Moulton and Pimm, 1986; Loockwood *et al.*, 1997). On the other hand, there are also many examples where significant ecomorphological patterns were sought, but not found (e.g. Scheibe, 1987; Simberloff and Boecklin, 1991).

Taken in whole, ecomorphological patterns exist, but are not ubiquitous (Weiher and Keddy, 1995b).

Both random and non-random processes can influence community structure (Weiher and Keddy, 1995b). The aim, therefore, should be to determine the relative importance of these processes in structuring communities, testing both random and non-random hypotheses to obtain an accurate portrayal of the processes that structure communities (Algar *et al.*, 2005).

The ensuing debate has played a pivotal role not only in the development of several components of community ecology (e.g. geographical and functional ecology), but also the introduction and development of ecologically explicit null models (Gotelli, 2004).

Some rules presented here have received significantly more attention than others, a fact evident by the amount of publications and the constancy in being referenced in the community assembly literature of the last three decades. Whereas more evidences be gathered, more groups be evaluated and more regions be included, assembly rules such as Nestedness, Favored States and Co-occurrence seem to continue receiving more support. For example, Colorado and Rodewald (2015) tested assembly models of co-occurrence, guild proportionality and constant body-size ratios in avian mixed-species flocks across the Andes. Overall, they found support for deterministic-assembly patterns, related to competitive interactions. On the other hand, some of the stated rules will possibly tend to disappear in the near future, either by their lack of consistency (e.g. variance in richness rule) or because they might be merged into more significant and better-tested rules (e.g. the guild proportionality into the favored states). To date, few studies have incorporated habitat and environmental variables in the analyses of assembly rules, as well as their temporal and spatial variation. This is particularly necessary in a context of environmental degradation and climate change, where evaluating other factors affecting the assembly of natural communities will provide a more comprehensive understanding of how ecological communities are structured.

## REFERENCES

Abrams, M. D.; Sprugel, D. G., and Dickmann, D. I. (1985). Multiple Successional Pathways on Recently Disturbed Jack Pine Sites in Michigan. *Forest Ecology and Management,* 10(1-2), February, pp.31-48.

Abrams, P. (1984). Variability in Resource Consumption Rates and the Coexistence of Competing Species. *Theoretical Population Biology,* 25(1), February, pp. 106-124.

Albrecht, M., and Gotelli, N. J. (2001). Spatial and Temporal Niche Partitioning in Grassland Ants. *Oecologia,* 126, pp. 131-141.

Algar, A. C.; Sleep, D. J. H., and Nudds, T. D. (2005). Niches, Null Models, and Forest Birds: Testing Competing Community Assembly Hypotheses in Disturbed and Undisturbed Hardwood Forest. *Ecoscience,* 12(4), pp. 574-580.

Armesto, J. J., and Pickett, S. T. A. (1985). Experiments on Disturbance in Old-Field Plant Communities: Impact on Species Richness and Abundance. *Ecology, 66*, pp. 230-240.

Atmar, W., and Patterson, B. D. (1993). The Measure of Order and Disorder of the Distribution of Species in Fragmented Habitat. *Oecologia,* 96, July, pp. 373-382.

Barkai, A., and McQuaid, C. D. (1988). Predator-Prey Role Reversal in a Marine Benthic Ecosystem. *Science,* 242(4875), October, pp. 62-64.

Bellwood, D. R., *et al.* (2002). Assembly Rules and Functional Groups at Global Biogeographical Scales. *Functional Ecology*, 16(5), October, pp. 557-562.

Belyea, L. R. and Lancaster, J. (1999). Assembly Rules Within a Contingent Ecology. *Oikos,* (86), September, pp. 402-416.

Blackburn, T. M. and Gaston, K. J. (2001). Local Avian Assemblages as Random Draws From Regional Pools. *Ecography,* 24(1), February, pp. 50-58.

Blake, J. G. (1991). Nested Subsets and the Distribution of Birds on Isolated Woodlots. *Conservation Biology,* 5(1), March, pp. 58-66.

Blaustein, L. and Margalit, J. (1996). Priority Effects in Temporary Pools: Nature and Outcome of Mosquito Larva-Toad Pole Interactions Depend on Order of Entrance. *Journal of Animal Ecology,* 65(1), January, pp. 77-84.

Bolger, D. T.; Alberts, A. C. and Soule, M. S. (1991). Occurrence Patterns of Bird Species in Habitat Fragments: Sampling, Extinction, and Nested Species Subsets. *American Naturalist,* 137, February, pp. 155-166.

Booth, B. D. and Larson, D. W. (1999). Impact of Language, History and Choice of System on the Study of Assembly Rules. *Ecological Assembly Rules: Perspectives, Advances, Retreats,* pp. 206-227.

Booth, B. D. and Swanton, C. J. (2002). Assembly theory applied to weed communities. *Weed Science,* (50), pp. 2-13.

Bowers, M. A., and Brown, J. H. (1982). Body Size and Coexistence in Desert Rodents: Chance or Community Structure? *Ecology,* 63(2), April, pp. 391-400.

Box, E. (1981). *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography.* The Hague: Junk Publishers. 258 p.

Briand, F. and Cohen, J. E. (1984). Community Food Webs Have Scale-Invariant Structure. *Nature,* 307(5948), January, pp. 264-267.

Brown, J. H.; Fox, B. J. and Kelt, D. A. (2000). Assembly Rules: Desert Rodent Communities are Structured at Scales from Local to Continental. *American Naturalist,* 156(3), September, pp. 314-321.

Brown, V. K. (1985). Insect Herbivores and Plant Succession. *Oikos,* 44(1), March, pp. 17-22.

Burns, K. C. (2007). Patterns in the Assembly of an Island Plant Community. *Journal of Biogeography,* 34(5), May, pp. 760-768.

Buss, L. W. and Jackson, J. B. C. (1979). Competitive Networks: Non-Transitive Competitive Relationships in Cryptic Coral Reef Environments. *American Naturalist,* 113(2), February, pp. 223-234.

Calmé, S. and Desrochers, A. (1999). Nested Bird and Microhabitat Assemblages in a Peatland Archipelago. *Oecologia,* 118(3), February, pp. 361-370.

Case, T. J. (1983). Niche Overlap and the Assembly of Island Lizard Communities. *Oikos,* 41(3), December, pp. 427-433.

Case, T. J., Faaborg, J. and Sidell, R. (1983). The Role of Body Size in the Assembly of West Indian Bird Communities. *Evolution,* 37(5), September, pp. 1062-1074.

Chase, J. M. (2003). Community Assembly: When Should History Matter? *Oecologia,* 136(4), August, pp. 489-498.

Chase, J. M. and Leibold, M. A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches.* Chicago, IL: University of Chicago Press. 221 p.

Chesson, P. and Huntly, N. (1997). The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities. *American Naturalist,* 150(5), November, pp. 519-553.

Clements, F. E. (1916). *Plant Succession: An Analysis of the Development of Vegetation.* Washington: Carnegie Institution of Washington., 658 p.

Cole, B. J. (1983). Assembly of Mangrove Ant Communities: Colonization Abilities. *Journal of Animal Ecology,* 52(2), June, pp. 349-355.

Colorado, G.J. y Rodewald, A.D. 2015. Assembly Patterns of Mixed-Species Avian Flocks in the Andes. *Journal of Animal Ecology,* 84(2), March, pp. 386–395.

Connell, J. H. (1980). Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. *Oikos,* 35(2), October, pp. 131-138.

Connolly, S. R., *et al.* (2005). Community structure of corals and reef fishes at multiple scales. *Science,* 309(5739), August, pp. 1363-1365.

Connor, E. F. and Simberloff, D. (1984). Neutral Models of Species Co-Occurrence Patterns. In D. R. Strong, D. Simberloff, L. G. Abele, & A. B. Thistle (Eds.), *Ecological Communities: Conceptual Issues and the Evidence.* (pp. 316-331). Princeton, NJ: Princeton University Press.

Connor, E. F. and Simberloff, D. (1979). The Assembly of Species Communities: Chance or Competition? *Ecology,* 60(6), December, pp. 1132-1140.

Darlington, P. J. (1957). *Zoogeography: The Geographic Distribution of Animals.* New, York, Wiley, 675 p.

Dayan, T. and Simberloff, D. (2005). Ecological and Community-Wide Character Displacement: The Next Generation. *Ecology Letters,* 8(8), August, pp. 875-894.

Dayan, T. and Simberloff, D. (1994). Morphological Relationships Among Coexisting Heteromyids: an Incisive Dental Character. *American Naturalist,* 143(3), March, pp. 462-477.

Diamond, J. M. (1975). Assembly of Species Communities. In M. L. Cody, & J. M. Diamond, *Ecology and Evolution of Communities* (pp. 342-444). Cambridge, Massachusetts, US: Harvard University Press. 545 p.

Diamond, J. M. and Gilpin, M. E. (1982). Examination of the "Null" Model of Connor and Simberloff for Species Co-Occurrences on Islands. *Oecologia,* 52(1), January, pp. 64-74.

Diamond, J. and Case, T. J. (1986). *Community Ecology.* Ney York, NY: Harper & Row. 665 p.

Diaz, S., Cabido, M. and Casanoves, F. (1999). Functional Implications of Trait-Environment Linkages in Plant Communities. In E. Weiher, & P. A. Keddy (Eds.), *Ecological Assembly rules: Perspectives, Advances, Retreats* (pp. 339-362). Cambridge: Cambridge University Press.

Drake, J. A. (1990). Communities as Assembled Structures: Do Rules Govern Pattern? *Trends in Ecology and Evolution,* 5(5), May, pp. 159-164.

Drake, J. A. (1991). Community-Assembly Mechanics and the Structure of an Experimental Species Ensemble. *American Naturalist,* 137 1), January, pp. 1-26.

Drake, J. A. (1990b). The Mechanics of Community Assembly and Succession. *Journal of Theoretical Biology,* 147(2), November, pp. 213-233.

Drake, J. A., *et al.* (1993). The Construction and Assembly of an Ecological Landscape. *Journal of Animal Ecology,* 62(1), January, pp. 117-130.

Elton, C. S. (1946). Competition and the Structure of Ecological Communities. *Journal of Animal Ecology,* 15(1), May, pp. 54-68.

Faaborg, J. (1982). Trophic and Size Structure of West Indian Bird Communities. *Proceedings of the National Academy of Sciences,* 79(5), March, pp. 1563-1567.

Feeley, K. (2003). Analysis of Avian Communities in Lake Guri, Venezuela, Using Multiple Assembly Rule Models. *Oecologia,* 137(1), September, pp. 104-113.

Fischer, J. and Lindenmayer, D. B. (2005). Perfectly Nested or Significantly Nested - an Important Difference for Conservation Management. *Oikos,* 109(3), June, pp. 485-495.

Fox, B. J. (1989). Small-Mammal Community Pattern in Australian Heathland: a Taxonomically Based Rule for Species Assembly. In D. W. Morris, Z. Abramsky, B. J. Fox, & M. R. Willig (Eds.), *The Structure of Mammalian Communities* (pp. 91-103). Lubbock: Texas Technical University.

Fox, B. J. (1987). Species Assembly and the Evolution of Community Structure. *Evolutionary Ecology,* 1(3), July, pp. 201-213.

Fox, B. J. (1999). The Genesis and Development of Guild Assembly Rules. In E. Weiher, & P. Keddy (Eds.), *The Search for Assembly Rules in Ecological Communities* (pp. 23-57). Cambridge: Cambridge University Press.

Fox, B. J. and Brown, J. H. (1993). Assembly Rules for Functional Groups in North American Desert Rodent Communities. *Oikos,* 67, pp. 358-370.

Fox, B. J. and Fox, M. D. (2000). Factors Determining Mammal Species Richness on Habitat Islands and Isolates: Habitat Diversity, Disturbance, Species Interactions and Guild Assembly Rules. *Global Ecology and Biogeography,* 9(1), January, pp. 19-37.

Fox, B. J. and Kirkland, G. L. (1992). North American Soricid Communities Follow Australian Small Mammal Assembly Rule. *Journal of Mammalogy,* 73, pp. 491-503.

Ganzhorn, J. U. (1997). Test of Fox's Assembly Rule for Functional Groups in Lemur Communities in Madagascar. *Journal of Zoology,* 241(3), March, pp. 533-542.

Gaston, K. J. and Lawton, J. H. (1989). Insect Herbivores on Bracken Do Not Support the Core-Satellite Hypothesis. *The American Naturalist,* 134(5), November, pp. 761-777.

Gilpin, M. E. and Diamond, J. M. (1984). Are Species Co-Occurrences on Islands Non-Random, and Are Null Hypotheses Useful in Communitiy Ecology? In *Ecological Communities: Conceptual Issues And the Evidence* (pp. 297-315). Princeton, NJ: Princeton University Press.

Gleason, H. A. (1926). The Individualistic Concept of the Plant Association. *Bulletin of the Torrey Botanical Club,* 53(1), January, pp. 7-26.

Gotelli, H. J. and Ellison, A. M. (2002). Assembly Rules for New England Ant Assemblages. *Oikos,* 99(3), December, pp. 591-599.

Gotelli, N. J. (2004). Assembly Rules. In M. V. Lomolino, D. F. Sax, & J. H. Brown, *Foundations of Biogeography* (pp. 1027-1040). Chicago, IL: The University of Chicago Press. 1328 p.

Gotelli, N. J. (1999). How Do Communities Come Together? *Science*, 286(5445), November, pp. 1684-1685.

Gotelli, N. J. and McCabe, D. J. (2002). Species Co-Occurrence: a Meta-Analysis of J.M. Diamond's Assembly Rules Model. *Ecology,* 83(8), August, pp. 2091-2096.

Gotelli, N. J. and Simberloff, D. (1987). The Distribution and Abundance of Tallgrass Prairie Plants: a Test of the Core-Satellite Hypothesis. *American Naturalist,* 130(1), July, pp. 18-35.

Grace, J. B. and Tilman, D. (1990). *Perspectives on Plant Competition.* San Diego: Academic Press. 504 p.

Grant, P. R. and Abbott, I. (1980). Interspecific Competition, Island Biogeography and Null Hypotheses. *Evolution,* 34(2), March, pp. 332-341.

Grover, J. P. (1994). Assembly Rules for Communities of Nutrient-Limited Plants and Specialists Herbivores. *American Naturalist,* 143(2), February, pp. 258-282.

Hanski, I. (1982a). Communities of Bumblebee: Testing the Core-Satellite Species Hypothesis. *Annales Zoologici Fennici,* 19(2), pp. 65-73.

Hanski, I. (1982c). Distributional Ecology of Anthropochorous Plants in Villages Surrounded by Forest. *Annales Botanni Fennici,* 19(1), pp. 1-15.

Hanski, I. (1982b). Dynamics of Regional Distribution: the Core and Satellite Species Hypothesis. *Oikos,* 38, pp. 210-221.

Holdaway, R. J. and Sparrow, A. D. (2006). Assembly Rules Operation Along a Primary Riverbed-Grassland Successional Sequence. *Journal of Ecology,* 94(6), November, pp. 1092-1102.

Holt, R. D. (1984). Spatial Heterogeneity, Indirect Interactions, and the Coexistence of Prey Species. *American Naturalist,* 124(3), September, pp. 377-406.

Hopf, F. A. and Brown, J. H. (1986). The Bull's-Eye Method for Testing Randomness in Ecological Communities. *Ecology,* 67(5), October, pp. 1139-1155.

Horn, H. S. and MacArthur, R. H. (1972). Competition Among Fugitive Species in a Harlequin Environment. *Ecology,* 53, pp. 749-752.

Hraber, P. T. and Milne, B. T. (1997). Community Assembly in a Model Ecosystem. *Ecological Modeling,* 104(2-3), November, pp. 267-285.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There so Many Kinds of Animals? *American Naturalist,* 93(870), May-June, pp. 145-159.

Jeffries, M. J. and Lawton, J. H. (1984). Enemy Free Space and the Structure of Ecological Communities. *Biological Journal of the Linnean Society,* 23(4), December, pp. 269-286.

Jeffries, M. J., and Lawton, J. H. (1985). Predator-Prey Ratios in Communities of Freshwater Invertebrates: the Role of Enemy Free Space. *Freshwater Biology,* 15(1), February, pp. 105-112.

Jenkins, D. G. (2006). In Search of Quorum Effects in Meta-Community Structure: Species Co-Occurrence Analysis. *Ecology,* 87(6), June, pp. 1523-1531.

Keddy, P. A. (1992b). A Pragmatic Approach to Functional Ecology. *Functional Ecology,* 6(6), pp. 621-626.

Keddy, P. A. (1992). Assembly and Response Rules: Two Goals for Predictive Community Ecology. *Journal of Vegetation Science,* 3(2), April, pp. 157-164.

Keddy, P., and Weiher, E. (1999). The Scope and Goals of Research on Assembly Rules. In E. Weiher, y P. Keddy (Eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats* (pp. 1-20). Cambridge, UK: Cambridge University Press.

Kelt, D. A., and Brown, J. H. (1999). Community Structure and Assembly Rules: Confronting Conceptual and Statistical Issues with Data on Desert Rodents. In E. Weiher, & P. Keddy (Eds.), *The Search for Assembly Rules in Ecological Communities* (pp. 75-107). Cambridge: Cambridge University Press.

Kelt, D. A., Taper, M. L., & Meserve, P. L. (1995). Assessing the impact of competition on the assembly of communities: a case study using small mammals. *Ecology ,* 76, 1283-1296.

Kneidel, K. A. (1983). Fugitive Species and Priority During Colonization in Carrion-Breeding Diptera Communities. *Ecological Entomology,* 8(2), May, pp. 163-169.

Kodric-Brown, A., and Brown, J. H. (1993). Highly Structured Fish Communities in Australian Desert Springs. *Ecology,* 74(6), pp. 1847-1855.

Law, R., and Morton, R. D. (1996). Permanence and the Assembly of Ecological Communities. *Ecology,* 77(3), April, pp. 762-775.

Lockwood, J. L., *et al.* (1997). Assembling Ecological Communities in Time and Space. *Oikos,* 80(3), December, pp. 549-553.

Lomolino, M. V. (1996). Investigating Causality of Nestedness of Insular Communities: Selective Immigrations or Extinctions? *Journal of Biogeography,* 23(5), September, pp. 699-703.

MacArthur, R. H. (1972). *Geographical Ecology.* Princeton, New Jersey: Princeton University Press.

MacArthur, R. H., and Levins, R. (1967). The Limiting Similarity, Convergence and Divergence of Coexisting Species. *The American Naturalist,* 101(921), September-October , pp. 377-385.

MacArthur, R. H., and Wilson, E. O. (1967). *The Theory of Island Biogeography.* Princeton, NJ: Princeton University Press.

Manly, B. F. J. (1995). A Note on the Analysis of Species Co-Occurrences. *Ecology,* 76, pp. 1109-1115.

Martinez-Morales, M. A. (2005). Nested Species Assemblages as a Tool to Detect Sensitivity to Forest Fragmentation: the Case of Cloud Forest Birds. *Oikos,* 108(3), March, pp. 634-642.

McBrien, H., Harmsen, R., and Crowder, A. (1983). A Case of Insect Grazing Affecting Plant Succesion. *Ecology,* 64(5), October, pp. 1035-1039.

McCune, B., and Allen, T. F. H. (1985). Will Similar Forests Develop on Similar Sites? *Canadian Journal of Botany,* 63(3), pp. 367-376.

McIntyre, S., *et al* (1999). Plant Functional Types and Disturbance Dynamics-Introduction. *Journal of Vegetation Sciences,* 10(5), October, pp. 604-608.

Meserve, P. L., and Glanz, W. E. (1978). Geographical Ecology of Small Mammals in the Northern Chilean Arid Zone. *Journal of Biogeography,* 5(2), June, pp. 135-148.

Meyer, C. F., and Kalko, E. K. (2008). Bat Assemblages on Neotropical Land-Bridge Islands: Nested Subsets and Null Model Analyses of Species Co-Occurrence Patterns. *Diversity and Distributions,* 14(4), July, pp. 644-654.

Mikkelson, G. M. (1993). How Do Food Webs Fall Apart? A Study of Changes in Trophic Structure During Relaxation on Habitat Fragments. *Oikos,* 67(3), September, pp. 539-547.

Mithen, S. J., and Lawton, J. H. (1986). Food-Web Models That Generate Constant Predator-Prey Ratios. *Oecologia,* 69 4), July, pp. 542-550.

Morris, D. W., and Knight, T. W. (1996). Can Consumer-Resource Dynamics Explain Patterns of Guild Assembly? *American Naturalist,* 147(4), April, pp. 558-575.

Moulton, M. P., and Pimm, S. L. (1986). The Extent of Competition in Shaping an Introduced Avifauna. In J. Diamond, & T. J. Case (Eds.), *Community Ecology* (pp. 80-97). New York, NY: Harper & Row.

Moyle, P. B., and Light, T. (1996). Biological Invasions of Fresh Water: Empirical Rules and Assembly Theory. *Biological Conservation,* 78(1-2), October-November, pp. 149-161.

Nobel, I. R., and Slatyer, R. O. (1980). The Use of Vital Attributes to Predict Successional Changes in Plant Communities Subject to Recurrent Disturbances. *Vegetatio,* 43(1), December, pp. 5-21.

Olff, H., Brown, V. K., and Dent, R. H. (Eds.). (1999). *Herbivores: Between Plants and Predators.* Oxford: Blackwell.

Orians, G. H., and Paine, R. T. (1983). Convergent Evolution at the Community Level. In D. J. Futuyma, & M. Slatkin (Eds.), *Coevolution* (pp. 431-458). Sunderland: Sinauer.

Pacala, S. W., and Tilman, D. (1994). Limiting Similarity in Mechanistic and Spatial Models of Plant Competition in Heterogeneous Environments. *American Naturalist,* 143(2), February, pp. 222-257.

Palmer, M. W., and van der Maarel, E. (1995). Variance in Species Richness, Species Association, and Niche Limitation. *Oikos,* 73(2), June, pp. 203-213.

Patterson, B. D. (1990). On the Temporal Development of Nested Subset Patterns of Species Composition. *Oikos,* 59(3), December, pp. 330-342.

Patterson, B. D. (1987). The Principle of Nested Subsets and its Implications for Biological Conservation. *Conservation Biology,* 1(4), December, pp. 323-334.

Patterson, B. D., and Atmar, W. (2000). Analyzing species composition in fragments. In G. Rheinwald (Ed.), *Bonn Zoological Monographs*, 46, pp. 1-16.

Patterson, B. D., & Atmar, W. (1986). Nested Subsets and the Structure of Insular Mammalian Faunas and Archipelagos. *Biological journal of the Linnean Society*, 28(1-2), May, pp. 65-82.

Patterson, B. D., and Brown, J. H. (1991). Regionally Nested Patterns of Species Composition of Granivorous Rodent Assemblages. *Journal of Biogeography,* 18(4), July, pp. 395-402.

Pielou, E. C. (1975). *Ecological Diversity.* New York: John Wiley.

Pimm, S. L., Lawton, J. H., and Cohen, J. E. (1991). Food Web Patterns and Their Consequences. *Nature,* 350, April, pp. 669-674.

Post, W. M., and Pimm, S. L. (1983). Community Assembly and Food Web Stability. *Mathematical Biosciences,* 64(2), June, pp. 169-192.

Ranta, E. (1982). Species Structure of North European Bumblebee Communities. *Oikos,* 38(2), March, pp. 202-209.

Ricklefs, R. E. (1987). Community Diversity: Relative Roles of Local and Regional Processes. *Science,* 235(4785), January, pp. 167-171.

Robinson, J. V., and Dickerson, J. E. (1987). Does Invasion Sequence Affect Community Structure? *Ecology,* 68(3), June, pp. 587-595.

Robinson, J. V., & Edgmon, M. A. (1988). An Experimental Evaluation of the Effect of Invasion History on Community Structure. *Ecology,* 69(5), October, pp. 1410-1417.

Roth, V. L. (1981). Constancy and Size Ratios of Sympatric Species. *American Naturalist ,* 118(3), September, pp. 394-404.

Roughgarden, J. (1989). The Structure and Assembly of Communities. In J. Roughgarden, R. M. May, & S. A. Levin (Eds.), *Perspectives in Ecological Theory* (pp. 203-226). Princeton, NJ: Princeton University Press.

Roughgarden, J., Gaines, S., and Pacala, S. W. (1987). Supply Side Ecology: the Role of Physical Transport Processes. In J. H. Gee, & P. S. Giller (Eds.), *Organization of communities past and present* (pp. 491-518). Oxford: Blackwell Scientific.

Sale, P. F. (1978). Coexistence of Coral Reef Fishes? A Lottery for Living Space. *Enviromental Biology of Fishes,* 3(1), March, pp. 85-102.

Sanders, N. J., and Gordon, D. M. (2004). The Interactive Effects of Climate, Life History, and Interspecific Neighbours on Mortality in a Population of Seed Harvester Ants. *Ecological Entomology,* 29(5), October, pp. 632-637.

Sanders, N. J., *et al.* (2003). Community Disassembly by an Invasive Species. *Proceedings of the National Academy of Sciences ,* 100 (5), pp. 2474-2477.

Sanders, N. J., *et al.* (2007). Assembly Rules of Ground-Foraging Ant Assemblages Are Contingent on Disturbance, Habitat and Spatial Scale. *Journal of Biogeography,* 34(9), September, pp. 1632-1641.

Sanderson, J. G., Moulton, M. P., and Selfridge, R. G. (1998). Null Matrices and the Analysis of Species Co-Occurrences. *Oecologia,* 116(1), August, pp. 275-283.

San-Jensen, K., and Mebus, J. R. (1996). Fine-Scale Patterns of Water Velocity Within Macrophyte Patches in Streams. *Oikos,* 76(1), May, pp. 169-180.

Scheibe, J. S. (1987). Climate, Competition and the Structure of Temperate Zone Lizard Communities. *Ecology,* 68, pp. 1424-1436.

Schluter, D. (1986). Tests for Similarity and Convergence of Finch Communities. *Ecology,* 67(4), August, pp. 1073-1085.

Schluter, D., and Grant, P. R. (1984). Determinants of Morphological Patterns in Communities of Darwin's Finches. *The American Naturalist,* 123(2), February, pp. 175-196.

Silvertown, J., and Dodd, M. (1996). Comparing Plants and Connecting Traits. *Philosophical Transactions of the Royal Society of London,* 351, pp. 1233-1239.

Simberloff, D. (1981). Community Effects of Introduced Species. In M. H. Nitecki (Ed.), *Biotic Crisis in Ecological and Evolutionary Time.* (pp. 53-81). New York, NY: Academic Press.

Simberloff, D., and Boecklen, W. (1981). Santa Rosalia Reconsidered: Size Ratios and Competition. *Evolution,* 35 6), November, pp. 1206-1228.

Simberloff, D., and Dayan, T. (1991). The Guild Concept and the Structure of Ecological Communities. *Annual Review of Ecology and Systematics,* 22, November, pp. 115-143.

Simberloff, D., Stone, L., and Dayan, T. (1999). Ruling Out a Community Assembly Rule: the Method of Favored States. In E. Weiher, & P. Keddy (Eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats* (pp. 58-74). Cambridge: Cambridge University Press.

Smith, T. M., Shugard, H. H., and Woodward, F. I. (Eds.). (1997). *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change.* Cambridge: Cambridge University Press.

Srivastava, D. S. (1999). Using Local-Regional Richness Plots to Test for Species Saturation: Pitfalls and Potentials. *Journal of Animal Ecology,* 68(1), January, pp. 1-16.

Stone, L., & Roberts, A. (1990). The Checkerboard Score and Species Distributions. *Oecologia,* 85(1), November, pp. 74-79.

Stone, L., Dayan, T., and Simberloff, D. (1996). Community-Wide Assembly Patterns Unmasked: the Importance of Species' Differing Geographical Ranges. *American Naturalist,* 148(6), December, pp. 997-1015.

Stouffer, P. C., and Bierregarrd, R. O. (1995). Use of Amazonian Forest Fragments by Understory Insectivorous Birds. *Ecology ,* 76 (8), December, pp. 2429-2445.

Strange, E. M. (1995). Pattern and Process in Stream Fish Community Organization: Field Study and Simulation Modeling. Ph D dissertation. Davis: University of California.

Strange, E. M., and Foin, T. C. (1999). Interaction of Physical and Biological Processes in the Assembly of Stream Fish Communities. In E. Weiher, & P. A. Keddy (Eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats* (pp. 311-337). Cambridge: Cambridge University Press.

Strong, D. R., *et al.* (1984). *Ecological Communities: Conceptual Issues and the Evidence.* Princeton, NJ: Princeton University Press.

Sutherland, J. P. (1974). Multiple Stable Points in Natural Communities. *American Naturalist,* 108(964), November-December, pp. 859-873.

Terborgh, J. (1974). Preservation of Natural Diversity: the Problem of Extinction Prone Species. *Bioscience,* 24(12), pp. 715-722.

Thompson, J. N., *et al.* (2001). Frontiers of Ecology. *Bioscience,* 51(1), pp. 15-24.

Thompson, K. (1987). Seeds and Seed Banks. *New Phytology,* 106(1), May, pp. 23-34.

Tilman, D. (1982). *Resource Competition and Community Structure.* Princeton: Princeton University Press. 296 pp.

Townsend, C. R. (1991). Exotic Species Management and the Need for a Theory of Invasion Ecology. *New Zealand Journal of ecology* ,15, January, pp.1-15.

Ulrich, W. (2004). Species Co-Occurrences and Neutral Models: Reassessing J.M. Diamond's Assembly Rules. *Oikos,* 107(3), December, pp. 603-609.

Ulrich, W., y Zalewski, M. (2006). Abundance and Co-Occurrence Patterns of Core and Satellite Species of Ground Beetles on Small Lake Islands. *Oikos,* 114(2), August, pp. 338-348.

van Breemen, N. (1995). How Sphagnum Bogs Down Other Plants. *Trends in Ecology and Evolution,* 10(7), July, pp. 270-275.

Watkins, A. J. and Wilson, J. B. (1992). Fine-Scale Community Structure of Lawns. *Journal of Ecology,* 80(1), March, pp. 15-24.

Weiher, E. A., *et al* (1999). Challenging Theophrastus: a Common Core List of Plant Traits for Functional Ecology. *Journal of Vegetation Sciences,* 10(5), October, pp. 609-620.

Weiher, E. and Keddy, P. A. (1999b). Assembly Rules as General Constraints on Community Composition. In E. Weiher, & P. A. Keddy (Eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats* (pp. 251-271). Cambridge: Cambridge University Press.

Weiher, E. and Keddy, P. A. (1995b). Assembly Rules, Null Models, and Trait Dispersion: New Questions From Old Patterns. *Oikos,* 74(1), October, pp. 159-164.

Weiher, E. and Keddy, P. A. (1999). *Ecological Assembly Rules: Perspectives, Advances, Retreats.* Cambridge, United Kingdom: Cambridge University Press.

Weiher, E. and Keddy, P. A. (1995). The Assembly of Experimental Wetland Communities. *Oikos,* 73(3), Septiembre, pp. 323-335.

Weiher, E., Clarke, P. and Keddy, P. A. (1998). Community Assembly Rules, Morphological Dispersion, and the Coexistence of Plant Species. *Oikos,* 81(2), March, pp. 309-322.

Wiens, J. A. (1991). Ecological Similarity of Shrub-Desert Avifaunas of Australia and North America. *Ecology,* 72(2), April, pp. 479-495.

Wiens, J. A. (1991b). Ecomorphological Comparisons of the Shrub-Desert Avifaunas of Australia and North America. *Oikos,* 60(1), February, pp. 55-63.

Wilbur, H. M. (1997). Experimental Ecology of Food Webs: Complex Systems in Temporary Ponds. *Ecology,* 78(8), December, pp. 2279-2302.

Wilbur, H. M. and Alford, R. A. (1985). Priority Effects in Experimental Pond Communities: Responses of Hyla to Bufo and Rana. *Ecology,* 66(4), August, pp. 1106-1114.

Wilson, J. B. (1989). A Null Model of Guild Proportionality, Applied to Stratification of a New Zealand Temperate Rain Forest. *Oecologia,* 80(2), August, pp. 263-267.

Wilson, J. B. (1999). Assembly Rules in Plant Communities . In *Ecological Assembly Rules: Perspectives, advances, retreats* (pp. 130-164). Cambridge: Cambridge University Press.

Wilson, J. B. (1995). Null Models for Assembly Rules: the Jack Horner Effect is More Insidious Than the Narcissus Effect. *Oikos,* 72(1), February, pp. 139-144.

Wilson, J. B. (1996). The Myth of Constant Predator: Prey Ratios. *Oecologia,* 106(2), April, pp. 272-276.

Wilson, J. B. and Gitay, H. (1995a). Community Structure and Assembly Rules in a Dune Slack: Variance in Richness, Guild Proportionality, Biomass Constancy and Dominance/Diversity Relations. *Vegetatio,* 116(2), February, pp. 93-106.

Wilson, J. B. and Gitay, H. (1995b). Limitations to Species Coexistence: Evidence for Competition From Field Observations, Using a Patch Model. *Journal of Vegetation Science,* 6(3), June, pp. 369-376.

Wilson, J. B. and Roxburgh, S. H. (1994). A Demonstration of Guild-Based Assembly Rules for a Plant Community, and Determination of Intrinsic Guilds. *Oikos,* 69(2), March, pp. 267-276.

Wilson, J. B., & Whittaker, R. J. (1995). Assembly Rules Demonstrated in a Saltmarsh Community. *Journal of Ecology,* 83(5), October, pp. 801-807.

Wilson, J. B., Agnew, A. D., y Partridge, T. R. (1994). Carr Texture in Britain and New Zealand: Convergence Compared with a Null Model. *Journal of Vegetation Science,* 5(1), February, pp. 109-116.

Wilson, J. B., Sykes, M. T. and Peet, R. K. (1995). Time and Space in the Community Structure of a Species-Rich Grassland. *Journal of Vegetation Science,* 6, pp. 729-740.

Wilson, J. B., *et al.* (1996). Are There Assembly Rules for Plant Species Abundance? An Investigation in Relation to Soil Resources and Successional Trends. *Journal of Ecology,* 84(4), August, pp. 527-538.

Withgott, J. (2000). Botanical Nursing. *Bioscience ,* 50 (6), pp. 478-484.

Worthen, W. B., Jones, M. T. and Jetton, R. M. (1998). Community Structure and Environmental Stress: Desiccation Promotes Nestedness in Mycophagous Fly Communities. *Oikos,* 81(1), February, pp. 45-54.

Wright, D. H., *et al.* (1998). A Comparative Analysis of Nested Subset Patterns of Species Composition. *Oecologia,* 113(1), December, pp. 1-20.