

OLM 10.5. Niche segregations

While niche and niche-segregation are defined in a model-independent way (Ch10Niche) it is far from being an easy task to understand coexistence of natural populations in terms of their niches. Identification and characterization of the regulating feed-back loops is a complex task that would require field-experiments and large-scale comparative studies of population growth. The technical difficulties as well as conceptual ambiguities (Ch10Niche) may explain why niches are usually determined with other methods. Besides functional-trait based approaches, the realised relative abundances of the species are studied in relation to the suspected limiting environmental conditions (like studies of adaptations within populations; Ch5Toler) instead of population dynamics and feed-backs. Studies in small communities of extreme habitats like deserts or comparisons of closely related species or ecotypes provide some examples in which the mechanisms of coexistence or the drive for niche segregation are well understood.

The classic comparative studies of lizard communities, which evolved independently in similar desert environments on three continents, were based on direct observation of the behaviour, activity pattern, place and food of individuals (Pianka 1973). Pianka interpreted the differences among sympatric species as differences in their niches and calculated niche breadth and overlap directly from the distributions of the observed characteristics. A robust view emerged in conclusion: “lizards in deserts partition environmental resources in three major ways: by being active at different times, by spending time in different places, and by eating different foods.” (Pianka 1988).

A similar functional trait-based approach was followed in a study of sand dune plant community consisting of 9 species (Stubbs & Wilson 2004). The patterns of associations at four spatial scales (up to 50 m²) revealed that plants with similar functional characters less often associated than expected at random. The 24 characters included in the analysis were chosen to represent modes of resource acquisition (Table 10.5.1). Species with different water-use pattern tended to co-occur which indicates that water is the limiting resource for this sand dune vegetation where the mean annual rainfall is 590 mm.

Table 10.5.1 List of the characters included in the models (Stubbs & Wilson 2004).

Character	Functional importance
Plant height	Light capture; growth strategy
Number of leaves on the terminal shoot ¹	Light capture; plant architecture
Support fraction ²	Growth strategy; leaf longevity
Leaf inclination from the horizontal	Light capture; water retention
Leaf area	Heat load; water retention; gas exchange
Leaf area ratio (LAR = leaf area/total mass)	Growth strategy
Leaf thickness (measured with a micrometer)	Light capture; gas exchange; water retention
Leaf shape (length/width)	Gas exchange; heat load
Leaf lobation: ($\pi \times \text{length} \times \text{width}$)/area	Heat load; gas exchange; water retention
Leaf succulence (fresh mass/dry mass)	Water retention
Specific leaf area (SLA: leaf area/leaf mass)	Photosynthetic capacity; leaf longevity; stress tolerance
Total chlorophyll content of the leaves ³	Light capture; growth strategy
Chlorophyll <i>a:b</i> ratio	Growth strategy
Nitrogen content of leaves ⁴	Photosynthetic capacity; leaf longevity
Phosphorus content of leaves ⁴	Leaf longevity
Number of primary root axes ⁵	Nutrient & water acquisition & storage
Horizontal root system extent	Nutrient & water acquisition
Vertical root system extent	Nutrient & water acquisition
Root diameter of the thickest root	Nutrient storage
Rhizome diameter	Nutrient storage
Presence/absence of tap roots ⁶	Water acquisition
Presence/absence of tubers ⁶	Nutrient storage
Root profile ⁷	Nutrient & water acquisition

In a recent reciprocal seed transplantation experiment of two xerophytic desert trees *Haloxylon ammodendron* and *H. persicum* not only some candidate functional characters were measured but the selective environmental conditions were also characterized (Xu et. al. 2014). The *Haloxylon* genus consists of these two species and distributed in southwest and Central Asia. The study area covered dune and interdune habitats in the sandy Gurbantonggut Desert, where *H. ammodendron* occupies interdunes and the flat slopes of dunes while *H. persicum* occurs mainly on the top of dunes. The physical and chemical properties as well as the nutrient contents differed at these habitats. The soil on the dune was less saline but had less nutrients and lower water availability compared to the interdune. Accordingly, seeds and seedlings of *H. ammodendron*, which lives under saline conditions, tolerated salinity better than *H. persicum* in former laboratory experiments. As

expected, each species' recruitment was better in its own habitat than in the other one in the transplantation experiments (Figure 10.5.1).

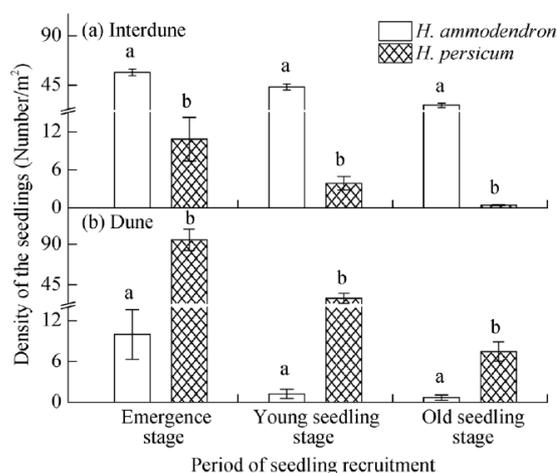


Figure 10.5.1 Germination rate and seedling survival in the transplant experiment (Xu et. al. 2014)

Seedling recruitment in a) interdune and b) dune habitats. 400 seeds were sown at 10 plots/habitat type for each species. Whiskers denote SE.

H. persicum is more adapted than *H. ammodendron* to water stress and nutrient shortage by having lower total dry biomass but allocating a higher percentage of it to roots in its water- and nutrient-limited environment (Figure 10.5.2). This study suggests that the agents of selection responsible for the spatial segregation of these tree species -as well as for the differences in their functional characters - are water shortage and salinity.

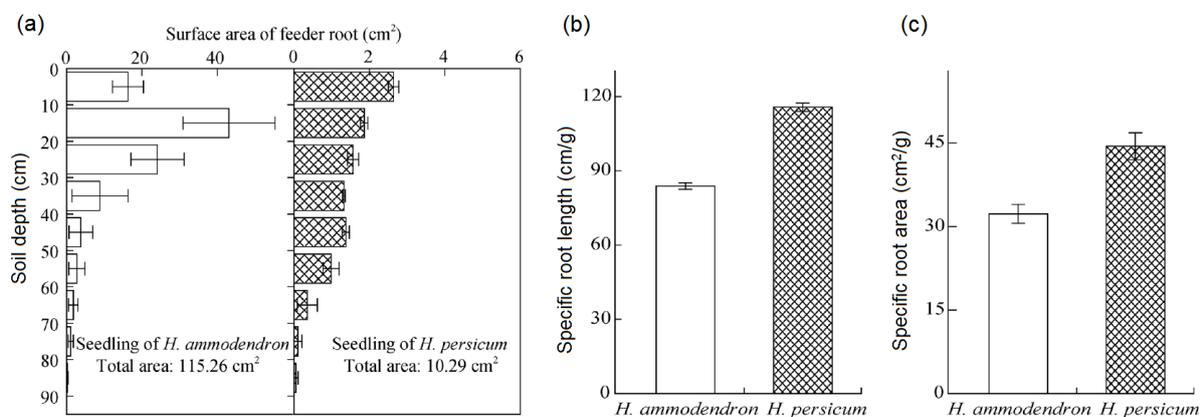


Figure 10.5.2. Morphological comparisons of the *Haloxylon* species (Xu et. al. 2014).

a) Root growth profile (Mean±SE, n=5) and b)-c) root growth characteristics (Mean±SE, n=3) of *H. ammodendron* and *H. persicum* in their own habitat types at age of one year. Note the different scales on the two horizontal axes in the growth profile panels.

While the harsh physical conditions and the scarcity of resources dominate the niche structure of the extreme environments like deserts, the situation gets more complex where biotic interactions regulate the populations mainly. We discussed that many studies have

indicated that soil humidity may be a decisive regulating factor of plant populations under a wide range of conditions (Silvertown et al. 2015; Ch10Niche p.212). This might be the case of goldenrods, which are intensively studied plant species under various conditions. Many of them coexist both in virgin tall-grass prairie and old-field communities. The old-field communities are transitional, the co-occurrence of *Solidago* species characterize the mid-parts of the successional gradient, whereas the undisturbed prairie vegetation is considered to be stable (“climax community”). Species abundances as well as physical conditions differ, therefore different niches and different adaptations have been expected in these habitats. Werner and Platt (1976) measured the water content of 50 (in prairie) and 70 (in old fields) soil samples per species below randomly chosen plants, at the level of main rhizomes along a slope. They characterized the species distributions along a moisture gradient based on these data. Their results are illustrated in Figure 10.5.3. As old fields are in succession and provide young habitats also in evolutionary sense the perennial, long-lived *Solidago* species must be in population dynamic as well as population genetic transient states there. These transient states might explain the co-occurrence and the large, supposedly transient, overlap of species distributions in themselves if priority effects (Ch12Divers, p.269), small selection coefficients (Ch8Excl, Tbox7.1, p.123) and the long expected-lifespan of *Solidago* genets are taken into consideration. The nice segregation of the six species in the prairie is assumed to be the result of competition in a stable community thus these abundance-based realized ecological tolerances (Ch5.2.2, p.84) were interpreted as results of niche segregation. The importance of soil characteristics for the distribution of goldenrods was reinforced by a more recent study of five co-occurring goldenrod species as well (Abrahamson et al. 2005). The 20 included homogeneous old fields were characterized by their mean soil textures, nutrients, pH, and moisture in this study. Moreover, a monographic study of the ground vegetation layer of 12 remnant oak-savanna sites in southern Wisconsin revealed that 14 pairs from six occurring *Solidago* species had significantly different positions along the two-dimensional gradients of soil texture and potential light availability.

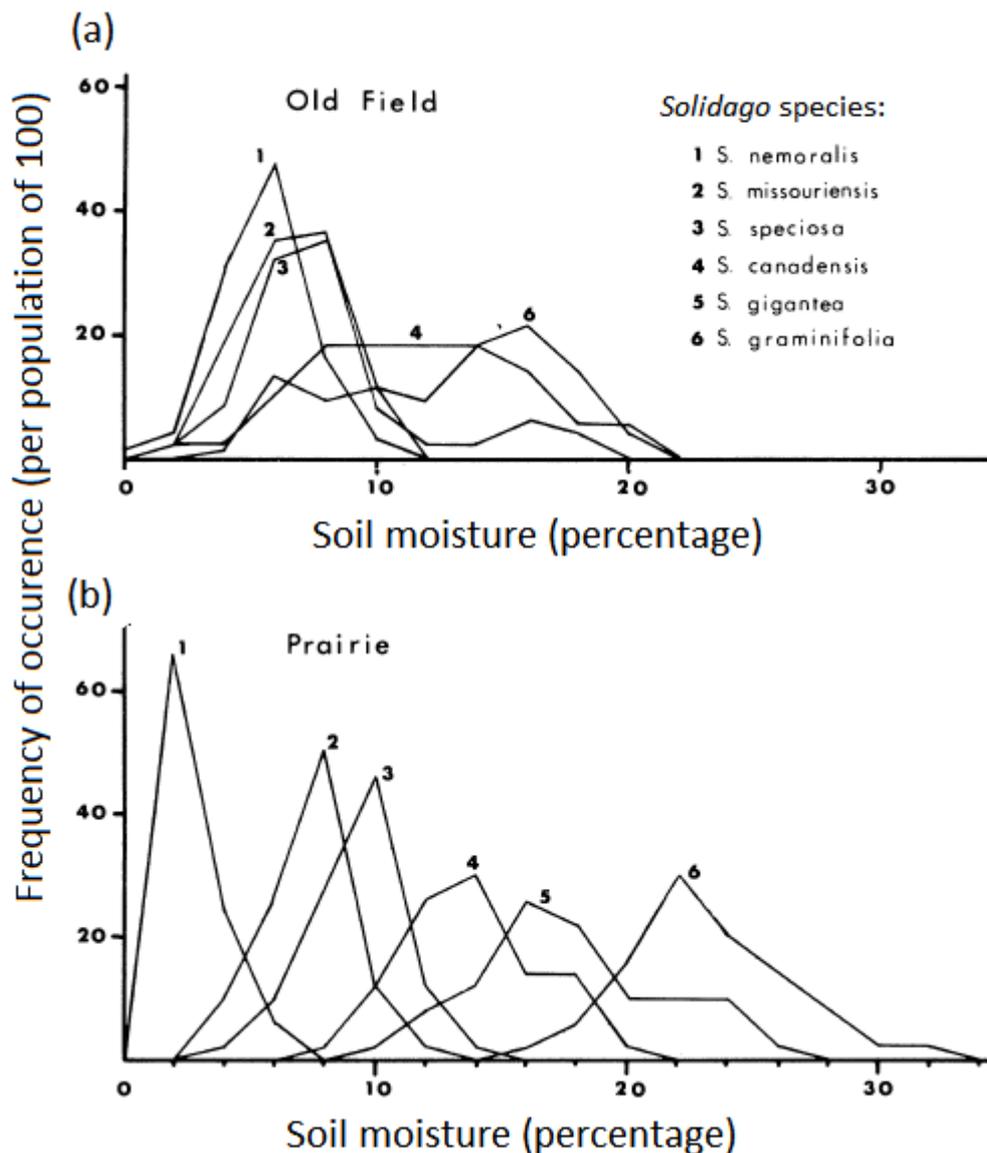


Figure 10.5.3. Realized abundance based ecological tolerances of 6 *Solidago* species in two habitat types (Werner and Platt 1976).

However, unlike the case of the *Haloxylon* trees the explanation of the coexistence of the *Solidago* species is far from being straightforward in terms of the species functional characters or life-history traits. Potvin and Werner (1983, 1984) did not find differences in the water use pattern of the seedlings or clonal transplants of *S. altissima* and *S. juncea* in the greenhouse though these species positions differ on the soil moisture gradient. Both species could maintain the standard physiological responses over a wide range of water availability. A possible explanation for the lack of a clear adaptive pattern is that there must be other players in the regulation of species abundances in this habitat type which were not included in the experiments. Competition for light or pollinators, against insect herbivores or

parasites, allelopathy, interactions with mycorrhizae may not only play a part in regulation via density-dependent feed-backs but may also modulate the response to water stress. Considering the results of long-series of field observations and experiments of several research groups none of these options can be excluded.

For instance, dominance in competition for light and intensive clonal growth from rhizomes seems to explain the widespread success of *Solidago altissima*, the tall goldenrod, whose dense stands decrease light intensity below them to such a low level what no other herbs or grasses can tolerate. However, these dense stands may attract herbivorous insects (e.g. chrysomelid beetles) who can regulate their host's populations and increase the diversity of the plant community by defoliating the goldenrods in such an extent that they cannot overshadow their competitors any more. Thus, some specialist herbivores can change the species composition of the plant communities by affecting the dominant plants and these species may even accelerate the speed of succession (Carson & Root 2000).

Not only *S. altissima* excels at light competition but its close relatives *S. canadensis*, *S. rugosa*, *S. gigantea*, and *Euthamia graminifolia*, are also rather good at shading (Figure 10.5.4). This can explain why the *Solidago* gang excludes the earlier arriving *Aster* species from old-fields in the mid-stage of succession (Banta et. al. 2008) but does not explain their coexistence. Still, as herbivores affect *Solidago* species differently and the plants have different means of defence, herbivory should contribute to their coexistence in principle.

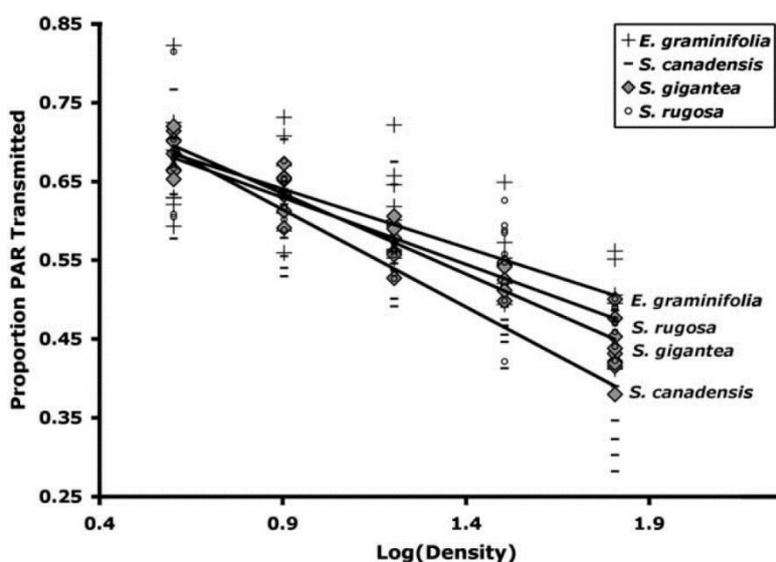


Figure 10.5.4 Light attenuation in monocultures of four naturally occurring goldenrod species (*Solidago canadensis*, *S. gigantea*, *S. rugosa*, and *Euthamia graminifolia*) at different densities on Beagle Road (Banta et. al. 2008). The proportion of photosynthetically active radiation transmitted to the soil surface (PPAR) in 71 x 71 cm plots. Density-gradient was created by removing other species and thinning. Density is measured in stems/m².

Finally, one should not forget about allelopathy and its consequences. The amount of the produced allelochemicals can be regulating variables as their production is affected by

several biotic and abiotic environmental conditions, the availability of resources and the pressures from herbivores among others (Figure 10.5.5). Specifically, a recent study showed that soil microbial communities alter the production of allelopathic chemicals of *Solidago* and *Aster* species (Meiners et. al. 2017).

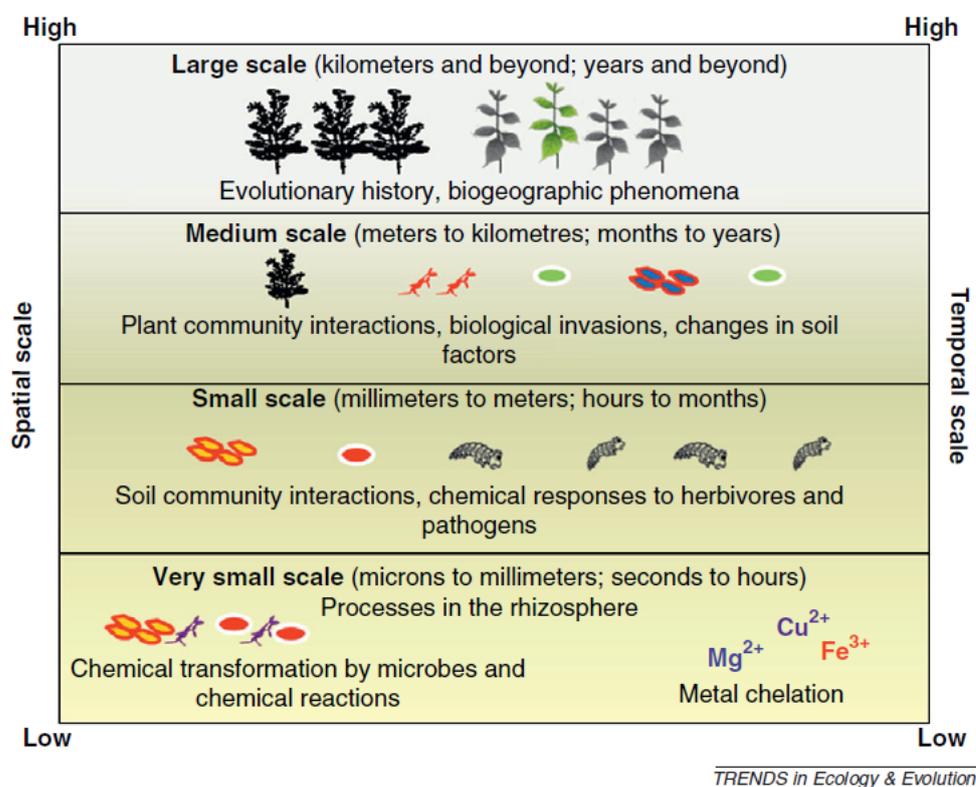


Figure 10.5.5 Several conditions influence the production and concentration of allelochemicals in the environment on various spatial and temporal scales (Inderjit et. al. 2011).

In addition to these opportunities for niche segregation, we should not forget that the competition-colonisation trade-off offers a further one (Ch9.2.3, p. 186) that can be highly relevant in case of old fields. When the mean weight of the propagules in old-field and prairie populations of six *Solidago* species were compared it was found that the propagules are 3 times heavier on average in the prairie than in the old field (Werner & Platt 1976). The rates of fall of the propagules were also measured as these are related to dispersal distance via the length of time that a propagule may be expected to remain in the air. The rate of fall was on average smaller in each of the old-field populations of the six *Solidago* species measured, and significantly so in 5 of them. Thus, we might interpret the difference between the old-field and prairie „ecotypes” as results the colonisation-competition trade-off species by species. Genetic differences between the conspecific populations (or adaptive phenotypic plasticity) might have evolved because types with higher dispersal rate become successful old-field colonizers but the type with smaller seeds is (or would be) outcompeted in

undisturbed, closed vegetation of the natural prairies. However, the competition-colonisation trade-off and asymmetric competition cannot explain the common co-occurrence of these species within old fields as there is no sign of such trade-off among the species in the old fields in this study. The populations on old-fields compose a distinct group with high variation in the number of propagules (*achene + pappus*; note the logarithmic scale on the figure) but lacking any relation between propagule size and number (Figure 10.5.6).

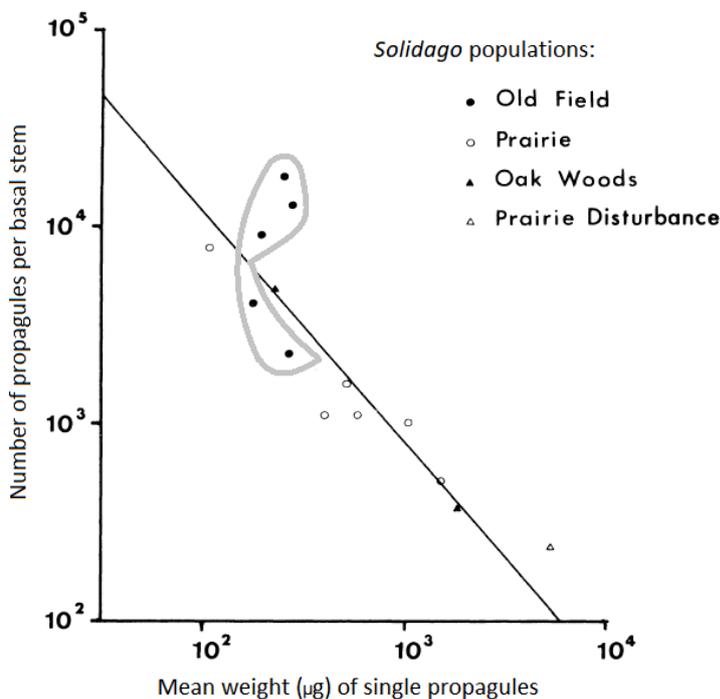


Figure 10.5.6 Propagule size and number trade-off with exceptions (Werner and Platt 1976).

Each point refers to mean value of a population. Old field populations are encircled. The authors did not exclude these records from the analysis of regression, which yielded the equation: $\log N = 5.2909 - 1.1950 (\log W)$; $r = -0.8622$.

Research of the intensively studied *Solidago* species rich in exciting results, still the mosaics do not provide a consistent picture. How to dissect this seemingly tangled web of interactions? The strength of these studies is their focus on the morphology, physiology, chemistry of individual plants and on the details of interactions with their surroundings. However, the regulating population dynamic feed-backs have remained hidden in the majority of these studies (for a counter example see Carson & Root 2000). Physiological proxies or vital rates have been measured in place of the *pgr* response functions (Ch5Toler; Figure 5.17, p.88). In this way it is difficult to determine the relative importance of the studied interactions in the actual community and to find the decisive ones. In a large community with many potential interactions it would be essential to link studies of interactions on the individual level with the actual population dynamics of the species in focus in order to reveal their niches, i.e. their places in the community.

Ecological studies of sympatric speciation provide excellent opportunities to study niche segregations *in statu nascendi*. The advantage of this situation is that less number of traits are affected, their genetic background can often be found and the driving selecting agents – i.e., regulating factors - can be also identified (pollination Rodríguez-Gironés & Santamaría 2007; segregation by macrohabitat Savolainen et. al. 2013; segregation by prey size Kingston & Rossiter 2004; Siemers & Schnitzler 2004; limnetic-benthic segregation Barluenga et. al. 2006; soil type Savolainen et. al. 2006).

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