OLM 10.2. The requirement/impact niche concept of Leibold: similarities and differences

The niche theory presented in TBE is compared to the niche concept introduced in the theoretical paper of Leibold (1995) which was elaborated and generalized in a book eight years later (Chase and Leibold 2003). This supplementary material is aimed at clarifying and emphasizing the most important conceptual and technical differences between the concepts of *niche space*, *impact niche* and *sensitivity niche* introduced in TBE and those of Leibold's *requirement niche* and *impact niche*.

The 1995 paper of Leibold was introduced by Nelson G. Hairston, J. as follows:

Editor's Note

Ecology's love–hate relationship with the niche concept has been long and not especially pretty. Whereas some ecologists continue to see value in the concept, others have despaired of ever finding an expression that is both general and non-circular. Part of the problem, originating early in our science, has been that different investigators have meant different things by "niche." Here, Leibold uses resource-based competition theory to produce a single construct that accommodates the earlier differences in meaning, while at the same time permitting measurement and experimentation. Although attempts to define *the* niche of a species may still prove fruitless, Leibold's contribution is to suggest that it is nevertheless possible to delineate niche parameters relevant to a variety of ecological interactions.

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The reputation of the niche concept aptly described by Hairston has not changed much during the past two decades (McInerny and Etienne 2012a, b, c) despite Leibold's theory having been explicitly connected to the models of basic interaction modules in Chase és Leibold (2003) and the development of a general theory of coexistence that makes the metaphoric, intuitive concept of niche operational in any coexistence model at least in principle (Meszéna et al. 2006, Szabó and Meszéna 2006, Parvinen and Meszéna 2009, Szilágyi and Meszéna 2009, Szilágyi and Meszéna 2010, Barabás et al. 2014). We wish to contribute to changing this state of affairs, i.e., to the stabilisation of the niche concept by connecting it to the concept of *population regulation* and the general theory of coexistence based on it. Ch10Niche presents the theory, supported by empirical studies demonstrating niche segregation in different taxa. This text and

OLM 10.6 attempts to compare the niche theory in TBE to earlier concepts, mainly with those readers in mind who have already encountered the latter.

The best known current niche theory is the one published in Leibold (1995), which we will refer to as L in the following. This approach was then presented in more detail and applied to a number of ecological situations in a book (Chase and Leibold 2003) referred to as CL hereafter. This approach is similar to ours in that it defines two complementary niche components: the requirement niche and the impact niche, and illustrates them with Tilman's explicit resource regulation model (cf. Figure 9.11). The definitions of niche space and niche partitioning are different from ours. The most significant of these differences is the one in niche space definition, therefore we start the comparison with that.

The typical niche representation found in basic ecology textbooks is that of Hutchinson's multidimensional niche space, and the niche of a species is a subset of that space. The interpretation of the dimensions (axes) of the niche space has been the subject of long debates. In 1995 Leibold argued that the appropriate niche axes should be the values of the modifying factors and the densities of the regulating variables (like resource concentrations or predator densities). He thought that Hutchinson's assumption that the niche axes are scales of the *qualities* (like seed *size*), not the *quantities* (like seed *density*) of the resources, was inconsistent, because it is the quantity, not the quality of the resources that has to exceed a threshold level (R^*), in order to secure the survival (i.e., the requirement) of the population. In accordance with this interpretation, Chase and Leibold consider the space of the regulating variables as the niche space (CL p. 55) at fixed values of the modifying variables, and they consider the use of qualitative variables as niche space axes to be a matter of mathematical convenience, whereby an infinite number of different quantitative axes can be lumped into a single continuous qualitative axis. Leibold and Chase are right in that the continuous qualitative axes like that of seed size are indeed simplifications representing an infinite number of regulating variables. They are also right in assuming that we need to know the quantities of seeds of different sizes in order to be able to evaluate the criteria of persistence for the population feeding on the seeds (Ch5Toler).

However, by claiming the use of qualitative variables (the index variables of the actual regulating factors) as niche axes to be a mistake they miss the point that a sufficient condition of coexistence is that the regulating variables be different. This means the consumption of seeds of different sizes in our example, which in turn represents complete segregation along the seed size axis. By discretizing the continuous qualitative variable to two dimensions, the density of small seeds will be one

regulating variable and that of large seeds will be the other. This simplification does not always work, however; it definitely breaks down if the consumptions are overlapping and the question we try to answer regards the number of possible parts into which a qualitative continuum can be subdivided among robustly coexistent populations (Meszéna et al. 2006). The determination of the conditions of coexistence requires the identification and appropriate modelling of the regulating variables. Resource particle size or, in other cases, any other continuous qualitative variable like temperature, is the index variable of the regulating resource – or, in case of temperature, rather the regulating space.

 Even though the role of competitive exclusion is not completely clear in the theory of Leibold and Chase (CL p. 42; the expression does not even occur in L), they agree that considering the niche as a place (Hutchinson) or role (Elton) in a community assumes that each of the coexistent populations have their own niche. We have shown in Ch9Coex that the populations of a community are differently regulated: either their growths are regulated by different factors or, in case of competing populations regulated by the same factors, the way of their regulations, i.e., the components of their regulatory loops are different. This is why we have defined the ecological niche as the mode of population regulation (including the determination of the regulating variables). We have demonstrated how this niche can be derived from the principles. The niche space represents the possibilities within the given community in this theoretical framework. The niche space can be defined by enumerating the regulating factors; if the number of regulating factors is infinite, then by specifying the corresponding index variable (OLM 5.1). For example, if the regulating factor is the density of seeds, then the index variable is seed size; if it is the density of free sites, then it can be indexed with the maximum temperature of the sites (Figure 5.21, TBox 10.1). This niche space is partitioned by coexistent populations, in a way analogous to companies trying to avoid competition for customers by partitioning them along certain traits (customer allocation by trait) or divide sales territories geographically (market division on a geographic basis). The counter-argument of Leibold and Chase is that it is only quantities that can be partitioned or competed for, not qualities. It is again true from a certain aspect, but it has to be noticed that populations competing for identical resources or sites and facing the same natural enemies under identical conditions have no chance to coexist, according to the principle of competitive exclusion. On the other hand, niche segregation, i.e., partitioning the regulating factors, just like market division, alleviates competition, leading to peaceful coexistence.

To our knowledge it was Leibold who, based on a historical and conceptual analysis and also referring to models, has separated and interpreted two types of niche – the requirement niche and the impact niche – for the first time. He has illustrated these concepts with Tilman's explicit resource partitioning model (two resources; *exploitative competition*) and predation-induced coexistence model (*keystone predation*).

According to Chase and Leibold

„*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 impacts of the species on these environmental conditions*" (CL 2003. p.19.)

is the niche of a species.

With modifying factors fixed in the two models mentioned above the requirement niche (*the environmental conditions that allow a species to satisfy its minimum requirements)* is equal to the resource concentrations sufficient to maintain a positive equilibrium population density, or to the maximum density of the regulating enemy (ZNGI-s on the graphs). The impact niche (*set of per capita impacts of the species on these environmental conditions*) is characterized by the per capita consumption vectors in the resource competition model, for example. Since the modifying factors are all fixed in all the examples of Leibold and Chase, in fact they determine the requirement niches and the impact niches for just the regulating variables.

As the above definition indicates, Leibold's niche concept is primarily aimed at finding conditions (resource densities, predator densities) for the persistence of particular species, with or without competing species present. Based on the Tilman model CL explains in detail, and it is also visible on our Figure 9.11, that for this it is necessary to determine the equilibrium isoclines (ZNGIs) of all the species and the vectors of their effects on the regulating factors (impact vectors). In contrast, the theory-based niche we propose specifies the conditions of sufficiently robust coexistence, for which the qualities of the regulating factors and the mode of population regulation must be determined in the community under study. The differences in the definitions of niche space is partly due to this difference in objectives.

Next we analyse the connection between Leibold's requirement niche (ZNGI) and our theory-based sensitivity niche concepts. Technically, sensitivities are derivatives specifying the change in fitness at equilibrium in response to small changes in the regulating variables (e.g. Eq. 6.35). For example, if there are two different resources

regulating population growth, then the sensitivity of the population is a gradient vector (Eq. 9.17) which is perpendicular to the tangent of the equilibrium isocline (cf. linearization: TBox 1.2), since "If Joe walks perpendicularly to the gradient ($\alpha = 90°$, cos $\alpha = 0$), then his vertical speed is zero." (TBox 2.2, p.24 and TBox 9.2, p.182). That is, the sensitivity vector determines the steepness of the ZNGI at the fixed point. It is the loss rate that determines the position of the ZNGI, independently of its steepness (e.g. Eq.6.28), and the position changes with the modifying factors affecting population growth. The shapes and the positions of the ZNGIs together determine whether they will intersect, that is, if a common equilibrium is possible at all. For the stability of the coexistence it is sufficient (besides the appropriate directions of the consumption vectors, to which we shall return later during the discussion of the impact niche) that the steepness's of the ZNGIs be different at the fixed point, which is rather probable for two different species. However, for the coexistence to be robust enough, the difference must be sufficiently large so that it can withstand the perturbations of the growth rates occurring in the natural environments of the populations (TBox 9.3). The same applies to impacts, whose definitions are not identical in the two systems either. The theory-based impact measures the effect of changes in population density on the regulating variable at equilibrium, which is not identical to the per capita consumption vectors in the Tilman model, for example, though it is a function of them (TBox 9.3. and OLM 9.3). Leibold and Chase have identified the impact niche with the consumption vectors in this model. For local coexistence to be robust enough it is necessary that the differences between both the impacts and the sensitivities be sufficiently large – a decrease in any one of them weakens robustness.

The limitations of the approach assuming only two regulating factors are most conspicuous when it is attempted to apply to determine the conditions of regional coexistence, instead of local coexistence with fixed external conditions, to which it is appropriate. In assessing the robustness of regional coexistence, the niches or even the chances of persistence (requirements) of the different variants within a region where the densities of non-consumed resources show spatial variation, it is necessary to consider dispersal as well, besides the environmental heterogeneity of the region. Thus, it is the impacts and the sensitivities of the populations structured accordingly in space that must be calculated, to which we have provided an example in TBox 10.3.

Let us assume for now that the dispersal rates are negligibly small. The quality of the different parts of the area is their non-consumed resource concentration. Supposing that there is no other difference between the parts of the area, the isoclines and the consumption vectors may be the same in all of them. Figure 10.2.1 shows which species may persist in which numbered sub-region of the resource space, assuming

simple exploitative competition. Notice that in this case the species compete for the sub-regions of different qualities (S_1, S_2; site limitation). The number of potentially different sites is infinite, given that concentration is a continuous variable. That is, Leibold himself has substituted an infinite number of regulating variables with a single axis, and the niche space he defines for this situation is a space of index variables. (For sake of clarity of the message we disregard the question how realistic this model can be.)
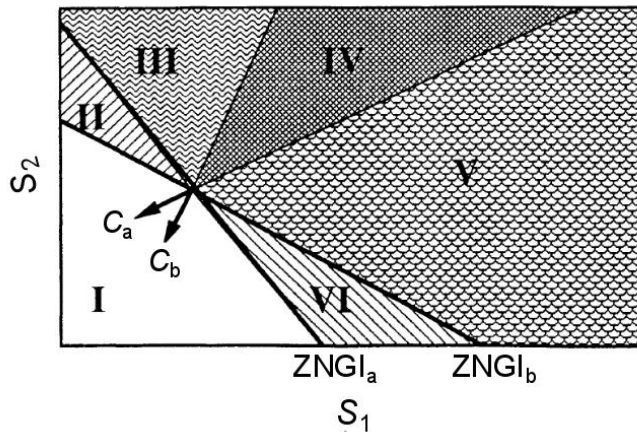

Figure 10.2.1: Spatial niche segregation in Tilman model of resource competition

According to Tilman model of coexistence on two different resources the numbered sub-regions show which species can persist on which combinations of non-consumed resource concentrations (S_1, S_2). C_a and C_b denote the consumption vectors of species a and b, respectively. The requirements of species b are met in the presence of species a in II, III, IV; species a persists in the presence of species b in IV, V and VI. In sub-regions III and V one species excludes the other (Leibold 1995).

The fact that the niche of both structured and fluctuating populations can be calculated with our approach enables us to precisely determine the niche of any particular reproductive unit on different spatial and temporal scales.

According to Chase and Leibold, the concept of an empty niche is nonsense, because, for example, the composition of a community might be determined by the actual order of species arrivals (Ch.9.4), meaning that there are no fixed niches. We agree in this latter statement. In our view the niche space is *ab ovo* dependent on the species already present in the community, so that it changes with the actual conditions (*Pseudomonas* example p. 201-2, 204, OLM 6.3). However, this does not mean that determining empty niches suitable for occupation would be nonsense. The comparative study of similar communities may be of help in such a task. It may be possible to tell in a specific situation whether there is a possibility for the addition of a new species to the community, either by speciation (Ch10.2.6) or by colonisation, and if so, what traits the new species should have. The conceptual difference between the two approaches is again that we, unlike Leibold, do not focus on the determination of the requirements of a particular species in general; therefore, we do not consider the

Theory-Based Ecology: A Darwinian approach

niche to be an *epitheton ornans* of a certain species. A certain reproductive unit may play different roles in many different communities, but the variants of the same community must have different niches. For those who look for rigorously species specific ecological traits we suggest the use of *ecological tolerance* as defined by response functions (Ch5Toler) instead of the niche.

References

Barabás, G., Pásztor, L., Meszéna, G. and Ostling, A. (2014). Sensitivity analysis of coexistence in ecological communities: theory and application. *Ecology Letters*, 17(12): 1479-94.

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

Leibold, M.A. (1995). The Niche Concept Revisited - Mechanistic Models and Community Context. *Ecology*, 76(5): 1371-82.

McInerny, G.J. and Etienne, R.S. (2012a). Pitch the niche–taking responsibility for the concepts we use in ecology and species distribution modelling. *Journal of Biogeography*, 39(12): 2112-18.

McInerny, G.J. and Etienne, R.S. (2012b). Ditch the niche–is the niche a useful concept in ecology or species distribution modelling? *Journal of Biogeography*, 39(12): 2096-102.

McInerny, G.J. and Etienne, R.S. (2012c). Stitch the niche–a practical philosophy and visual schematic for the niche concept. *Journal of Biogeography*, 39(12): 2103-11.

Meszéna, G., Gyllenberg, M., Pásztor, L. and Metz, J.A.J. (2006). Competitive exclusion and limiting similarity: a unified theory. *Theor Popul Biol*, 69(1): 68-87.

Parvinen, K. and Meszéna, G. (2009). Disturbance-generated niche-segregation in a structured metapopulation model. *Evolutionary Ecology Research*, 11: 651-66.

Szabó, P. and Meszéna, G. (2006). Limiting similarity revisited. *Oikos*, 112(3): 612-19.

Szilágyi, A. and Meszéna, G. (2009). Limiting similarity and niche theory for structured populations. *Journal of Theoretical Biology*, 258(1): 27-37.

Szilágyi, A. and Meszéna, G. (2010). Coexistence in a fluctuating environment by the effect of relative nonlinearity: A minimal model. *Journal of Theoretical Biology*, 267(4): 502-12.