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## Chapter 26

# The Ecological Niche: History and Recent Controversies

Arnaud Pocheville

**Abstract** In this chapter, we first trace the history of the concept of ecological niche and see how its meanings varied with the search for a theory of ecology. The niche concept has its roots in the Darwinian view of ecosystems that are structured by the struggle for survival and, originally, the niche was perceived as an invariant place within the ecosystem, that would preexist the assembly of the ecosystem. The concept then slipped towards a sense in which the niche, no longer a pre-existing ecosystem structure, eventually became a variable that would in turn have to be explained by the competitive exclusion principle and the coevolution of species. This concept, while more operational from an empirical point of view than the previous one, suffered from an ill-founded definition. A recent refoundation by Chase & Leibold enabled to overcome some of the definitional difficulties.

We then present how, in contemporary ecology, the niche concept is recruited to explain biodiversity and species coexistence patterns. In parallel, neutralist models, by successfully explaining some ecological patterns without resorting to explanations in terms of niche, have questioned the explanatory virtues of the niche concept.

After this presentation, it seems that the fortunes and misfortunes of the niche concept can be seen as a reflection of the difficulties of ecology to give birth to a theory that would be both predictive and explanatory.

The niche concept pervades ecology. Like the fitness concept in evolutionary biology, it is a core concept, whose meaning is sometimes made little explicit, prompt to slippages, and that has been called tautological. As a rough preliminary definition, let us say that the niche is what describes a species' ecology, which may mean its habitat, its role in the ecosystem, etc. The niche concept, inspired by darwinian biology, has had a growing fortune during the twentieth century, at the crossroads of the developing ecological disciplines, before falling out of favor in the 1980s.

In the first part of this chapter, we will trace the history of the concept and of its various fortunes and misfortunes. In the second part, we will examine more closely the relationships between the concept and the explanations of coexistence and

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diversity. In the third part, we will expose the recent controversy between theories based on the niche concept and neutral theory, and will discuss the legitimacy of such a controversy. To conclude, we will come back on the merits and difficulties of the diverse meanings of the concept.

## 1 History of the Niche Concept

### 1.1 *The Concept Before the Word*

The idea that a species has an habitat or a role has long preceded post-darwinian biological studies, and runs across history – although the filiation between its various incarnations is not always obvious.

Many religious myths, especially in the West, the Genesis, attribute to each species a place within a harmonious system. Since ancient times we find, in the Greek philosophers and naturalists, explanations of the multiplicity of forms of life and very accurate descriptions of what we would now call the “ecology” of organisms, including their diet, their habitat, their behavior, the influence of seasonality, their distribution, etc. (e.g. Aristotle, 4th century BC., 1883, esp. book VIII). In the eighteenth century, Linnaeus (Linné 1744–1972: 57) brought together the divine harmony of Genesis and the work of contemporary naturalists in its definition of the “economy of nature”, in which natural beings are complementary and tend to a common purpose.

The ideas of the relation to the environment and the interdependency of the elements of the natural system can be read in the writings of nineteenth century naturalists, in various forms such as the definition of biotic relation types (parasitism, commensalism, mutualism) (Beneden 1878), the concept of biocoenosis (Möbius 1877), the quantified studies of trophic chains (Forbes 1880, 1887; Semper 1881), the study of vegetal successions and of the feedback between soil and plants (Cowles 1899), or the notion of limiting factor (Liebig 1841: xcii,c) (see McIntosh 1986, esp. chap I & II). Darwin provided, in addition, the idea that living organisms have a place in the economy of nature to which *they are adapted by natural selection*: this is what he explicitly called the “*line of life*”, (e.g. Darwin 1859: 303; Stauffer 1975: 349, 379) like the “*line of work*” refers to the profession of a person (Chase and Leibold 2003: 6). For Darwin’s successors, the “economy of nature” had been laicized and one must seek mechanical causes to it (Haeckel 1874: 637).<sup>1</sup>

### 1.2 *Grinnell and Elton, the Nucleation of the Concept*

The first use of the word “niche” in the meaning of the place occupied by a species in the environment is probably due to Roswell Johnson (1910: 87); but Joseph Grinnell (Grinnell and Swarth 1913: 91, quoted in Schoener 1989: 80) was the first

<sup>1</sup> Julve (2005) provides a synthetic list of actors of seemingly ecological ideas since ancient times.

to insert the concept in a research program, and explicitly described the niches of a variety of species (Griesemer 1992: 232). Grinnell dealt with the influence of environment on the distribution of populations and their evolution, following the traditions of biogeography, of systematics, and of Darwinian evolution (Grinnell 1917; Griesemer 1992: 233). For Grinnell, the term “niche” encompassed everything that conditioned the existence of a species at a given location, including abiotic factors such as temperature, humidity, rainfall and biotic factors such as the presence of food, competitors, predators, shelters, etc.. In fact, his niche concept was closely linked to his idea of competitive exclusion (Grinnell 1904: 377), an idea more readily attributed to Gause (1934: V), although already very pregnant in Darwin (1872: 85): the niche was a complex of environmental factors, a place, according to which species would evolve and exclude each other.

In order to explain the distribution and properties of the species, Grinnell developed an ecological hierarchy, parallel to the systematic hierarchy. While the systematic hierarchy subdivided the living from the reigns to the subspecies (and beyond), the ecological hierarchy subdivided the distribution of biotic and abiotic factors into realms, regions, life zones, faunal areas, (plant) associations and ecological or environmental niches (Grinnell 1924: 227, quoted in Schoener 1989: 83). The higher levels, such as kingdoms, regions, areas of life, had an explicit geographical connotation and were rather associated with abiotic factors. Conversely, the lower levels, including the niche, were rather associated with biotic factors and had no explicit geographical connotation (Grinnell 1928, cited in Griesemer 1992: 233). In this context, the niche was seen as the “ultimate” unit of association between species (e.g. Grinnell and Swarth 1913: 91; Grinnell 1917: 433, 1924: 277, 1928: 193 quoted in Schoener 1989: 84) or of distribution (1928) or of occurrence (Grinnell and Storer 1924: 12, quoted in Schoener 1989: 88), and Grinnell posed that “[i]t is, of course, axiomatic that no two species regularly established a single fauna have precisely the same niche relationships” (Grinnell 1917: 433).

Moreover, by comparing communities in different regions, Grinnell imagined that some niches that are occupied in a region may be vacant in another, because of the limitations in dispersal due to geographical barriers. The comparison of communities also lead him to bring his attention to ecological equivalents that, by evolutionary convergence, are driven to occupy similar niches in different geographical areas (1924: 227, quoted in Schoener 1989: 83).

Charles Elton (1927: chap. V), who is perceived as the second father of the niche concept, also focused on ecological equivalents, but in a different research program. Elton looked for invariances of community structures through four areas of study that focused on the trophic relations: (a) food-chains, that combine to eventually form a whole food-cycle, (b) the relation between the size of an organism and the size of its food, (c) the niche of an organism, that is, “the animal’s place in its community, *its relations to food and enemies*, and to some extent to other factors also”, and (d) the “pyramid of numbers” (the fact that organisms at the base of food chains are more abundant, by a certain order of magnitude, than the organisms at the end of the chain) (Elton 1927: 50, 64, his italics). The niche was thus defined mainly by the position in trophic chains (such as carnivore, herbivore, etc.); although other factors such as the micro-habitat could also be included (Elton 1927: 65). Elton

gave many examples of organisms occupying similar niches, such as the Arctic fox that feeds on eggs of guillemots and remains of seals killed by polar bears, and the spotted hyena that feeds on eggs of ostriches and remains of zebras killed by lions (Elton 1927: 65; see also Schoener 1989: 86).

Although some later commentators (e.g. Whittaker et al. 1973), and specifically textbooks authors (e.g. Ricklefs 1979: 242; Krebs 1992: 245; Begon et al. 2009: 31), have forced the distinction between Grinnell's and Elton's concepts, by respectively renaming them "habitat niche" and "functional niche", both concepts appear to be very similar (Schoener 1989: 86–87).<sup>2</sup> So similar indeed, that it may have seemed questionable that they were independently formulated (Schoener 1989: 88).

The word "niche" was also used by contemporaries in animal ecology in a way similar to Grinnell and Elton (Schoener 1989: 84–85).<sup>3</sup> In vegetal ecology, concepts that were close but often dressed in a different terminology were developed in studies that were later ignored, but that preceded similar works on the niche coming several decades later (Chase and Leibold 2003: 7).<sup>4</sup>

<sup>2</sup>For both authors: (1) the ecological equivalents were the rationale for the concept, as an evidence that similar niches existed in different places, (2) the niche was seen as a place that existed independently of its occupant, (3) food was a major component of the niche but the niche was not restricted to food, as it also included the micro-habitat factors and the relationship to predators. However, Elton's definition being more vague, several species could share the same niche (Griesemer 1992: 235). In addition, Elton explicitly excluded macro-habitat factors, which was not the case for Grinnell. (See Schoener 1989: 86–87 for a detailed discussion of the relationship of these two concepts.)

Griesemer (1992: 235–236) notices that the two concepts are better distinguished with respect to the research programs in which they were inserted, rather than to differences between some of their respective definitions: Grinnell focused on the environment to explain speciation, while Elton focused on the structure of the communities.

<sup>3</sup>Schoener (1989: 85), acknowledging Gaffney (1973, here cited as 1975), notices in particular the precedence of Johnson (1910). Johnson used the word in a way similar to Grinnell's concept: species must occupy different niches in a region, because of the importance of competition in the Darwinian theory. However, Johnson observed that the lady-beetles he studied did not seem to show a clear niche distinction – an observation, Schoener remarks, that was to be repeated many times on arthropods in later studies. Hutchinson (1978: 156), who studied the books available to Grinnell from 1910 to 1914, did not find Johnson's work in them (Schoener 1989: 85).

Schoener also reports the work of another contemporary, Taylor (1916), who worked with Grinnell, and who also focused on ecological equivalents (Schoener 1989: 84). Taylor however, Schoener notices, rather than imagining that the repetition of local adaptive radiations to similar niches between different locations would lead to convergences, suggested that the same group of organisms would fill the same niche in different geographical areas. Barriers to dispersal could thus prevent some niches to be filled.

<sup>4</sup>In their historical introduction, Chase and Leibold (2003: 7–8) give a quick and edifying portrait of such studies in vegetal ecology: "For example, Tansley (1917) performed experiments that showed how plant species competed and coexisted, in a sense vying for shared niche space. Tansley also explicitly contrasted the conditions in which a species could theoretically exist with the actual conditions in which it did exist: ideas generally attributed to Hutchinson (1957) in his discussion of "fundamental" and "realized" niches (...). Salisbury (1929) furthered this distinction and suggested that the similarity in species requirements was strongly related to the intensity of their competition – much the same concept as appears in the more widely appreciated work of Gause (1936)" (referred here as Gause 1934).

### 1.3 George Hutchinson and the Competitive Exclusion Principle

In the 1930s, Georgyi Gause conducted a series of empirical studies on the dynamics of populations of paramecia in competition or suffering predation from *Didinium*, to test the predictions of the differential equations of Vito Volterra (1926) and Alfred Lotka (1924). He identified Elton's niche (Gause 1934: chap. II) to the competition coefficients in Lotka-Volterra's model (*ibid.*: chap. III<sup>5</sup>) and concluded that two species occupying the same niche in a homogeneous environment cannot coexist, one excluding the other (*ibid.*: chap. V<sup>6</sup>). Related experiments were conducted by Thomas Park (1948, 1954) on beetles and led to similar conclusions. In so doing, the niche got phagocytized by population dynamics, as it was seen as the determinant of competitive exclusion – the integration of which to a Grinnell-like evolutionary vision having been evacuated (Griesemer 1992: 236–237).

As a result of these studies, the impossibility of the coexistence of several species on the same niche, which had been previously “regarded by all as obvious and not particularly interesting” (Kingsland 1985: 156), eventually appeared reinforced as a principle derived from an empirical generalization (Gause 1939: 255, quoted in Kingsland 1985: 157) – though it was not so, however, before the works of Hutchinson (e.g. 1944: 120, 1948: 238, 1957: 417–421) and Lack (1947: 18; see Hardin 1960: 1294; Kingsland 1985: 162).<sup>7</sup> This principle would be later designated, among other names, Gause's principle, or competitive exclusion principle. Although it created difficulties and encountered resistance (Hardin 1960: 1297), it is still fundamental today both in textbooks (e.g. Begon et al. 2009: 238), and in research papers (e.g. Meszéna et al. 2006).

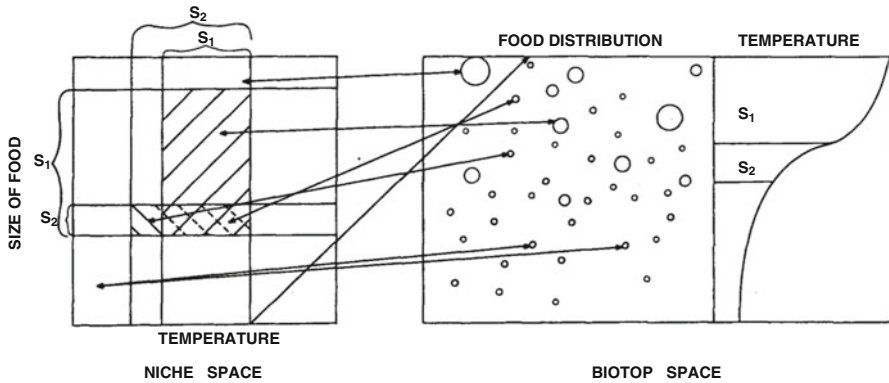
In 1957, Hutchinson caused an additional shift by formalizing the niche concept as an attribute of the species, not of the environment (Hutchinson 1957: 416). The niche was described in a space of environmental variables, biotic and abiotic, some of which representing the limits of species viability.<sup>8</sup> The area included between

<sup>5</sup>“... if the species lay claim to the very same “niche”, and are more or less equivalent as concerns the utilization of the medium, then the coefficient  $\alpha$  [in Lotka-Volterra's equations] will approach unity” (Gause 1934: chap. III).

<sup>6</sup>“It appears that the properties of the corresponding [Lotka-Volterra] equation of the struggle for existence are such that if one species has any advantage over the other it will inevitably drive it out completely (Chapter III). It must be noted here that it is very difficult to verify these conclusions under natural conditions. (...) There being but a single niche in the conditions of the experiment it is very easy to investigate the course of the displacement of one species by another.” (Gause 1934: chap. V)

<sup>7</sup>By contrast, in France, L'Héritier and Teissier (1935), who carried out experiments on the coexistence of two species of *Drosophila*, came (in agreement with some experimental results of Gause 1934) to the conclusion that “two species sharing the same resource in an environment and using it in an apparently identical way may survive side by side in a state of approximate balance.” (see Gayon and Veuille 2001: 88). On the status of the competitive exclusion principle, seen as an *a priori*, and therefore irrefutable, principle, see Hardin (1960: 1293).

<sup>8</sup>The first formulation of the niche concept by Hutchinson is to be found in a footnote, in a paper in limnology (Hutchinson 1944: 20). Schoener (1989: 91) reports a very similar formulation



**Fig. 26.1** Original illustration of Hutchinson's niche concept (1957: fig. 1): "Two fundamental niches defined by a pair of variables in a niche space in two dimensions. Only one of the two species is expected to persist in the region of intersection. The *lines* joining equivalent points in niche space and biotop space indicate the relationship between the two spaces. The distribution of the two species involved is shown in the *right panel* in relation to a standard curve of temperature versus depth in a lake in the summer"

these limits, corresponding to "a state of the environment which would permit the species to exist indefinitely", was named *the fundamental niche* (Fig. 26.1). The niche actually occupied by the species, restricted to the regions of the fundamental niche where the species is not excluded by its competitors, was named *the realized niche* (Hutchinson 1957: 417). Contrary to the fundamental niche, the realized niche is contingent on a given set of competitors.

While Grinnell and Elton emphasized the similarity of the niches occupied by ecological equivalents in different geographic areas, Hutchinson emphasized the similarity of the niches of species in a same location, and how species come into competition – although other niche factors were also considered, such as predation and environmental variability (Griesemer 1992: 238). In Hutchinson, competition (for resources) could change the niche of a species – in the sense of a reduction in similarity. The following authors would focus on competition for resources and combine the two words, niche and competition, in more and more intimate combinations (Chase and Leibold 2003: 12: fig. 1.4).<sup>9</sup>

The shift operated by Hutchinson, from the niche offered by the environment to the niche of a species, has sometimes been described as revolutionary (Schoener 1989: 90). It would be crystallized in the distinction between *environmental niche*

(in french) in a book by Kostitzin (1935: 43): "Imagine a multi-dimensional symbolic space representing the vital factors: p=pressure, T=temperature, I=illumination, etc.. In this space every living creature at a given time occupies a point, a species may be represented by a set of points.". Hutchinson (1978: 158, quoted in Schoener 1989: 91) acknowledged having been informed of Kostitzin's work in the 1940s, without, however, remembering it when formulating his definition in 1944.

<sup>9</sup>Note that predation will also be set aside in the development of the neutral theory.

and *populational* niche (Colwell 1992: 242–243). In fact, it may seem natural to shift, at least verbally, between “the niche occupied by a species” and “the niche *of* that species”. Hutchinson himself seemed to return to the environmental niche when he discussed the problem of a biotope saturation, speaking of “empty niches” (1957: 424), and said he “merely” formalized the concept already in use (1957: 416).<sup>10</sup> With this formalization, the concept allowed to consider quantifications and predictive theories; however, it still presented some operational difficulties.<sup>11</sup>

Two years later, by more precisely questioning the causes of the number of species in a biotope and their degree of similarity, Hutchinson noted that when two similar species coexist, the average ratio of the size of the largest to the size of the smallest is approximately 4/3 (Hutchinson 1959: 150–154). This ratio, that would soon to be known as the Hutchinsonian ratio (Lewin 1983: 637), consumed, for many years, much of the theoretical and experimental impulses in ecology (Kareiva 1997: §1), paving the way for flourishing researches on the causes and consequences of diversity (Chase and Leibold 2003: 10).

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<sup>10</sup> The environmental and populational niches are however incommensurable if one holds the view that species make some ecological factors relevant that could not be suspected to be so before observing the species (that is, if species and niches are co-constituted, see e.g. similar views in Drake et al. 2007; Longo et al. 2012).

<sup>11</sup> The operational difficulties of Hutchinson’s concept come from the (binary) formalism of the set theory he used. They are already partly mentioned by Hutchinson (1957: 417) and discussed in length by Schoener (1989: 93).

All points of the fundamental niche represent the possibility of indefinite existence while all points outside the fundamental niche represent non-indefinite viability. Now, for the ecologist, the performance of a species cannot be reduced to a binary variable. (I thank François Munoz for an insightful comment on this point.) Despite this simplification, a major difficulty is to empirically determine the environmental states that allow the population to survive, because the viability of a population is difficult to assess – especially in the field. Similarly, it is physically impossible to measure the survival of a population at *one* point of the environmental values, and less precise measurements are likely to ignore the extent of the impact of competing species on the realized niche. Hutchinson (1978: 159, quoted in Schoener 1989: 93) proposed to use the average values instead, but this would lack both biological relevance (the same average can represent very different biological realities) and relevance for the limiting similarity (the niche width and overlap would not be represented).

Another difficulty concerns the nature of the environmental variables considered: strictly speaking, it is the occurrence of a factor (for example, the frequency of the seeds of a certain size) that is one axis of the niche, and not the measurement of this factor (seed size) (see Hutchinson 1957: 421, fig. 1 shown above: the axes are respectively “temperature” and “size of food”). This is because organisms compete, if any competition, for places in the biotope space, not for places in the niche space. This gets particularly clear if one considers possible biotopes where the places corresponding to the intersection of the two fundamental niches would be non-limiting. As Schoener (1989: 94) puts it: “Hutchinson’s formulation of niche overlap acts as if competing species are placed together in arenas having single values of such niche dimensions as food size or temperature. (...) But real arenas where populations interact are characterized by distributions of values over axes of resource availability, not by single values.”. A similar problem exists with the concept of utilization niche, as it also uses the measurement of a factor and not the measurement of its occurrence (see below).



## 1.4 *The Golden age: The Niche Theory*

In the 1960s, Robert MacArthur, Richard Levins and colleagues extended Hutchinson's approach and recast the niche concept again (MacArthur and Levins 1967). Hutchinson's concept – the range of environmental states, specific to a species, which allowed its existence – was replaced by the concept of resource utilization distribution. The niche, defined for a specific population, was equivalent to the frequency of utilization of a resource ordered on one or more dimensions, and could be simply represented by a histogram (where the maximum utilization for each class of a given resource would be 100 % for a given species). The axes of the niche could be very diverse, including notably food (frequency of consumption of items sorted by size, for example), space and time (frequency of occurrence or activity according to places and/or circadian, seasonal rhythms,, etc.) (Schoener 1989: 91).

The niche as a utilization distribution was an “eminently operational concept” (Schoener 1989: 93). Easy to measure compared to earlier authors' niches, it got readily used in many empirical studies and initiated a soon fertile family of models, known today as the theory of niche (reviewed in Vandermeer 1972; Schoener 1989: 96–106). Niche theory essentially dealt with competition (Schoener 1989: 106). It aimed to explain the rules of assembly and coexistence of communities, their degree of saturation or invasibility, the number, abundance and the degree of similarity of species composing them (Schoener 1989: 102,106). *Via* this program, the niche concept got firmly nested in most environmental issues (Chase and Leibold 2003: 11), although some ecologists found the concept “confusing” (and yet important) (Root 1967: 317), “tautological” (Peters 1976: 5–6), to be avoided “whenever possible” (Williamson 1972: 111), or that it would “probably turn out to be unnecessary” (Margalef 1968: 7, quoted in Griesemer 1992: 231).<sup>12</sup>

Models of the niche theory are based on Lotka-Volterra's equations (MacArthur and Levins 1967: 377). Further developments would show that more mechanistic descriptions of the resources dynamics would produce similar behaviors, at equilibrium, to those represented by Lotka-Volterra's equations (Tilman 1982: chap. 7, see also MacArthur and Levins 1964<sup>13</sup>). The models crucially rely on the assumption that the overlap of utilization niches allows to calculate the coefficients of competition (MacArthur and Levins 1967: 380).<sup>14</sup> In turn, the limiting values of the coeffi-

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<sup>12</sup> Besides, niche theory was considered as inappropriate or of limited use by some botanists, who insisted on the fact that all autotrophic plants “need light, carbon dioxide, water and the same mineral nutrients” (Grubb 1977: 107) and that a substantial partitioning of these resources seems impossible (but see Sect. 3.4.3). Among them, Grubb pleaded for an extended definition of the niche, including notably the regeneration niche – that is, the way plants colonize the gaps arising in the environment (Grubb 1977: 119). Fagerström and Agren (1979) have used models to show how different regeneration properties (i.e. temporal average and variance, and phenology, of diaspore production) could enable coexistence.

<sup>13</sup> See also the treatment by Looijen (1998: Chap. 11, esp. pp. 184–185).

<sup>14</sup> See the review by Schoener (1989: 97), and the discussions by e.g. Schoener (1974), Neill (1974), May (1975), and references therein.

cients allowing coexistence in a model can be converted into resources utilizations properties, giving the expected limiting similarity of species. The limiting similarity can be expressed as the ratio between the width of the niche, defined as the variety of resources used by the species (for example, the standard deviation of the distribution) and the distance between the distribution modes of each species (Schoener 1989: 93–94,97).

In ecological models, niches of species do not evolve (in the sense of long term evolution by natural selection). These models aim at determining, for a given community in equilibrium, if a species can invade or even persist, hence to formulate the rules of coexistence and assembly.<sup>15</sup>

In niche evolution models, the niche is defined at the organism level and such organism niches vary within a species. The niche of a species becomes a cloud of points or a density of utilization probability, which can be partitioned into “intra” and “inter” organism components (Griesemer 1992: 239, see e.g. Roughgarden 1972; Ackermann and Doebeli 2004). These models deal with the evolution of niche properties such as its width and the position of the mode, the distance/width ratio at the evolutionary equilibrium, i.e. the displacement and the divergence/convergence of characters – such as size ratios (Roughgarden 1972, 1976; Case 1981, 1982<sup>16</sup>).

Initially, the theory has generally been applied to pre-existing data sets, but it also stimulated new empirical studies for the field ecologists (Schoener 1989: 100). The limiting similarity was a notable part of these investigations, and was a difficult one because the theory did not predict a single value for it, even less for the *realized* limiting similarity (reviewed in Abrams 1983; Schoener 1986, cited in Schoener 1989: 100). After Hutchinson’s publication on the 4/3 size ratios, many empirical studies were conducted in an attempt to determine whether, on this dimension (i.e. size), niches are non-randomly spaced – with both positive and negative results (Schoener 1989: 100). Some empirical studies targeted specific predictions of the theory, such as the co-evolution of size among different species, or the expected overlap according to the grain of the considered habitat (Schoener 1989: 102).

## 1.5 The 1980s: The Downfall<sup>17</sup>

The enthusiasm for the competition-centered niche theory has been followed by a backlash in the 1980s. Authors, including Simberloff (1978) and Strong (1980),<sup>18</sup> showed that many studies on patterns of competition did not involve adequate null hypotheses, thereby questioning their validity and the importance of the theory

<sup>15</sup> See Schoener (1989: 97), Chase and Leibold (2003: 13), and references therein.

<sup>16</sup> These and other models are briefly reviewed in Schoener (1989: 98–99).

<sup>17</sup> The word comes from Chase and Leibold (2003: 11).

<sup>18</sup> Pielou (1975: e.g. 80, 1977) seems to have been a pioneer (Keddy 1998: 753) who has been overlooked, which might be brought into perspective with Simberloff’s style, which was “perceived as arrogant and combative” (Lewin 1983: 639).

(Chase and Leibold 2003: 12). The debate on the form of null model would generate tensions (e.g. Lewin 1983: 638–639; Strong et al. 1984: chap. 1, quoted in Hubbell 2001: 9), and remains a source of conflicts today.<sup>19</sup> The difficulty to have to first show the presence of competition, or falsify his absence (e.g. Schoener 1983a; Connell 1983), could also have resonated with the load carried by Gould and Lewontin (1979), in evolutionary biology, against the “hard” adaptationist program,<sup>20</sup> and the emergence of the neutral theory in population genetics (Kimura 1968, 1983).

The niche theory had also been weakened by its own developments: each new treatment appearing to produce new and unexpected results, which did not converge to a general or usable theory (Schoener 1989: 103). Meanwhile, the emphasis on competition decreased as a more pluralistic vision of coexistence developed, with models taking into account predation, abiotic stresses,<sup>21</sup> mutualism, or the extrinsic and intrinsic spatio-temporal heterogeneity.<sup>22</sup> This seemed to mark a return to the first Grinnellian and Eltonian conceptions, though it did not prevent the niche concept to remain, overall, closely entangled with competition (Colwell 1992: 247; Chase and Leibold 2003: 14).

However, these developments of the theory were not intimately connected to empirical work (Chase and Leibold 2003: 14), the volume of which, by the way, decreased (Schoener 1989: 102). Empirical ecologists were now skeptical about the usefulness of the theory and focused on testing very basic hypotheses with rigorous null models on the presence or absence of species interactions – mostly competition (Chase and Leibold 2003: 14). This empirical attitude was concomitant with the breakthrough of statistical and experimental rigor in ecology (Chase and Leibold 2003: 14). Studies of species diversity, abundance, distribution at large scales were abandoned in favor of studies of local interactions, more suitable for experiments (Chase and Leibold 2003: 13). And among those interested in large spatial scales, Hubbell (1979) explicitly avoided to use niche differences to explain the distribution patterns (see Sect. 3).

## 1.6 Chase and Leibold, the Renovation

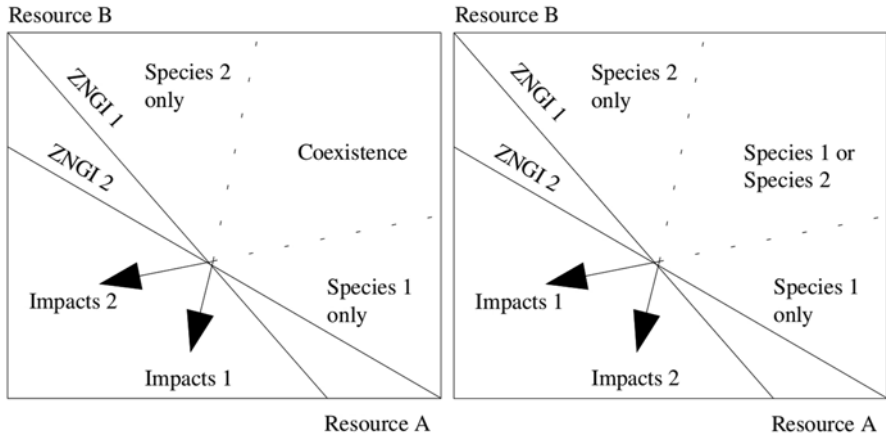
After the loss of momentum of the niche concept in the literature, Matthew Leibold (1995) and Jonathan Chase, who grant this concept a useful and synthetic role in ecology (Chase and Leibold 2003: 17), proposed an ultimate revision, based on

<sup>19</sup> See e.g. Gotelli and Graves (1996: chap. 1), Looijen (1998: chap. 13), Chase and Leibold (2003: 13), and references therein.

<sup>20</sup> On adaptation, See Grandcolas, and Downes, this volume (*Ed. note*)

<sup>21</sup> Stress: a factor having a negative impact on the organism and on which the organism has no impact (*sensu* Chase and Leibold 2003: 26, table 2).

<sup>22</sup> See Chase and Leibold (2003: 13–14) and references therein.



**Fig. 26.2** Niche theory according to Chase and Leibold (2003): This chart shows the responses and impacts of two species 1 and 2 from, and on, two substitutable resources A and B. *Arrows*: vectors summarizing the impact of each species on resources A and B. *Lines*: zero net growth isoclines (ZNGI). In this example, the growth rate is negative under the ZNGI and positive above, the half-plane above the ZNGI hence represents the area of viability of the species. Last, the higher the intersection of a species' ZNGI with a resource axis, the higher its needs of that resource. *Left*: 1 needs more B and depletes B the more, conversely 2 needs more A and depletes A the more; the direction of the impact vectors and the intersection point of the isoclines define an area of coexistence. *Right*: the vectors of impacts have been reversed: the zone of coexistence has evolved into an exclusion zone. The range of environmental values that species are experiencing depends on the species characteristics, but also on the intrinsic dynamics of the environment, such as the rate of resource renewal (After Chase and Leibold 2003: 34 fig. 2.8)

Tilman's mechanistic formalism (Tilman 1982: 6<sup>23</sup>). They showed that, within the ecology of an organism, we must distinguish the impacts of a given ecological factor on this organism, that is to say its response to the factor – in particular its needs – and the impacts of the organism on the ecological factor (Chase and Leibold 2003: 14). They defined the niche as the union of the responses of the organism and its impacts<sup>24</sup> (Fig. 26.2). In this formalism, Chase and Leibold presented a bestiary of ecological factors depending on the types of the impacts, positive, null or negative, *from* and *on* the organism.<sup>25</sup> They emphasized in particular resources, predators and stresses.<sup>26</sup> The axes of the niche should be quantitative measures of the occurrence

<sup>23</sup> See also e.g. MacArthur and Levins (1964: 1208), MacArthur (1972: e.g. 37–40) and other predecessors cited in Chase and Leibold (2003: 16).

<sup>24</sup> To be precise, Leibold (1995) and Chase and Leibold (2003: 15–61) refer to the union of the *requirements* of the organism and its impacts: “[the niche is] the joint description of the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita effects of that species on these environmental conditions” (p. 15). The generalization of the definition to the organism *responses* seems natural (see e.g. Meszéna et al. 2006).

<sup>25</sup> See Chase and Leibold (2003: chap. 2, esp. table 2, p. 26).

<sup>26</sup> See e.g. Chase and Leibold (2003: fig. 2.4 p. 27, p. 44).

of environmental factors, not just measures of the factors as in the utilization-distribution niche (Leibold 1995: 1373; Chase and Leibold 2003: 55). In this way, Chase and Leibold produce an elegant synthesis of a century old history.

Chase and Leibold incorporated their new concept into an inclusive research program that aimed to free niche theory from the focus on competition and local interactions. Breaking the association with competition must help save the niche terminology from its replacement by synonyms of cosmetic value, and improve the readability of previous studies by contemporary ecologists (Chase and Leibold 2003: 17–18), who are less fond of the history of their discipline than their evolutionist colleagues (Griesemer 1992: 240). Finally, they highlighted the integration of their concept into the exploration of multi-scale heterogeneous processes, which must meet the challenges of contemporary ecology such as habitat degradation, extinctions, invasions, etc. (Chase and Leibold 2003: 16,40–41,139,155). At this stage, Chase and Leibold's revision was not directly empirically interpretable (Chase and Leibold 2003: chap. 4, Cadotte 2004: 1792). They considered their revision as a framework to build more specific hypotheses and to compare broad ecological patterns (Chase and Leibold 2003: 61).

### ***1.7 The Theory of Niche Construction and the Stem Cell Niche***

The niche concept has recently experienced two additional extensions: niche construction in evolutionary biology, and the stem cell niche in cell biology.

The research program on niche construction arose from an opposition to the externalist program in evolutionary biology, where the environment is conceived as a non-modifiable entity causing the evolutionary change in organisms (Lewontin 1983: 274; Godfrey-Smith 1998: 142). Proponents of the constructionist program point out, conversely, that by their activities (construction of burrows, secretion of chemical substances, consumption of preys, etc.), organisms modify their environment in such a way that the selection pressures they undergo can in turn be modified. The niche is defined as the set of evolutionary pressures, and construction refers to their modification (Odling-Smee et al. 2003: 419). The program is presented as a generalization of existing models in evolutionary biology, such as models of coevolution, frequency-dependent selection and maternal effects. In ecology, a branch of the program calls for increased consideration of ecosystem engineering in the models.

The main epistemological novelty (and difficulty) of this research program is to insistently introduce construction as an evolutionary process that is symmetrical to natural selection, none of them being subordinated to the other, in particular as regards the production of adaptation (e.g. Odling-Smee et al. 2003: 19,289–290; Day et al. 2003: 89). In principle, it is a revolutionary difference with previous approaches. However, to our knowledge, models and examples of niche construction given by these authors always call for an invariant entity that can be considered as the selection pressure (e.g. the matrix of gains in a game) and other entities that may be considered as variables (e.g. frequencies of strategies). Therefore, the externalist perspective of

the extended phenotype, considering non-modifiable selective pressures which can act on phenotypes that are both external (like activities) and internal to the organism, does not seem surpassed (Dawkins 1982: chap. 11 & 14, 2004: 378–381).<sup>27</sup>

In cell biology, yet another niche concept has been used to explain the apparent immortality of certain stem cells<sup>28</sup> (Schofield 1978: 13–15, 1983: 277).<sup>29</sup> The stem cell niche is defined as the tissular microenvironment that is required for cells to acquire or retain their stem cell characteristics, and which control their numbers. The stem cell niche constitutes “*a basic unit of tissue physiology*” (Scadden 2006: 1075, my emphasis). In case of a vacancy, the stem cell niche may force differentiated cells to adopt characteristics of stem cells (Scadden 2006: 1078). Conversely, stem cells can induce the formation of niches (Bendall et al. 2007). The stem cell niche is localized in space (Powell 2005: 269), it is a three-dimensional structure (Powell 2005: 270) consisting of other cells and their signals, of extracellular materials, it is the target of signals from the nervous system and is associated with the circulatory system (Scadden 2006: 1077, fig. 3). It has a functional dimension (Li and Xie 2005: 622; Scadden 2006: 1078). Because of its impact on the tissue that surrounds it, the stem cell niche is considered a promising therapeutic target (Li and Xie 2005: 623; Scadden 2006: 1078). The word “niche” is also used in oncology, by analogy with stem cell biology: on the one hand, the alteration of the niche of a stem cell is considered as a possible etiology of cancer, on the other hand, cancer cells can also induce the formation of so-called pre-metastatic niches (that is, modified environments facilitating the establishment of tumoral cells<sup>30</sup>) and metastatic niches (*via* for example the development of blood vessels in the vicinity) (Psaila and Lyden 2009).<sup>31</sup>

<sup>27</sup> Pocheville (2010: chap. 2, esp. pp. 75–77) provides a more thorough critique of the symmetry between niche construction and natural selection. This point will be further deepened in a forthcoming paper, aimed at showing in which cases niche construction theory produces radical theoretical novelty.

<sup>28</sup> Watt and Hogan (2000: 1427) give the following definition: “Although [the question of what a stem cell is] remains contentious after 30 years of debate (...) the prevailing view is that stem cells are cells with the capacity for unlimited or prolonged self-renewal that can produce at least one type of highly differentiated descendant. Usually, between the stem cell and its terminally differentiated progeny there is an intermediate population of committed progenitors with limited proliferative capacity and restricted differentiation potential, sometimes known as transit amplifying cells.” Laplane (2013) provides a thorough discussion of the stem cell concept.

<sup>29</sup> Though the stem cell niche concept has been later claimed to come by analogy with the ecological niche concept (e.g. Powell 2005: 268, see also Papayannopoulou and Scaddeb 2008), it does not seem to have been imported from the ecological literature by Schofield. I thank Lucie Laplane for drawing my attention to this point.

<sup>30</sup> It has been shown that tumoral cells can mobilize normal bone marrow cells, have them migrate to particular regions and change the local environment so that it attracts and supports the development of a metastasis (Steeg 2005).

<sup>31</sup> Work on cell niche sometimes explicitly refers to the concept of ecological niche (e.g. Powell 2005: 269). Work on the “niche construction” by the cells, however, does not seem to have been inspired by Odling-Smee’s and colleagues’ program (e.g. Bershad et al. 2008).

Though the importation of ecological (and evolutionary) thinking in cell biology seems promising, it does not come without difficulties.<sup>32</sup> Here, while both the ecological niche concepts and the (stem and cancer) cell niche concepts are aimed to describe how the environment can be impacted and impact a living system, it should be noticed that they do not have similar explanatory purposes: the ecological niche concepts deal with *fitness* issues, while the stem cell niche concepts deal with *fate* issues.

## 2 The Niche Concept and Coexistence Theories

From Grinnell's times, the niche has been an *explanans* of diversity: diverse species coexist because each occupies its own niche. In this section we mainly follow Chesson's (2000) framework to show how the concept is integrated with current explanations of coexistence, which will allow us to better understand the controversy generated by the neutral theory (Sect. 3).<sup>33</sup>

First, let's underline that the explanations of diversity that could be invoked in coexistence theories vary depending on the fact that the coexistence of different species in the same locality is supposed to be unstable or stable. There are many concepts of stability, the analysis of which cannot be included in this chapter (see e.g. Ives and Carpenter 2007: 58). As a rough definition, let's say that coexistence is unstable when populations are not each maintained on the long term. Conversely, coexistence is stable when the frequency or density of each population does not show any trend over the long term, or at least, when populations tend to not disappear (Chesson 2000: 344).<sup>34</sup>

The "mechanisms"<sup>35</sup> that promote coexistence can have *equalizing* or *stabilizing* effects. The mechanisms are equalizing when they reduce the differences in average fitness<sup>36</sup> between competitors (Chesson 2000: 347). The mechanisms are stabilizing

<sup>32</sup> We briefly discussed this point in Pocheville (2010: chap. III).

<sup>33</sup> See Delord, Chap. 25, this volume. (*Ed. note*)

<sup>34</sup> See Meszéna et al. (2006) for an examination of the structural stability (robustness of coexistence against changes of parameters) of models of stable coexistence.

<sup>35</sup> Here, we use the word "mechanism" in the – very broad – sense used in ecology: practically any form of generation of a pattern can be considered as a mechanism (e.g. Strong et al. 1984: 5&220, Bell 2000: 606, Hubbell 2001: 114, Leigh 2007: 2087; see the brief discussions in Turner et al. 2001: 53 and McGill et al. 2007: 1001). For example, the intensity of competition in a Lotka-Volterra model can be seen, in our view, as a mechanism for the exclusion of two species, while the consumption of the same resource by two species in a Tilman model can be seen as a mechanism, among other possible mechanisms, for the intensity of competition (Tilman 1982: 6, 1987: 769; Chesson 2000: 345). In this sense we say that a Tilman model is "more mechanistic" than a Lotka-Volterra model (e.g. Chase and Leibold 2003: 13), qualified as "more phenomenological" (see Mikkelsen 2005: 561).

<sup>36</sup> We draw reader's attention to the fact that here, fitness is not averaged over time but over all environmental states, e.g. the different values of resource availability (Chesson 2000: 346–7353) or the relative frequency of species (Adler et al. 2007: 96: fig. 1, 97: fig. 2). Last, we also speak of



when they involve negative feedback loops on frequencies (Chesson 2000: 343).<sup>37</sup> Such loops exist when intraspecific interactions (direct or apparent competition, for example) are “more negative” than interspecific interactions (Chesson 2000: 345). Equalizing mechanisms and stabilizing mechanisms, *together*, increase the probability or durability of coexistence (Chesson 2000: 347; Adler et al. 2007: 102, 2010: 1020). Equal fitnesses and the absence of stabilizing mechanisms are at the core of the neutral theory (Fig. 26.3, see also Sect. 3).<sup>38</sup>

Niche partitioning is likely to create negative, stabilizing feedbacks: it occurs when the impacts of each species are negatively correlated to its responses to each factor, and when this impact/response pattern is proper to each species (Chase and Leibold 2003: 43).<sup>39</sup> This applies, for example, when species are limited by a variety of resources and when each species decreases the most (negative impact) the availability of its most needed resource (positive response), if the most needed resource is proper to each species (Chase and Leibold 2003: 34: fig. 2.8). This is also true when species suffer predation of several predators or parasites and when each species increases the most (positive impact) the population of the predator or parasite that limits the species the most (negative response), if, once again, the most limiting predator or parasite is proper to each species (Chase and Leibold 2003: 36: fig. 2.9<sup>40</sup>). With regard to the negative feedback factors (e.g. limiting factors), the smaller the niche overlap, *i.e.* the more the responses are opposed to the impacts and the more they are specific to each species, the more stabilizing the niche partitioning. Recall that the limiting similarity that allows stable coexistence depends on equalizing mechanisms that exist otherwise (Chesson 2000: 346) and on the robustness<sup>41</sup>

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an average fitness in the sense of the per capita growth rate, averaged among individuals within a population.

<sup>37</sup> Negative frequency-dependence : most frequent populations are disadvantaged. Negative density-dependence: for each population, the *per capita* growth rate decreases as density increases. While negative frequency-dependence can emerge from negative density-dependence (e.g., when each species has a specific niche which can support a given maximum density), density-dependence is not sufficient to generate frequency-dependence: each species must, in addition, reduce its own growth more than those of others (Chesson 2000: 348; Adler et al. 2007: 97). (Note that density-dependence is not necessary for frequency-dependence to occur: for instance rock-paper-scissors games can arise without any obvious link to underlying limiting conditions (e.g. Sinervo and Lively 1996).)

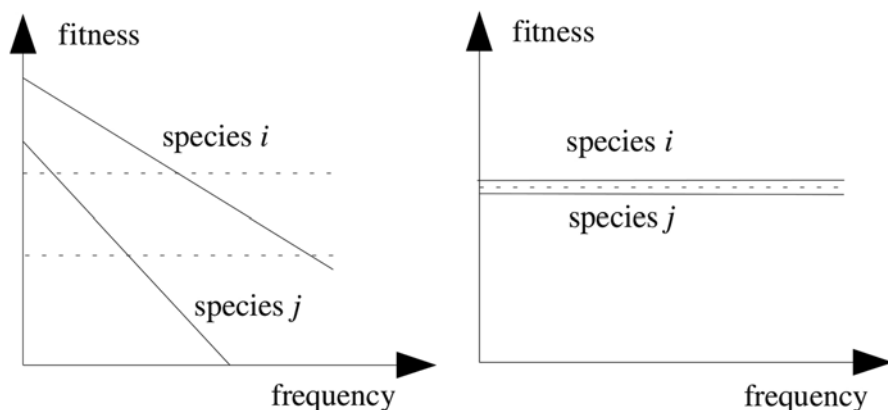
<sup>38</sup> In neutral theory, fitness equality is defined at the individual level (regardless of the species), which implies equality at the population level (the reverse is not true).

<sup>39</sup> We would like to draw once again the reader's attention to the fact that these stabilizing feedbacks are not sufficient in themselves to ensure the stability of coexistence. Put in the graphical terms of Fig. 26.2 given here, niche partitioning will be expressed as a correlation between zero net growth isoclines and impact vectors, and equalizing mechanisms as a proximity of the intercepts of the zero net growth isoclines (Chase and Leibold 2003: 43).

<sup>40</sup> On predation and parasitism see also Chesson (2000: 356–357) and references therein.

<sup>41</sup> Robustness here is meant in the sense of structural stability (model robustness to parameters changes) (Mészéna et al. 2006: 69–70). On the concept of model robustness see Levins (1966: 423–427) and for instance, the critique by Orzack and Sober (1993: 538), and the account by Lesne (2012: 1–3).





**Fig. 26.3** Diagram illustrating the typical assumptions of the niche theory (*left*) and the neutral theory (*right*); for the neutral theory, cf. Sect. 3. *Left*: species have different average fitness (*dotted lines*) but each undergoes a negative frequency-dependence (*solid line*), which stabilizes coexistence (the slope of the *line* represents the intensity of stabilization). *Right*: species show no frequency-dependence, but have equal average fitness (After Adler et al. 2007)

of the desired stability (Meszéna et al. 2006: 695). The limiting similarity and limiting diversity may also be affected by the minimum of viability of a population: the more similar to a competitor's or the more limited a population's niche, other things being equal, the lower the population, which is therefore even more prone to Allee<sup>42</sup> effects (Hopf and Hopf 1985; Hopf et al. 1993) or stochastic extinctions (Turelli 1980; see Chesson 2000: 360).

Niche partitioning is not the only possible stabilizing mechanism. For instance, predators and parasitoids stabilize the coexistence of preys when they have frequency-dependent responses, that is, when they affect the dominant whatsoever, even if all prey species are otherwise ecologically similar (see Chesson 2000: 357 and references therein).<sup>43</sup>

Last, various mechanisms can affect niche partitioning, and interspecific competition is just one of them (e.g. niche partitioning<sup>44</sup> can be caused by “the necessity to specialize in order to guarantee survival in a particular microhabitat, and mate finding”<sup>45</sup>). This said, competition leads to a segregation of niches: even when no

<sup>42</sup> A population is subject to an Allee effect when “the overall individual fitness, or one of its components, is positively related to population size or density” (Courchamp et al. 2008: 4, see also p. 10: box 1.1). This effect can be explained by difficulties in finding breeding partners, or by the need for a group to reach a critical mass to be able to exploit a resource or deal with predation (Courchamp et al. 2008: chap. 2).

<sup>43</sup> We draw reader's attention to the fact that this stabilizing mechanism is different from the niche partitioning with respect to predation exposed above.

<sup>44</sup> To be precise, in this case we would speak of niche restriction rather than niche partitioning (e.g. Rohde 2005: 51–52).

<sup>45</sup> See Rohde (2005: chap. 5, quoted here from p. 82) and other works in the 1970s by the same author (e.g. Rohde 1979).

species is excluded, each species has its utilization of overlap zones reduced by the presence of interspecific competitors. However, a consequence of this is that if overlap, *ceteris paribus*, increases competition, competition in turn, *ceteris paribus*, reduces overlap, both on the ecological time, by the modification of the realized niches, and on the evolutionary time by the modification of the fundamental niches (Schoener 1989: 105 fig. 4.4). Because of this negative feedback of competition on itself *via* its impact on overlap and the multiplicity of mechanisms that can also affect niche partitioning, assessing the importance of competition in niche partitioning is difficult and controversial<sup>46</sup>.

### 3 Neutral Theory and Adventitious Controversies

Hubbell recently challenged dramatically the niche concept,<sup>47</sup> by providing a neutral theory of diversity (here defined in terms of the distribution and abundance of species), in which species have the same niche, and where individuals have the same fitness regardless of the species (e.g. Hubbell 2001: 8–9). In this theory, the dynamics of the community is random and does not depend on its composition. The neutral theory thus proposes, in ecology, nothing less than the negation of the Darwinian approach, in which the very patterns of competition within and between species determine the assembly of a community (Leigh 2007: 2081). Moreover, in the Darwinian approach this assembly was assumed to be reproducible (e.g. Darwin 1859: 74–75), in such a way that communities have sometimes even been considered as superorganisms (Clements 1916: xvii).

The success of the theory on the cases studied by Hubbell and his colleagues, including the highly diverse tropical rainforests, have put the niche concept in serious trouble. Nevertheless, we will see that neutral theory and niche theory<sup>48</sup> do not oppose in the most obvious way. The strength of the controversy can be attributed in part to the denial of the selectionist intuitions (Sect. 3.2), but also to the ambiguous status of the debate, which oscillates between difficulties in distinguishing the predictions of neutral models from those of niche models (Sect. 3.3), and epistemological questions such as the nature of randomness (Sect. 3.4).

<sup>46</sup> See e.g. the discussion by Looijen (1998: chap. XIII).

<sup>47</sup> “I believe that community ecology will have to rethink completely the classical niche-assembly paradigm from first principles.” (Hubbell 2001: 320).

<sup>48</sup> For simplicity, we use in this section the term “niche theory” in a broad sense (equivalent to the *niche-assembly perspective* in Hubbell’s terms, 2001: 8), to mean the corpus of models that are based on the niche concept – and not, in the strict sense, the research program of MacArthur & Levins evoked in Sect. 1.4.

### 3.1 *Neutral Theory Ante Litteram*

Hubbell's neutral theory provides a synthesis of ideas and data published in the 1960s–1980s.<sup>49</sup> As Bell et al. (2006: 1379) notice, the issue of explaining seemingly too high levels of diversity had been already raised in two classic articles by Hutchinson (1959: 154, 1961: 137<sup>50</sup>). MacArthur and Wilson themselves, in their theory of island biogeography, explained the large-scale distribution patterns by assuming that the species undergo fluctuations (following a probability distribution) of colonization and extinction (MacArthur and Wilson 1963; Wilson and MacArthur 1967). Ironically, it does not seem that MacArthur sought to elaborate on a possible link between biogeography theory and niche theory.<sup>51</sup> In population genetics, Kimura (1968, 1983), inspired by Haldane's (1957) calculations on the cost of natural selection and Wright's (1931) works on genetic drift,<sup>52</sup> proposed a theory of neutral evolution of allele frequencies where alleles have the same fitness, the only causes of change being mutation, migration and demographic stochasticity.<sup>53</sup> Kimura thus proposed a null hypothesis, of which the alternative would be the presence of natural selection at the scale of the genome. These works were transposed in ecology (Watterson 1974; Caswell 1976), considering the abundance of species instead of allele frequencies.<sup>54</sup> Hubbell (1979: 1306) expanded these models, following the intuition that limited dispersal, in addition to drift, was a major factor in the assembly of communities,<sup>55</sup> which would explain the agglutinated distribution of conspecific trees that he observed in the Barro Colorado forest.

Besides, in parallel with the decline of the niche concept, the competitive exclusion principle was undermined by works in spatial ecology, that showed that limited

<sup>49</sup>To be precise, we already find the idea of neutral variation in Darwin (e.g. 1859: 46): “These facts [an inordinate amount of variation in some genera] seem to be very perplexing, for they seem to show that this kind of variability is independent of the conditions of life. I am inclined to suspect that we see in these polymorphic genera variations in points of structure which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection (...)”

<sup>50</sup>However, Hutchinson still considered the competitive exclusion principle as a starting point (Hutchinson 1961: 143), envisaging to explain unexpectedly high levels of diversity in functional terms, among others: non-equilibrium competitive dynamics (Hutchinson 1941, cited and deepened in Hutchinson 1961: 138), the mosaic nature of the environment (Hutchinson 1959: 154), and the supposed stability of more complex trophic relationships (Hutchinson 1959: 150).

<sup>51</sup>Schoener (1983b) cited in Loreau and Mouquet (1999: 427), Chase and Leibold (2003: 177–178).

<sup>52</sup>Drift: variation in frequency (here, allelic frequency) due to a random sampling effect in the population: the offspring population of alleles represents a (finite) sample of the parental population. In virtue of the law of large numbers, the larger the sample, the more representative it is.

<sup>53</sup>On neutrality in population genetics, see Leigh (2007: 2076), and references therein.

<sup>54</sup>See Chave (2004: 244) for a discussion on the emergence of neutral models in ecology. Alonso et al. (2006: 452: table 1) provide a useful comparison of the main parameters used in the two neutral theories.

<sup>55</sup>Migration had already been studied in population genetics, but never had a central status as in Hubbell's theory (Alonso et al. 2006: 452).

dispersal might *ad infinitum* delay the exclusion of one species by another, even in the absence of any trade-offs (Hurtt and Pacala 1995). Hubbell found his intuitions reinforced by these works (e.g. Hubbell 2001: 344), being one of those who believe that competitive exclusion is not sufficiently documented in the empirical literature (Hubbell 2001: 11&328, 2005: 167). He recast neutralist models in a monograph, *The Unified Neutral Theory of Biodiversity and Biogeography* (Hubbell 2001<sup>56</sup>), which quickly became a “best seller” (Leigh 2007: 2075) and generated an abundant controversy.

### 3.2 *Characteristics of Neutral Models*

A neutral model describes a community of individuals (belonging to genotypes/species) having symmetrical behavior (see below), which is subject to the apparition of new types (by mutation/speciation) and loss of types by stochastic drift.<sup>57</sup> The diversity of individuals is a dynamical balance between the extinction of the residents and the appearance of new types. Complex interactions are possible between individuals, as long as they are symmetric, *i.e.*, as long as the type of an individual (e.g. species in Hubbell) has no effect on the fate of the individual or on that of other individuals in the community (Hubbell 2001: 28). Typically, in neutral theory, the community is defined as a set of species of similar trophic level and individuals compete symmetrically with each other (Hubbell 2001: 28). Competition is usually carried out by assuming that the total number of individuals is constant (zero-sum game) (Hubbell 2001: 53). Trophic relationships, which are asymmetrical, and mutualism (symmetric or asymmetric) are not treated (Bell 2001: 2413).

Symmetry (also called equivalence) can be confusing in niche/neutrality debates. Symmetry can be defined at several levels: intraspecific level (Kimura), interspecific level (Hubbell), etc. Asymmetry at one level can be, in principle, compatible with symmetry at another level (see e.g. Chesson and Rees 2007).<sup>58</sup> In addition, symmetry can be defined for different properties: ecological equivalence (*sensu* here the

<sup>56</sup> See also Hubbell (1997).

<sup>57</sup> See Hubbell (2001: esp. chap. 1,5,6) and the presentations by Chave (2004: esp. p. 245.: fig. 2) and Leigh (2007). Beeravolu et al. (2009) provide a remarkable review of neutral models. McGill et al. (2006: table 1) provide a usefull comparison of existing neutral models.

<sup>58</sup> It is in particular the case when two species are exactly similar (for instance, if they have exactly the same genes and allelic frequencies as for the functional aspects) and are only inter-sterile: there would be intraspecific, but not interspecific, competition. Hubbell (2006) proposed (without, however, stating it explicitly) such a mechanism to explain the evolution of neutrality at the interspecific level. (A similar result would probably be obtained assuming no limitation on (epi)mutations at the intraspecific level.) Chave (2004: 249) quickly discusses how restrictive the assumption of individual equivalence is.

lack of stabilizing mechanisms<sup>59</sup>) does not entail an equivalence of fitnesses<sup>60</sup> (existence of equalizing mechanisms). Probably, Hubbell's and others' use of terminology, equating ecological, functional, and demographic equivalence,<sup>61</sup> in addition to some of Hubbell's arguments on niche convergence where he (more or less explicitly) discards the principle of competitive exclusion (e.g. Hubbell 2005: 169), may have fueled the controversy. To put it in a nutshell, neutral models are models of complete niche overlap and symmetric fitnesses.<sup>62</sup>

One strength of neutral theory is to provide implicit and explicit spatial models, in which assembly is determined by dispersal (dispersal assembly), and not by adaptation to a local environment (niche assembly).<sup>63</sup> Implicit spatial models consider local communities that exchange individuals, according to a given migration rate, with a global community (admittedly not much empirically identifiable, Leigh 2007: 2081).<sup>64</sup> These models describe local communities as *samples* of the global community, which allows a direct confrontation with the

<sup>59</sup> Bell (2000: 613) proposed a different – and compatible – definition: “Even the notion of ecological equivalence is rather vague; I shall take it to refer to a set of species for each member of which no interaction with another member is positive. If community structure is determined to some extent by competition, then at least one interaction for each member is negative; the neutral model is the limiting case in which all interactions are negative and equal.”

<sup>60</sup> Neutral theory considers fitness equivalence at the individual level (e.g. Hubbell 2001: 6), which implies fitness equivalence at the population level.

<sup>61</sup> On the use of these terms, see e.g. Hubbell (2001: 6, 2005: 166, 2006), and the discussion in Clark (2009: 9). For instance Hubbell's following statement shows a slippage between demographic and functional equivalence: “These life history trade-offs equalize the per capita relative fitness of species in the community, which set the stage for ecological drift.” (Hubbell 2001: 346, briefly discussed in Alonso et al. 2006: 455, similar statements can be found elsewhere in the literature, see e.g. Kraft et al. 2008: 582: note 11). Notice, however, that a full ecological drift would in addition require the absence of any stabilizing mechanisms (an absence that seems to be implicitly hypothesized by Hubbell 2001: 327–328). The word trade-off itself is ambiguous, as trade-offs can theoretically produce both equalizing and/or stabilizing effects (Chesson 2000: 346–347), be they trophic (e.g. Clark et al. 2003) or life-history trade-offs (e.g. Clark et al. 2004). Chase and Leibold (2003), as for them, seem to use trade-offs (here in niche use) as *explanantes* of stabilization in their whole book: “That is, Hubbell's hypothetical species show no niche differences or trade-offs.” (p. 42, note the contrast with Hubbell's quote above). Clark (2009: 9) shows, using Lotka-Volterra equations, how species can have identical parameters (demographic equivalence) while displaying stable coexistence, in particular if there are trade-offs that entail that each species negatively impacts itself more than it impacts the other (functional differences). (Functional equivalence would in this case be represented by an equivalence of the intra- and inter-specific competition terms for each, and all, species. Notice that, still, it would not imply that species be ecologically equivalent, as Lotka-Volterra parameters can be ecologically multiply realized (see Clark 2009: fig. 1).)

<sup>62</sup> That is, complete overlap of responses and impacts to environmental factors in Chase's and Leibold's (2003: 23) account. Note that with this concept, two species having exactly the same niche behave neutrally, and the only “competitive exclusion” occurring is mere drift.

<sup>63</sup> See Chave (2008: 18–20) for a short comparison of niche vs dispersal assembly frameworks. See Beeravolu et al. (2009: 2605–7) for a review of the different kinds of spatial neutral models.

<sup>64</sup> See esp. Hubbell (2001: chap. 5) and the quick and didactic presentation by Alonso et al. (2006: 453: box 2).

sampling data of a community (Alonso et al. 2006: 454). Explicit spatial models specify population dynamics and dispersal in an explicit space, which generates autocorrelated distributions in space and time, that is, non-random patterns.<sup>65</sup> These models differ significantly from earlier so-called “null models”, that were based on the generation of random patterns of spatial distribution – the presence of autocorrelation in the data was then interpreted as an effect of environmental heterogeneity.<sup>66</sup>

### 3.3 *Area of Relevance of Neutral Theory*

#### 3.3.1 *Quality of the Hypotheses*

It is a truism that assumptions of a scientific theory are, because of their ideal character, strictly speaking false. Neutral theory is no exception (e.g. Alonso et al. 2006: 451), and its ability to describe the distributions of abundance *despite* the assumption of niche overlap and the assumption of individual fitness equivalence, has raised questions about the necessity to appeal to niche theory to explain other kinds of observations.

Concerning the hypothesis of niche equivalence, the existence of differences in niches hardly seems debatable even to tenors of neutrality (e.g. Hubbell 2005: 166; Engelbrecht et al. 2007: 80) – on the other hand, they insist on the fact that *not* every difference in phenotypes or in distribution does reflect a difference in niches (e.g. Hubbell 2006: 1389).<sup>67</sup> Among the observations that require explanation in terms of niche let’s mention, without aiming at being exhaustive<sup>68</sup>: (1) differences, and consistencies, in responses of different species to environmental changes in space and time, (2) overyielding,<sup>69</sup> observed in mixtures of species relative to monocultures in the lab or in the field, which has been used in polycultures since the Middle Ages

<sup>65</sup> See Bell (2001: 2417), Bell et al. (2001: 121–128), Bell (2005).

<sup>66</sup> See Gotteli and Graves (1996: chap. I), Bell (2001: 2416), Bell (2005: 1757–1758) and references therein.

<sup>67</sup> As we have seen, Darwin (1859: 46, quoted above) already acknowledged the possibility of neutral differences in phenotypes; he however supposed that the abundances of species in an ecosystem could not be explained by chance, but by the struggle between kinds: “When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this! Every one has heard that when an American forest is cut down, a very different vegetation springs up; but it has been observed that the trees now growing on the ancient Indian mounds, in the Southern United States, display the same beautiful diversity and proportion of kinds as in the surrounding virgin forests. What a struggle between the several kinds of trees must here have gone on during long centuries, each annually scattering its seeds by the thousand; (...)” (Darwin 1859: 74–75).

<sup>68</sup> See Bell et al. (2006) and Leigh (2007: 2081), for reviews.

<sup>69</sup> Overyielding: positive correlation between the productivity and the diversity of a community.

(Derville 1999: 277), and which is interpreted in terms of a complementarity in resource use – note that overyielding falls outside the scope of neutral theory in that there is, by definition, no impact of diversity on the size of the community (assumed to be constant, by the way, in most current models) (Mikkelsen 2005: 563<sup>70</sup>), (3) stability of community composition (which we detail in Sect. 3.3.2; see e.g. Levine and HilleRisLambers 2009).

As for the hypothesis of average fitness equivalence, in the absence of stabilizing mechanisms very slight deviations from this assumption lead to completely different predictions with monospecific dominance, in accordance with the principle of competitive exclusion (see e.g. Zhou and Zhang 2008).

The parameters of neutral models can be difficult to interpret empirically, and thus difficult to measure *a priori*<sup>71</sup> – which would nevertheless enrich the family of the predictions of the theory. Implicit spatial models (e.g. Hubbell 2001: chap. 5), for example, are not really enlightening about what the migration rate stands for; the migration rate is, besides, seldom measured (Leigh 2007: 2082, Beeravolu et al. 2009: 2608). Similarly, the assumption that every new tree has a given probability of belonging to a new species bothers some environmentalists, who however grant it to be operative in the case of small isolated populations (Leigh 2007: 2084). Finally, the estimated parameters may vary depending on the estimation methods for the same data set without the reason for this being clear, and they sometimes vary by several orders of magnitude depending on the study, which bothers the intuition: for example, the rate of speciation estimated retrospectively for Panama is 1300 times the one obtained for the Yasuni forest (Amazonian Ecuador) and 2.6 million times the speciation rate of the Manu forest (Southeast Amazon, Peru) (Leigh 2007: 2082).<sup>72</sup>

Because of these limitations, a concern with neutral theory is that reliable predictions and extrapolations of this theory may be limited to a certain area of parameter values that may seem highly improbable and require, at least, verification (Zhang and Lin 1997). This concern is important as regards the application of neutral theory (Leigh 2007: 2085), for instance to conservation biology – which is one of the rationales of Hubbell's work (Hubbell 2001: ix,26; Hubbell et al. 2008).

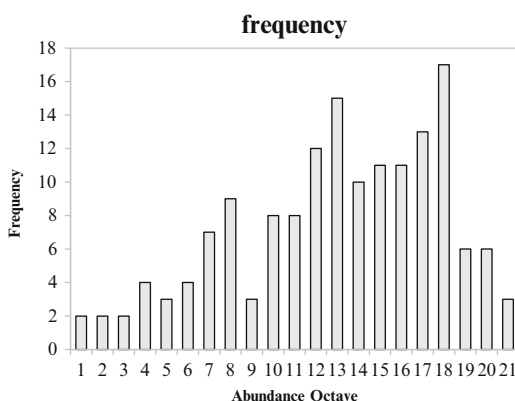
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<sup>70</sup> Hubbell (2006: 1395) argues that he found no evidence for overyielding in the tropical forest on Barro Colorado Island.

<sup>71</sup> See Beeravolu et al. (2009: 2607).

<sup>72</sup> Munoz et al. (2007) have proposed an approach that relaxes the speciation modalities and do not imply any estimation of the speciation parameter. The estimation of the speciation parameter seems generally highly unreliable, contrary to the estimation of the migration parameter, that seems more robust (on parameter estimation, see also Beeravolu et al. 2009). I thank François Munoz for an insightful comment on this point.

**Fig. 26.4** Example of a SAD (Species Abundance Distribution), showing the frequency of diverse classes of abundance of 146 bird species that reproduce in Great-Britain. The occasional reproducers are excluded, which depresses the distribution on the left. Abundances are ranked by octaves of power 2 (After Nee et al. (1991a, b: fig. 4), and Bell (2000: fig. 1:B))



### 3.3.2 Quality of Predictions<sup>73</sup>

Neutral theory has originally been developed to describe relative species abundance patterns on a plot (Fig. 26.4).<sup>74</sup> The scope of application has then been extended to species area curves,<sup>75</sup> to abundance-range size relationships, to the interpretation of spatial patterns (spatial autocorrelation) and of temporal patterns (time autocorrelations in the composition and diversity of a community, and in their spatial patterns).<sup>76</sup>

The remarkable success of neutral theory in predictions of species abundance distributions (SADs) has caused astonishment: why, despite its assumptions, does this theory succeed so well?<sup>77</sup> This point was central in the controversy, although, as regards aggregate properties such as SADs, neutral theory and niche theory are more or less tied.<sup>78</sup> Neutral theory interprets the abundances distribution in terms of the number of individuals of novel types occurring at each generation (by speciation and/or migration) (Bell et al. 2006: 1380), while niche theory assumes that the abundances distribution is determined by the distribution of niches (e.g. Pueyo et al. 2007). Echoing the historical skepticism toward the relevance of SADs to judge the

<sup>73</sup> Unless explicitly stated, this part draws on the remarkable review by Bell et al. (2006).

<sup>74</sup> E.g. Watterson (1974), Caswell (1976), Hubbell (1979, 1997, 2001: 11&17, chap. 5), Volkov et al. (2003).

<sup>75</sup> E.g. Bramson et al. (1996, 1998), Hubbell (2001: chap. 6), but see Leigh (2007: 2080).

<sup>76</sup> See e.g. Bell (2001, 2005), Bell et al. (2006).

<sup>77</sup> See e.g. Hubbell (2001: 320–321), or this interview of Hubbell by Baker (2002): “Look, I think the biggest question to come out of the neutral theory is: “Why does it work so well?” I’m as puzzled as the next person. But one idea is these trade-offs.” (Notice that here Hubbell still seeks to explain neutrality in functional terms, while a possibly more neutral explanation would be that environmental variations in space and time are such that the environment is not selective, as for instance with fractal perturbations; a case briefly discussed in Pocheville 2010: 85–86).

<sup>78</sup> See Pueyo et al. (2007: 1017), McGill et al. (2007: esp. 1001) and references therein; see also Chave (2004: 247–248).



underlying mechanisms (MacArthur 1966<sup>79</sup>), Pueyo et al. (2007) have used the maximum entropy formalism<sup>80</sup> to show that the SAD generated by a model is a log-series when the model contains no information about the abundances of species: this is the case of a strictly neutral model (where the abundances are the result of a random demographic process), but also of a model of idiosyncratic niches (where the abundances are the result of a process of a random allocation of niches). Models that deviate from this null information generate power laws or log-normal SADs. Hubbell's model, in particular, when it generates a log-normal-like SAD for the local community, introduces information at the level of the characteristic area of the local community, which is not necessarily a mechanism more general than others (Pueyo et al. 2007: 1023) (Hubbell's model generates a log-serie for the global community<sup>81</sup>). Despite this qualitative equality, the descriptive quality of neutral theory on SADs and its ease of implementation may make it appear as the best current method of interpolation to estimate the diversity of a plot (e.g. Hubbell et al. 2008).

Another objective of neutral theory is to explain the agglutinated distribution of conspecific organisms (spatial autocorrelation) (e.g. Hubbell 1979). The traditional interpretation in terms of niches consisted in assuming that the non-random spatial distribution of organisms reflected local adaptation to environmental factors that were themselves non-randomly distributed, remote sites being more likely to be different.<sup>82</sup> Conversely, neutral theory assumes that the agglutinated distribution is to be explained in terms of local dispersion, the more distant sites exchanging fewer migrants (e.g. Bell 2001: 2415). Qualitatively, spatially explicit neutral models can generate patterns of apparent local adaptation, by introducing local dispersal alone (Bell et al. 2001: 127;<sup>83</sup> Bell 2001: 1381–1382). The question then arises as to determine how community composition can be explained by local adaptations or dispersal limitation (Bell et al. 2001: 126). An intuitive solution could be to look for correlations between environmental factors and species distribution. This solution

<sup>79</sup> The controversy about SADs draws back to Fisher et al. (1943) and Preston (1948). According to Fisher et al. (1943) the expected number  $N$  of species having  $n$  individuals in a sample can be described by a log-serie:  $N = \alpha^n/n$ , where  $\alpha$  (a parameter now known as Fisher's  $\alpha$ ) is a measure of species diversity. According to Preston (1948), the log-serie lacked the bell-shape he observed in his data on bird abundances, a phenomenon he attributed to the presence of trully rare species that are hardly detectable in small samples (a concept now known as Preston's veil line). Preston (1948) remarked that, by contrast, a log-normal distribution fitted his data. See Hubbell (2001: 31–37) and McGill et al. (2007: 998–999, 1004–1005) for short historical introductions, emphasizing respectively the theoretical and empirical sides.

<sup>80</sup> The maximum entropy technique consists in describing the microscopic degrees of freedom of a system (e.g. the species abundances) by the probability distribution that maximizes the Shannon entropy, under a set of macroscopic constraints (such as bounded mean abundance). On entropy maximization in ecology, see also Banavar and Maritan (2007), Banavar et al. (2010), Dewar and Porté (2008) and the controversy between Shipley et al. (2006) and Shipley (2009), and Haegeman and Loreau (2008, 2009). Haegeman and Loreau (2008) provide a nice and critical introduction to the technique.

<sup>81</sup> See Hubbell (2001: 125–126, 150, chap. 6, 280).

<sup>82</sup> E.g. Hengeveld and Haeck (1981, cited in Brown 1995: 24, 1982), Brown (1995: 32, et al. 1996)

<sup>83</sup> Note that qualitative patterns (e.g. Bell et al. 2001: 133) could be an insufficient method to detect selective processes.

can be inconclusive because (1) on the one hand, the lack of correlation may simply mean that the relevant factors were not considered (here we face a similar algorithm than the adaptationist algorithm) (Bell et al. 2001: 119, 2006: 1382), (2) on the other hand, contrary to our intuition, a species-factors correlation can also be explained by dispersal limitation in a spatial neutral model – in the sense, at least, where many species will occupy only a fraction of the possible environments and will thus show an apparent specialization (Bell et al. 2001: 129). Highlighting the consistency of occupancy of possible environments by organisms requires studies of sufficiently high resolution, both spatially (number of sampling sites and surface of the study area), temporally, taxonomically (refinement of the taxonomy used relative to the proximity of organisms sampled), and environmentally (variety of factors measured and sensitivity of measurement for each factor).<sup>84</sup> From this point of view, the neutral stance consists in asking a question: at which resolution (for example, which temporal or spatial scale<sup>85</sup>) can the pattern be considered neutral<sup>86</sup>?

The supposed stability of coexistence of a set of species, however, is the rationale for niche theory. Neutral theory explicitly assumes that the composition of a community undergoes drift, that is, it undergoes a random walk. Therefore, the composition of a neutral community does not show equilibrium nor resilience (although, of course, it is characterized by temporal autocorrelations because of population dynamics). Note that, conversely, the *diversity* of the community tends towards a dynamic speciation (or migration)/drift equilibrium.<sup>87</sup> This aspect of neutral theory makes it an interesting null hypothesis to test departures from drift, within a community or between communities (Sect. 3.4.2). Composition stability and resilience after a disturbance, too short to be neutral extinction times that are found in the fos-

<sup>84</sup> See Bell et al. (2001: 129,132), Bell (2003), Bell (2005), Bell et al. (2006: 1380–1381, 1383–1384)

<sup>85</sup> See McGill et al. (2006: 1414). Such a question is already mentioned by MacArthur (1972: 21), and is repeated, in a less general form, in Chesson and Huntly (1997: 520), quoted in Hubbell (2001: 9–10). Leigh (2007: 2080) raises, in passing, a similar question. Hubbell (1997: S9) interprets the niche assembly perspective of ecologists (vs the dispersal assembly perspective of biogeographers) as a mark of the different processes occurring on the respective scales of these disciplines. See also the three-levels spatially implicit neutral model of Munoz et al. (2008: 117)

<sup>86</sup> A major difficulty of this research program is to separate the effects of the environmental variability (on fitness) from the effects of physical/biological distances (on dispersal), for there is a covariation between environment similarity and distance in natural landscapes: environmental variability tends to increase with the geographic distance, and the biologically perceived distance tends to increase with environmental variability (due to barriers to dispersal for instance – such barriers need not be, of course, purely “neutral”, i.e., equivalent for all species). For short discussions of this issue, see Bell (2006: 1382), Chave (2008: 21–23). Borcard et al. (1992, see also Legendre and Legendre 2012) proposed a method to statistically partition environment from distance, implemented in Gilbert and Lechowicz (2004: 7653) who found “strong evidence of niche-structuring but almost no support for neutral predictions” (2004: 7651). Jeliaskov (2013: Chap. III) performed an implementation in a similar vein, finding that the environment explained a major part of the community variation only when it was joined to a spatial component. On dispersal as a non-neutral phenomenon see Clark (2009: 12).

<sup>87</sup> In other terms, while the *composition* of a neutral community does not show any equilibrium nor resilience, it is not the case for the *characteristics* of this composition (species number, relative frequencies, etc.).

sil records (Leigh 1981, cited in 2007: 2082; Ricklefs 2003, 2006), resistance to invasion (Fargione et al. 2003) and, on the other side, demographic explosions of invasive species (e.g. Crook and Soulé 2001), argue, in this regard, for an explanation in terms of niches.

The concept of community drift has been applied to study the divergence of isolated communities. If communities get completely isolated, neutral theory predicts that the summed diversity of the communities increases over time (up to a maximal summed diversity where communities have no more species in common and have each reached a speciation/extinction equilibrium), while niche theory predicts that the compositions of similar communities should remain similar, at least over the ecological time (due to stabilizing mechanisms) (Clark and McLachlan 2003: 638). Unfortunately, even in the neutral situation, a few migrants per generation and per community is enough to homogenize the compositions of each community (Volkov et al. 2004), making the neutral and niche predictions, once again, indistinguishable (Bell et al. 2006: 1382<sup>88</sup>).

### 3.4 *Nature of the Opposition Between Neutral Theory and Niche Theory*

The difficulty to decide between the theories was already present in the controversy between neutralism and selectionism in population genetics (see Lewontin 1974: 4, chap. 5<sup>89</sup>). It has been circumvented there by the development of a synthetic model, the so-called nearly-neutral model, which takes into account the effects of drift and selection (Ohta 1973, 1992: 271: fig. 2). Such a model has also been developed in community ecology (Zhou and Zhang 2008), but it does not evade the difficulty of determining the origin (selection or drift) of the observed patterns, nor the difficulty of the status of stochasticity.

#### 3.4.1 *Status of Stochasticity*

The status of stochasticity (*sensu* randomness) has probably generated significant confusion in the debate, which can be illustrated by the use of an unfortunate terminology: the *stochastic* or *neutral* forces (e.g. demographic stochasticity) are

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<sup>88</sup> A similar counterargument has been opposed by Hubbell (2001: 330–331) to the conclusions reached by Terborgh et al. (1996) on floodplain forests and Pandolfi (1996) on a paleo-reconstruction of coral reefs. Leigh (2007: 2082) points to the fact that Hubbell's (2001: 331) and Volkov et al.'s (2004) arguments rely on "the fictitious concept of a panmictic source pool", a fiction that contrasts with a – desirable – approach studying the long-range correlations produced by local dispersal alone (as hypothesized by Bell et al. 2006: 1382). As another step in the controversy, Dornelas et al. (2006) have shown that Indo-Pacific coral communities exhibit far more variable, and lower on average, community similarities than expected by neutrality.

<sup>89</sup> The debate is quickly summarized in Bell et al. (2006: 1379) and Leigh (2007: 2081–2082).

opposed to *deterministic* forces (e.g. selection).<sup>90</sup> Without elaborating on the presence, irreducible or not, of randomness in biology,<sup>91</sup> note that the term “stochastic force” is an oxymoron: stochasticity is precisely that which is not directional.<sup>92</sup> In fact, the stochastic terms of a neutral model can be considered to reflect unknown or ignored mechanisms.<sup>93</sup> In other words, the stochastic terms represent the part of missing information in the model, and have no other explanatory value than estimating the part of the unknown in the result. One should not leave aside certain deterministic terms for the benefit of stochastic terms solely to gain parsimony, without ensuring that the *explanandum* of interest has not been abandoned in the interval. For example, neutral theory leaves out a significant *explanandum*: it does not, because of symmetry, predict *which* species will be rare or common.<sup>94</sup>

As such, the increasingly consensual *continuum* (e.g. Chase and Leibold 2003: 179; Gravel et al. 2006; Gewin 2006) between determinism and stochasticity, interpreted as a *continuum* of causality (every force determining the dynamics to varying degrees) is rather to be considered as a *continuum* of the amount of information introduced into a model (see Clark et al. 2007: 656–657; Clark 2009: 10–11).<sup>95</sup>

### 3.4.2 Neutral Theory: A Null Hypothesis?

Neutral theory has shown the non-necessity of niche theory to explain, at least qualitatively, some spatial and diversity patterns, both at global (Bell 2001) and local (Bell 2003) scales – except, indeed, in case of strong selection or at large spatial scales (Bell 2005: 1758; Leigh 2007: 2080). Because of this, and because of its

<sup>90</sup> E.g. Hubbell (2001: 220), McGill et al. (2005: 16706), Bell et al. (2006: 1379), Gewin (2006: 1309), Daleo et al. (2009: 547). These terms are not new, as in the 1970s Lewontin for instance could write: “Genetic variation is removed from populations by both random and deterministic forces” (Lewontin 1974: 192).

<sup>91</sup> See Malaterre & Merlin, Chap. 17, this volume (Ed. note)

<sup>92</sup> We mean here by “directional” a direction in the composition dynamics (of alleles or species frequencies for instance) or in spatial patterns of distributions. Drift, by contrast, can be considered as a noise: it “explains” to what extent we cannot know the direction. (This, of course, does not hold for parameters that are *explananda* of neutral theory, such as the number of alleles/species, mentioned in the preceding section.)

<sup>93</sup> This notion of epistemic randomness is, to our knowledge, the most common notion of randomness in ecology (e.g. Clark 2009: 10: “First, there is no evidence for stochasticity in nature at observable scales. Stochasticity is an attribute of models”). To be precise, random terms could also be considered to reflect deterministically random phenomena, as in classical physics, or intrinsically random phenomena, as in quantum physics. Other concepts of randomness could be developed for ecology. The distinction between direction/dispersion proposed here holds for epistemic randomness.

<sup>94</sup> This explanandum is significant in, for instance, the review by Lavergne et al. (2010).

<sup>95</sup> Huneman (2012) questions in the same vein the conception of causation (counterfactual vs statistical) required to make sense of natural selection (by contrast with drift) in evolutionary biology.

parsimony, neutral theory is often regarded as a null hypothesis to, possibly, refute (e.g. Nee 2005: 176; Leigh 2007: 2082).<sup>96</sup>

Typically, models of neutral theory rely on two assumptions: (1) a double assumption of equivalence of species: ecologically (no stabilization) and competitively (equal mean fitnesses), (2) and for (explicitly or implicitly) spatial models, an assumption of limited dispersal.

An alternative hypothesis of (1) is an assumption that species are not equivalent, at the competitive and/or ecological level; it is the hypothesis supposed by models of coexistence based on the niche concept. As such, testing how a community drifts or not in time amounts to testing a null hypothesis with respect to niche models (e.g. Clark and McLachlan 2003).

The case of space is more ambiguous. Hypothesis (2) is, in the case of spatially explicit models, an assumption of connectivity in space.<sup>97</sup> Its alternative hypothesis is, at first glance, a lack of connectivity (that is to say an unlimited (or null) dispersion), not the assumption of heterogeneity of species' ecologies and of environmental factors in space, that suppose niche based models of repartition. The difficulty to reject a neutral or a niche model by examining spatial patterns also invites us to prefer, rather than a test of null hypothesis, an approach of model selection, in which competing hypotheses are confronted simultaneously with data and classified according to criteria such as likelihood, parsimony, etc. (see Johnson and Omland 2004; Clark et al. 2007: 656).

### 3.4.3 Models Dimensionality

Clark et al. (2004, 2007) and Clark (2009) provided an interesting insight about the contrast between the niche and neutral models. According to them, each type of model fails to explain diversity: niche models, because we observe too few trade-offs and too great overlaps in the field by comparison with the requisites of the models, and neutral models, because they do not explain the observed stability and resilience of communities (Clark et al. 2007: 648). According to Clark et al., this

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<sup>96</sup> Neutral theory has not always been perceived as a null hypothesis. Bell (2001: 2418) distinguishes two versions of the theory: "The weak version recognizes that the NCM [neutral community model] is capable of generating patterns that resemble those arising from survey data, without acknowledging that it correctly identifies the underlying mechanism responsible for generating these patterns. The role of the NCM is then restricted to providing the appropriate null hypothesis when evaluating patterns of abundance and diversity. (...) The strong version is that the NCM is so successful precisely because it has correctly identified the principal mechanism underlying patterns of abundance and diversity. This has much more revolutionary consequences, because it involves accepting that neutral theory will provide a new conceptual foundation for community ecology and therefore for its applied arm, conservation biology."

<sup>97</sup> A similar argument would hold for implicitly spatial models (involving limited dispersal without necessarily defining a distance between communities): dispersal, even symmetric, is not "null" regarding the niche.

epistemic failure is due to the low dimensionality of these models, even in niche theory (Clark 2009: 13). The low dimensionality is favored in ecology for several reasons: the models must be tractable, only few resources axes and trade-offs are perceived (Clark et al. 2007: 648), finally, the selection criteria of models that rely on parsimony and eliminate all non-significant effects, as do fitting deterministic relationships with a residual noise, make relationships appear low-dimensional (Clark et al. 2007: 656).

Clark et al. propose an alternative: to explicitly explore processes that are misrepresented or set aside, and to consider complex models. Using bayesian hierarchical models as an inference method (Clark 2003; Clark et al. 2004), they reveal high dimensionality differences of niches in two species of trees that apparently seemed ecologically equivalent (Clark et al. 2007). According to them, this call for an explanation in terms of high dimensionality echoes the seminal papers by Gleason (1926) and Hutchinson (1961) on the question of coexistence (Clark et al. 2007: 656; Clark 2009: 13).

From the perspective of the structure, neutral models and classical niche models belong to the same family of low-dimensional models and are to be opposed to high-dimensional models (Clark 2009: 14). By contrast, the niche models of low and high dimensionality target the same *explanandum*: to determine, for example, the abundance of *certain* species, or the outcome of given competitive situations.

## 4 Conclusions

### 4.1 Meanings of the Concept

Although the meaning of the word “niche” in ecology has substantially changed over a century of existence, its multiple meanings all revolve around the Darwinian view of ecosystems that are structured by the struggle for survival. Originally, the word meant a place in the ecosystem, in the sense of the relationship to resources, predators and habitat. Grinnell and Elton, when comparing communities, came to be interested in ecological equivalents, that is to say, species with similar niche in different locations or ecosystems: the word “niche” was tinged with connotations about the structural invariance of ecosystems.

The idea that two species coexisting in the same place must occupy different niches, already present in Darwin and his successors, including Grinnell, and later known as the competitive exclusion principle, provided the framework for the redefinition by Hutchinson. Hutchinson formalized the niche of a species as the volume, in the space of environmental variables, where the species can survive indefinitely (the fundamental niche), or the volume, limited because of interaction with present competitors, where the species actually survives (the realized niche). The niche was specific to each species, and the structural invariance of the ecosystem was not presupposed

any more. With this formalization, Hutchinson set the stage for the quantification of niche differences that allowed coexistence and similarities that lead to exclusion, a concern already present in Darwin (1859: 320). Besides, it is notable that in the history of research on competitive exclusion, particularly in the seminal paper by Hutchinson (1957: 417–418), the status of the principle has oscillated between an *a priori* principle<sup>98</sup> (the coexistence of species implies a certain dissimilarity, even if it is not detected) and an empirical principle (the goal is to predict *via* measures of niches either coexistence or exclusion, or *via* observations of coexistence, the existence of niche differences) (see also e.g. Hutchinson 1961: 143).<sup>99</sup>

Gradually, it appeared that the burgeoning niche theory had difficulties to produce general results. At the same time, a more mechanistic approach was emerging, that was based on the explication of the underlying mechanisms of competition and of other interspecific interactions, such as the dynamics of resource consumption (e.g. Tilman 1982). The use of the concept has been declining since the 1980s.

Although the mechanistic approach is in the lineage of the previous approaches, the niche concept is no longer central. However, it is from this mechanistic approach that Chase and Leibold produced their conceptual overhaul, aimed at giving back the niche concept its role of a framework for synthetic thinking in ecology. The niche is a visualization of the ecological mechanisms: it is the conjunction of the responses to, and of the impacts on, the environmental factors.

Whatever the differences between the multiple meanings of the concept, the niche is a model of the relationship between the organism and its environment: this model is limited to a sustainability area in Hutchinson's sense or a utilization distribution in the theory of niche, and incorporates the impacts of the organism on environmental factors in authors such as Grinnell, Elton, Chase and Leibold. This relationship cannot be changed; by contrast, the environmental conditions and the species' demography can change. By contrast in models of niche evolution, the relationship can change. In the niche construction program, the niche is modifiable, but the meaning oscillates between the model of the relationship with the environment (the set of selection pressures experienced by the organism, which can refer to the model's invariant) and the state of the environment (which is, in our sense, a variable). This oscillation generates confusion about the explanatory status of the niche, which alternatively stands for the *explanans* and the *explanandum*. In medicine, the niche of a cell is clearly identified as a physical structure, and considering its modification by the cell does not pose any epistemic problem.

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<sup>98</sup> The *a priori* principle belongs to the same family than the strong adaptationist principle, that can be formulated as, for example: "every trait is an adaptation to a selection pressure, even if this pressure is not shown", or: "it is the fittest who survives, even if fitness is not shown". (On adaptationism, see Orzack and Sober 2001, in particular the chapter by Godfrey-Smith.)

<sup>99</sup> I am indebted to Philippe Huneman for having drawn my attention to this point.



## 4.2 *Niche and Neutrality*

The niche concept was coined as part of an explanation of species *coexistence* despite their tendency, in principle, to exclude each other: the differences in niche act as factors stabilizing coexistence. Neutral theory, in contrast, explains the observed *diversity* without assuming differences in niches. The paradox is only apparent: coexistence, in the sense of a certain stability of the composition of a community, is not the *explanandum* of the neutral theory, which assumes instead that the composition drifts. Neutral theory is tailored to predict distributions of species abundance at the community level, not which species will be abundant or rare, which comes under the portfolio of a theory based on the niche concept (if successful). Despite some attempts by Hubbell (e.g. 2006), neutral theory does not explain why the principle of competitive exclusion should not apply, in other words, why the species should evolve towards equal fitnesses.

We have seen that diversity patterns are most often not discriminating about the assumptions of a community stabilization or an equivalence of species – which means that these patterns cannot be interpreted as evidences favoring either hypothesis (e.g. Bell et al. 2001: 132). As such, neutral theory has expanded the family of models able to explain the diversity patterns, which in turn helps to better understand the assumptions that are not necessary for the explanation of these patterns.

Most critics have focused on the hypothesis of fitness equivalence, which seems highly unlikely, while the assumption of stability is well documented both theoretically (Chesson 2000) and empirically (Bell et al. 2006). This equivalence assumption, however, is an operative approximation to derive a certain family of results in diversity studies, although it may decrease the robustness of the theory. The contributions of neutral theory is not limited to the assumptions of ecological and mean fitness equivalences: the emphasis on limited dispersal, on stochasticity and sampling effects are completely detachable from equivalence assumptions, and integrable into a mechanistic theory (Alonso et al. 2006: 455–456). Neutral theory thus represents a first entry into difficult theoretical areas, as analytical solutions of spatially explicit models (Bramson et al. 1996, 1998). The assumption of fitness equivalence, which was central at the origin, should then only appear as a limit case.<sup>100</sup>

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## References

- Abrams, P. (1983). The theory of limiting similarity. *Annual Review of Ecology and Systematics*, 14, 359–376.
- Ackermann, M., & Doebeli, M. (2004). Evolution of niche width and adaptive diversification. *Evolution*, 58, 2599–2612.
- Adler, P. B., HilleRisLambers, J., & Levine, J. M. (2007). A niche for neutrality. *Ecology Letters*, 10, 95–104.
- Adler, P. B., Ellner, S. P., & Levine, J. M. (2010). Coexistence of perennial plants: An embarrassment of niches. *Ecology Letters*, 13, 1019–1029.
- Alonso, D., Etienne, R. S., & McKane, A. J. (2006). The merits of neutral theory. *Trends in Ecology & Evolution*, 21, 451–457.
- Aristotle, & Jules Barthélemy Saint-Hilaire. (1883). *Histoire des animaux d'Aristote*. Paris: Hachette et cie., 1883. <http://remacle.org/bloodwolf/philosophes/Aristote/tableanimaux.htm>
- Baker, O. (2002). Interview with Steve Hubbell: Scientific American [WWW Document]. URL <http://www.scientificamerican.com/article.cfm?id=interview-with-steve-hubb&page=2>. Accessed 5 June 2013.
- Banavar, J., & Maritan, A. (2007). The maximum relative entropy principle. arXiv Preprint Cond-mat/0703622, 2007. <http://arxiv.org/abs/cond-mat/0703622>
- Banavar, J. R., Maritan, A., & Volkov, I. (2010). Applications of the principle of maximum entropy: From physics to ecology. *Journal of Physics: Condensed Matter*, 22, 063101.
- Beeravolu, C. R., Couteron, P., Péliissier, R., & Munoz, F. (2009). Studying ecological communities from a neutral standpoint: A review of models' structure and parameter estimation. *Ecological Modelling*, 220, 2603–2610.
- Begon, M., Townsend, C. R. & Harper, J. L. (2009). *Ecology: From individuals to ecosystems*. Wiley.
- Bell, G. (2000). The distribution of abundance in neutral communities. *The American Naturalist*, 155, 606–617.
- Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.
- Bell, G. (2003). The interpretation of biological surveys. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270, 2531–2542.
- Bell, G. (2005). The co-distribution of species in relation to the neutral theory of community ecology. *Ecology*, 86, 1757–1770.
- Bell, G., Lechowicz, M. J., & Waterway, M. (2001). The scale of local adaptation in forest plants. *Special Publication-British Ecological Society*, 14, 117–138.
- Bell, G., Lechowicz, M. J., & Waterway, M. J. (2006). The comparative evidence relating to functional and neutral interpretations of biological communities. *Ecology*, 87(6), 1378–1386.
- Bendall, S. C., Stewart, M. H., Menendez, P., George, D., Vijayaragavan, K., Werbowetski-Ogilvie, T., Ramos-Mejia, V., Rouleau, A., Yang, J., & Bossé, M. (2007). IGF and FGF cooperatively establish the regulatory stem cell niche of pluripotent human cells in vitro. *Nature*, 448, 1015–1021.
- Bershad, A. K., Fuentes, M. A., & Krakauer, D. C. (2008). Developmental autonomy and somatic niche construction promotes robust cell fate decisions. *Journal of Theoretical Biology*, 254, 408–416.
- Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73, 1045–1055.
- Bramson, M., Cox, J. T., & Durrett, R. (1996). Spatial models for species area curves. *The Annals of Probability*, 24, 1727–1751.
- Bramson, M., Cox, J. T., & Durrett, R. (1998). A spatial model for the abundance of species. *The Annals of Probability*, 26, 658–709.
- Brown, J. H. (1995). *Macroecology*. Chicago: University of Chicago Press.
- Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27, 597–623.

- Cadotte, M. W. (2004). Ecological niches: Linking classical and contemporary approaches. *Biodiversity and Conservation*, 13, 1791–1793.
- Case, T. J. (1981). Niche packing and coevolution in competition communities. *PNAS*, 78, 5021–5025.
- Case, T. J. (1982). Coevolution in resource-limited competition communities. *Theoretical Population Biology*, 21, 69–91.
- Caswell, H. (1976). Community structure: A neutral model analysis. *Ecological Monographs*, 46, 327–354.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. Chicago: University of Chicago Press.
- Chave, J. (2004). Neutral theory and community ecology. *Ecology Letters*, 7, 241–253.
- Chave, J. (2008). Spatial variation in tree species composition across tropical forests: Pattern and process. In W. Carson & S. Schnitzer (Eds.), *Tropical forest community ecology* (pp. 11–30). Oxford: Wiley Blackwell.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Chesson, P., & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*, 150, 519–553.
- Chesson, P., & Rees, M. (2007). Commentary: Resolving the biodiversity paradox. *Ecology Letters*, 10, 659–661.
- Clark, J. S. (2003). Uncertainty and variability in demography and population growth: A hierarchical approach. *Ecology*, 84, 1370–1381.
- Clark, J. S. (2009). Beyond neutral science. *Trends in Ecology & Evolution*, 24, 8–15.
- Clark, J. S., & McLachlan, J. S. (2003). Stability of forest biodiversity. *Nature*, 423, 635–638.
- Clark, J. S., Mohan, J., Dietze, M., & Ibanez, I. (2003). Coexistence: How to identify trophic trade-offs. *Ecology*, 84, 17–31.
- Clark, J. S., LaDeau, S., & Ibanez, I. (2004). Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*, 74, 415–442.
- Clark, J. S., Dietze, M., Chakraborty, S., Agarwal, P. K., Ibanez, I., LaDeau, S., & Wolosin, M. (2007). Resolving the biodiversity paradox. *Ecology Letters*, 10, 647–659.
- Clements, F. E. (1916). *Plant succession: An analysis of the development of vegetation*. Washington: Carnegie Institution of Washington.
- Colwell, R. K. (1992). Niche: A bifurcation in the conceptual lineage of the term. In E. F. Keller & E. A. Lloyd (Eds.), *The keywords in evolutionary biology*. Cambridge, MA: Harvard University Press.
- Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *American Naturalist*, 122, 661–696.
- Courchamp, F., Berec, L., & Gascoigne, J. (2008). Allee effects in ecology and conservation. *Environmental Conservation*, 36, 80–85.
- Cowles, H. C. (1899). *The ecological relations of the vegetation on the sand dunes of Lake Michigan*. Chicago: The University of Chicago Press.
- Crooks, J. A., & Soulé, M. E. (2001). Lag times in population explosions of invasive species: Causes and implications. In O. T. Sandlund, P. J. Schei, & Å. Viken (Eds.), *Invasive species and biodiversity management*. Dordrecht: Springer.
- Daleo, P., Alberti, J., & Iribarne, O. (2009). Biological invasions and the neutral theory. *Diversity and Distributions*, 15, 547–553.
- Darwin, C. R. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life* (1st ed.). London: John Murray.
- Darwin, C. R. (1872). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life* (6th ed.). London: John Murray.
- Dawkins, R. (1982). *The extended phenotype: The long reach of the gene*. Oxford: Oxford University Press.
- Dawkins, R. (2004). Extended phenotype—but not too extended. A reply to Laland, Turner and Jablonka. *Biology and Philosophy*, 19(3), 377–96.

- Day, R. L., Laland, K. N., & Odling-Smee, F. J. (2003). Rethinking adaptation: The niche-construction perspective. *Perspectives in Biology and Medicine*, 46, 80–95.
- Derville, A. (1999). *L'agriculture du nord au Moyen Age*. Septentrion: Presses Univ.
- Dewar, R. C., & Porté, A. (2008). Statistical mechanics unifies different ecological patterns. *Journal of Theoretical Biology*, 251, 389–403.
- Dornelas, M., Connolly, S. R., & Hughes, T. P. (2006). Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, 440, 80–82.
- Drake, J. A., Fuller, M., Zimmerman, C. R., & Gamarra, J. G. P. (2007). Emergence in ecological systems. In N. Rooney, K. S. McCann, & D. L. G. Noakes (Eds.), *From energetics to ecosystems: The dynamics and structure of ecological systems* (pp. 157–183). Dordrecht: Springer.
- Elton, C. S. (1927). *Animal ecology*. New York: The Macmillan Company.
- Engelbrecht, B. M., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., & Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447, 80–82.
- Fagerström, T., & Ågren, G. I. (1979). Theory for coexistence of species differing in regeneration properties. *Oikos*, 33, 1.
- Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences*, 100, 8916–8920.
- Fisher, R. A., Corbet, A. S., & Williams, C. B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *The Journal of Animal Ecology*, 12, 42–58.
- Forbes, S. A. (1880). On some interactions of organisms. *Illinois State Laboratory of Natural History Bulletin*, 1, 3–17.
- Forbes, S. A. (1887). *The lake as a microcosm*. Bulletin of the Peoria Scientific Association.
- Gaffney, P. M. (1975). Roots of the niche concept. *The American Naturalist*, 109, 490.
- Gause, G. F. (1934). *The struggle for existence*. Baltimore: Williams & Wilkins.
- Gause, G. F. (1939, January). Discussion of the paper by Thomas Park, 'analytical population studies in relation to general ecology'. *American Midland Naturalist*, 21(1), 235. doi:10.2307/2420382.
- Gayon, J., & Veuille, M. (2001). The genetics of experimental populations: L'Heritier and Teisser's population cages. In R. S. Singh, C. B. Krimbas, D. Paul, & J. Beatty (Eds.), *Thinking about evolution: Historical, philosophical, and political perspectives* (pp. 77–102). New York: Cambridge University Press.
- Gewin, V. (2006). Beyond neutrality—Ecology finds its niche. *PLoS Biology*, 4, e278.
- Gilbert, B., & Lechowicz, M. J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. *PNAS*, 101, 7651–7656.
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53, 7–26.
- Godfrey-Smith, P. (1998). *Complexity and the function of mind in nature*. Cambridge: Cambridge University Press.
- Gotelli, N. J., & Graves, G. R. (1996). *Null models in ecology*. Washington, DC: Smithsonian Institution Press.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 205, 581–598.
- Gravel, D., Canham, C. D., Beaudet, M., & Messier, C. (2006). Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters*, 9, 399–409.
- Griesemer, J. (1992). Niche: Historical perspectives. In E. F. Keller & E. A. Lloyd (Eds.), *The keywords in evolutionary biology*. Cambridge, MA: Harvard University Press.
- Grinnell, J. (1904). The origin and distribution of the chest-nut-backed chickadee. *The Auk*, 21, 364–382.
- Grinnell, J. (1917). The niche-relationships of the California Thrasher. *The Auk*, 34, 427–433.

- Grinnell, J. (1924). Geography and evolution. *Ecology*, 5, 225.
- Grinnell, J. (1928). Presence and absence of animals. *University of California Chronicle*, 30, 429–450.
- Grinnell, J., & Storer, T. I. (1924). *Animal life in the Yosemite: An account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada*. Berkeley: University of California Press.
- Grinnell, J., & Swarth, H. S. (1913). *An account of the birds and mammals of the San Jacinto area of southern California with remarks upon the behavior of geographic races on the margins of their habitats*. Berkeley: University of California Press.
- Grubb, P. J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, 52, 107–145.
- Haeckel, E. H. P. A. (1874). *Histoire de la création des êtres organisés d'après les lois naturelles*. Paris: C. Reinwald et cie.
- Haegeman, B., & Loreau, M. (2008). Limitations of entropy maximization in ecology. *Oikos*, 117, 1700–1710.
- Haegeman, B., & Loreau, M. (2009). Trivial and non-trivial applications of entropy maximization in ecology: A reply to Shipley. *Oikos*, 118, 1270–1278.
- Haldane, J. B. S. (1957). The cost of natural selection. *Journal of Genetics*, 55, 511–524.
- Hardin, G. (1960). The competitive exclusion principle. *Science*, 131, 1292–1297.
- Hengeveld, R., & Haeck, J. (1981). The distribution of abundance. II. Models and implications. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C*, 84, 257–284.
- Hengeveld, R., & Haeck, J. (1982). The distribution of abundance. I. Measurements. *Journal of Biogeography*, 9, 303.
- Hopf, F. A., & Hopf, F. W. (1985). The role of the Allee effect in species packing. *Theoretical Population Biology*, 27, 27–50.
- Hopf, F. A., Valone, T. J., & Brown, J. H. (1993). Competition theory and the structure of ecological communities. *Evolutionary Ecology*, 7, 142–154.
- Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203, 1299–1309.
- Hubbell, S. P. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16, S9–S21.
- Hubbell, S. (2001). *The unified neutral theory of biodiversity and biogeography* (MPB-32). Princeton: Princeton University Press.
- Hubbell, S. P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19, 166–172.
- Hubbell, S. P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology*, 87, 1387–1398.
- Hubbell, S. P., He, F., Condit, R., Borda-de-Agua, L., Kellner, J., & ter Steege, H. (2008). How many tree species are there in the Amazon and how many of them will go extinct? *Proceedings of the National Academy of Sciences*, 105, 11498–11504.
- Huneman, P. (2012). Natural selection: A case for the counterfactual approach. *Erkenntnis*, 76, 171–194.
- Hurtt, G. C., & Pacala, S. W. (1995). The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, 176, 1–12.
- Hutchinson, G. E. (1941). Ecological aspects of succession in natural populations. *The American Naturalist*, 75, 406–418.
- Hutchinson, G. E. (1944). Limnological studies in Connecticut. VII. A critical examination of the supposed relationship between phytoplakton periodicity and chemical changes in lake waters. *Ecology*, 25, 3–26.
- Hutchinson, G. E. (1948). Circular causal systems in ecology. *Annals of the New York Academy of Sciences*, 50, 221–246.

- Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, 93, 145–159.
- Hutchinson, G. E. (1961). The paradox of the plankton. *The American Naturalist*, 95, 137–145.
- Hutchinson, G. E. (1978). *An introduction to population ecology*. New Haven: Yale University Press.
- Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62.
- Jeliazkov, A. (2013). *Effets d'échelles dans les relations agriculture-environnement-biodiversité*. Paris: Université Pierre et Marie Curie.
- Johnson, R. H. (1910). *Determinate evolution in the color-pattern of the lady-beetles*. Washington, WC: Carnegie Institution of Washington.
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19, 101–108.
- Julve, P. (2005). *Écologie historique* [WWW Document]. [http://www.tela-botanica.org/page:ecologie\\_historique?langue=en](http://www.tela-botanica.org/page:ecologie_historique?langue=en). Accessed 19 Apr 2013.
- Kareiva, P. (1997). Why worry about the maturing of a science? Ecoforum discussions, 1997. <http://www.nceas.ucsb.edu/nceas-web/projects/resources/ecoessay/brown/kareiva.html>.
- Keddy, P. (1998). Null models in ecology. *The Canadian Field-Naturalist*, 112, 752–754.
- Kimura, M. (1968). Evolutionary rate at the molecular level. *Nature*, 217, 624.
- Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press.
- Kingsland, S. E. (1985). *Modeling nature*. Chicago: University of Chicago Press.
- Kostitzin, V. A. (1935). *Evolution de l'atmosphère: circulation organique: époques glaciaires, Exposés de biométrie et de statistique biologique*. Paris: Hermann.
- Kraft, N. J., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322, 580–582.
- Krebs, C. J. (1992). *Ecology: The experimental analysis of distribution and abundance*. New York: HarperCollins College Publishers.
- L'Héritier, P., & Teissier, G. (1935). Recherches sur la concurrence vitale. Etude de populations mixtes de *Drosophila melanogaster* et de *Drosophila funebris*. *Comptes Rendus de la Société de Biologie*, 118, 1396–1398.
- Lack, D. (1947). *Darwin's finches*. Cambridge: CUP Archive.
- Laplane, L. (2013). *Cancer stem cells: Ontology and therapies*. Paris: Université Paris-Ouest Nanterre.
- Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, 41, 321–350.
- Legendre, P., & Legendre, L. (2012). *Numerical ecology*. Amsterdam: Elsevier.
- Leibold, M. A. (1995). The niche concept revisited: Mechanistic models and community context. *Ecology*, 76, 1371–1382.
- Leigh, G., Jr. (1981). The average lifetime of a population in a varying environment. *Journal of Theoretical Biology*, 90, 213–239.
- Leigh, E. G. (2007). Neutral theory: A historical perspective. *Journal of Evolutionary Biology*, 20, 2075–2091.
- Lesne, A. (2012). *Robust Modeling in Natural Sciences*. In Annales de l'ISUP. Presented at the Les Journées de la Robustesse, Institut de statistique de l'Université de Paris, pp. 109–118.
- Levine, J. M., & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.
- Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, 54, 421–431.
- Lewin, R. (1983). Santa Rosalia was a goat. *Science*, 221, 636–639.
- Lewontin, R. C. (1974). *The genetic basis of evolutionary change*. New York: Columbia University Press.

- Lewontin, R. C. (1983). Gene, organism and environment. In D. S. Bendall (Ed.), *Evolution from molecules to men*. Cambridge: Cambridge University Press.
- Li, L., & Xie, T. (2005). Stem cell niche: Structure and function. *Annual Review of Cell and Developmental Biology*, 21, 605–631.
- Longo, G., Montévil, M., & Kauffman, S. (2012). *No entailing laws, but enablement in the evolution of the biosphere*. GECCO Proceedings, 2012. <http://onlinelibrary.wiley.com/doi/10.1046/j.1420-9101.2002.00437.x/full>
- Looijen, R. C. (1998). *Holism and reductionism in biology and ecology: The mutual dependence of higher and lower level research programmes*. Groningen: Rijksuniversiteit Groningen.
- Loreau, M., & Mouquet, N. (1999). Immigration and the maintenance of local species diversity. *The American Naturalist*, 154, 427–440.
- Lotka, A. J. (1924). *Elements of physical biology*. Baltimore: Williams & Wilkins.
- MacArthur, R. (1966). Note on Mrs. Pielou's comments. *Ecology*, 47(6), 1074. doi:10.2307/1935661.
- MacArthur, R. (1972). *Geographical ecology: Patterns in the distribution of species*. Princeton: Princeton University Press.
- MacArthur, R., & Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the United States of America*, 51(6), 1207.
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101, 377–385.
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387.
- Margalef, R. (1968). *Perspectives in ecological theory*. Chicago: University of Chicago Press.
- May, R. M. (1975). Some Notes on Estimating the Competition Matrix, a. *Ecology*, 56, 737.
- McGill, B. J., Hadly, E. A., & Maurer, B. A. (2005). Community inertia of Quaternary small mammal assemblages in North America. *PNAS*, 102, 16701–16706.
- McGill, B. J., Maurer, B. A., & Weiser, M. D. (2006). Empirical evaluation of neutral theory. *Ecology*, 87, 1411–1423.
- McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., & He, F. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, 10, 995–1015.
- McIntosh, R. P. (1986). *The background of ecology: Concept and theory*. Cambridge: Cambridge University Press.
- Meszéna, G., Gyllenberg, M., Pásztor, L., & Metz, J. A. J. (2006). Competitive exclusion and limiting similarity: A unified theory. *Theoretical Population Biology*, 69(1), 68–87.
- Mikkelsen, G. M. (2005). Niche-based vs. neutral models of ecological communities. *Biology and Philosophy*, 20, 557–566.
- Möbius, K. A. (1877). *Die Auster und die Austernwirtschaft*. Berlin: Verlag von Wiegandt, Hempel & Parey.
- Munoz, F., Couteron, P., Ramesh, B. R., & Etienne, R. S. (2007). Estimating parameters of neutral communities: From one single large to several small samples. *Ecology*, 88, 2482–2488.
- Munoz, F., Couteron, P., & Ramesh, B. R. (2008). Beta diversity in spatially implicit neutral models: A new way to assess species migration. *The American Naturalist*, 172, 116–127.
- Nee, S. (2005). The neutral theory of biodiversity: Do the numbers add up? *Functional Ecology*, 19, 173–176.
- Nee, S., Harvey, P. H., & May, R. M. (1991a). Lifting the veil on abundance patterns. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 243, 161–163.
- Nee, S., Read, A. F., Greenwood, J. J. D., & Harvey, P. H. (1991b). The relationship between abundance and body size in British birds. *Nature*, 351, 312–313.
- Neill, W. E. (1974). The community matrix and interdependence of the competition coefficients. *American Naturalist*, 108, 399–408.
- Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton: Princeton University Press.



- Ohta, T. (1973). Slightly deleterious mutant substitutions in evolution. *Nature*, 246, 96–98.
- Ohta, T. (1992). The nearly neutral theory of molecular evolution. *Annual Review of Ecology and Systematics*, 23, 263–286.
- Orzack, S. H., & Sober, E. (1993). A critical assessment of Levins's the strategy of model building in population biology (1966). *Quarterly Review of Biology*, 68, 533–546.
- Orzack, S. H., & Sober, E. (2001). *Adaptationism and optimality*. Cambridge: Cambridge University Press.
- Pandolfi, J. M. (1996). Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: Constancy during global change. *Paleobiology*, 22, 152–176.
- Papayannopoulou, T., & Scadden, D. T. (2008). Stem-cell ecology and stem cells in motion. *Blood*, 111, 3923–3930.
- Park, T. (1948). Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecological Monographs*, 18, 265–308.
- Park, T. (1954). Experimental studies of interspecies competition II. Temperature, humidity, and competition in two species of *Tribolium*. *Physiological Zoology*, 27, 177–238.
- Peters, R. H. (1976). Tautology in evolution and ecology. *American Naturalist*, 110, 1–12.
- Pielou, E. C. (1975). *Ecological diversity*. New York: Wiley.
- Pielou, E. C. (1977). *Mathematical ecology*. New York: John Wiley & Sons.
- Pocheville, A. (2009). La niche écologique: histoire et controverses récentes. In T. Heams, P. Huneman, G. Lecointre, & M. Silberstein (Eds.), *Les Mondes Darwiniens*. Paris: Syllepse.
- Pocheville, A. (2010). *La Niche Ecologique: Concepts, Modèles, Applications*. Thèse de doctorat, Ecole Normale Supérieure, Paris.
- Powell, K. (2005). Stem-cell niches: It's the ecology, stupid! *Nature*, 435, 268–270.
- Preston, F. W. (1948). The commonness, and rarity, of species. *Ecology*, 29, 254–283.
- Psaila, B., & Lyden, D. (2009). The metastatic niche: Adapting the foreign soil. *Nature Reviews Cancer*, 9, 285–293.
- Pueyo, S., He, F., & Zillio, T. (2007). The maximum entropy formalism and the idiosyncratic theory of biodiversity. *Ecology Letters*, 10, 1017–1028.
- Ricklefs, R. E. (1979). *Ecology* (2nd ed.). New York: Chiron.
- Ricklefs, R. E. (2003). A comment on Hubbell's zero-sum ecological drift model. *Oikos*, 100, 185–192.
- Ricklefs, R. E. (2006). The unified neutral theory of biodiversity: Do the numbers add up? *Ecology*, 87, 1424–1431.
- Rohde, K. (1979). A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *American Naturalist*, 114(5), 648–71.
- Rohde, K. (2005). *Nonequilibrium ecology*. Cambridge: Cambridge University Press.
- Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs*, 37, 317–350.
- Roughgarden, J. (1972). Evolution of niche width. *American Naturalist*, 106, 683–718.
- Roughgarden, J. (1976). Resource partitioning among competing species—A coevolutionary approach. *Theoretical Population Biology*, 9, 388–424.
- Salisbury, E. J. (1929). The biological equipment of species in relation to competition. *Journal of Ecology*, 17, 197–222.
- Scadden, D. T. (2006). The stem-cell niche as an entity of action. *Nature*, 441, 1075–1079.
- Schoener, T. W. (1974). Some methods for calculating competition coefficients from resource-utilization spectra. *American Naturalist*, 108, 332–340.
- Schoener, T. W. (1983a). Field experiments on interspecific competition. *American Naturalist*, 122, 240–285.
- Schoener, T. W. (1983b). Rate of species turnover decreases from lower to higher organisms: A review of the data. *Oikos*, 41, 372.
- Schoener, T. W. (1986). Resource partitioning. In J. Kikkawa & D. J. Anderson (Eds.), *Community ecology: Pattern and process* (pp. 91–126). Melbourne: Blackwell Scientific Publications.

- Schoener, T. W. (1989). The ecological niche. In J. M. Cherrett (Ed.), *Ecological concepts: The contribution of ecology to an understanding of the natural world, symposium British ecological society*. Cambridge: Blackwell Scientific Publications.
- Schofield, R. (1978). The relationship between the spleen colony-forming cell and the haemopoietic stem cell. *Blood Cells*, 4, 7.
- Schofield, R. (1983). The stem cell system. *Biomedicine & Pharmacotherapy = Biomedecine & Pharmacotherapie*, 37, 375.
- Semper, K. (1881). *The natural conditions of existence as they affect animal life*. London: C. Kegan Paul & Co.
- Shipley, B. (2009). Limitations of entropy maximization in ecology: A reply to Haegeman and Loreau. *Oikos*, 118, 152–159.
- Shipley, B., Vile, D., & Garnier, É. (2006). From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, 314, 812–814.
- Simberloff, D. (1978). Using island biogeographic distributions to determine if colonization is stochastic. *American Naturalist*, 112, 713–726.
- Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380, 240–243.
- Stauffer, R. C. (1975). *Charles Darwin's natural selection: Being the second part of his big species book written from 1856 to 1858*. Cambridge: Cambridge University Press.
- Steeg, P. S. (2005). Cancer biology: Emissaries set up new sites. *Nature*, 438, 750–751.
- Strong, D. R. (1980). Null hypotheses in ecology. *Synthese*, 43, 271–285.
- Strong, D. R., Lawton, J. H., & Sir, R. S. (1984). *Insects on plants: Community patterns and mechanisms*. Cambridge, MA: Harvard University Press.
- Tansley, A. G. (1917). On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. *The Journal of Ecology*, 5, 173–179.
- Taylor, W. P. (1916). *The status of the beavers of western North America with a consideration of the factors in their speciation....* Berkeley: University of California.
- Terborgh, J., Foster, R. B., & Nunez, P. (1996). Tropical tree communities: A test of the nonequilibrium hypothesis. *Ecology*, 77, 561–567.
- Tilman, D. (1982). *Resource competition and community structure*. Princeton: Princeton University Press.
- Tilman, D. (1987). The importance of the mechanisms of interspecific competition. *The American Naturalist*, 129, 769–774.
- Turelli, M. (1980). Niche overlap and invasion of competitors in random environments. II. The effects of demographic stochasticity. In W. Jäger, H. Rost, & P. Tăutu (Eds.), *Biological growth and spread: Mathematical theories and applications: Proceedings of a conference held at Heidelberg, July 16–21, 1979*. New York: Springer.
- Turner, M. G., Gardner, R. H., & O'Neill, R. V. (2001). *Landscape ecology in theory and practice: Pattern and process*. New York: Springer.
- Van Beneden, P. J. (1878). *Les Commensaux et les parasites dans le règne animal*. Paris: G. Baillière.
- Vandermeer, J. H. (1972). Niche theory. *Annual Review of Ecology and Systematics*, 3, 107–132.
- Volkov, I., Banavar, J. R., Hubbell, S. P., & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.
- Volkov, I., Banavar, J. R., Maritan, A., & Hubbell, S. P. (2004). The stability of forest biodiversity. *Nature*, 427(6976), 696–696.
- Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature*, 118, 558–560.
- Von Liebig, J. (1841). *Traité de Chimie Organique*. Bruxelles: A. Wahlen.
- von Linné, C. (1972). *L'équilibre de la nature*. Paris: Vrin.
- Watt, F. M., & Hogan, B. L. (2000). Out of Eden: Stem cells and their niches. *Science*, 287, 1427–1430.
- Watterson, G. A. (1974). Models for the logarithmic species abundance distributions. *Theoretical Population Biology*, 6, 217–250.



- [Whittaker, R. H., Levin, S. A., & Root, R. B. \(1973\). Niche, habitat, and ecotope. \*American Naturalist\*, 107, 321–338.](#)
- [Williamson, M. H. \(1972\). \*The analysis of biological populations\*. London: Edward Arnold.](#)
- [Wilson, E. O., & MacArthur, R. H. \(1967\). \*The theory of island biogeography\*. Princeton: Princeton University Press.](#)
- [Wright, S. \(1931\). Evolution in Mendelian populations. \*Genetics\*, 16, 97.](#)
- [Zhang, D.-Y., & Lin, K. \(1997\). The effects of competitive asymmetry on the rate of competitive displacement: How robust is Hubbell's community drift model? \*Journal of Theoretical Biology\*, 188, 361–367.](#)
- [Zhou, S.-R., & Zhang, D.-Y. \(2008\). A nearly neutral model of biodiversity. \*Ecology\*, 89, 248–258.](#)

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