Worldwide decline of specialist species: toward a global functional homogenization?

Joanne Clavel*, Romain Julliard, and Vincent Devictor

Specialization is a concept based on a broad theoretical framework developed by evolutionary biologists and ecologists. In the past 10 years, numerous studies have reported that – in many contexts – generalist species are "replacing" specialist species. We review recent research on the concept of the ecological niche and species specialization, and conclude that (1) the observed worldwide decline in specialist species is predicted by niche theory, (2) specialist declines cause "functional homogenization" of biodiversity, and (3) such homogenization may be used to measure the impact of disturbance on communities. Homogenization at the community level could alter ecosystem functioning and productivity, as well as result in the deterioration of ecosystem goods and services. We propose community-level specialization as an indicator of the impact of global changes (habitat and climate disturbances) on biodiversity.

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During the past decade, several important studies have revealed declines in specialist species, including plants (Rooney *et al.* 2004), coral reef fish (Munday 2004), birds (Julliard *et al.* 2004), and mammals (Fisher *et al.* 2003). Most of these studies have consisted of compilations of large datasets, involving long-term observations. Researchers suggest that the observed declines were related to disturbances to habitat and climate. Disturbances, directly and indirectly, may cause the decline of specialist species: habitat destruction (ie loss of habitat quantity) and degradation may lead to increased competition with generalists, as well as to extinction or extirpation of specialists otherwise unable to adapt to changing conditions.

Here, we used arguably the most influential concept of ecology – the ecological niche (Hutchinson 1957) – to investigate why specialists may be more sensitive than generalists to ongoing global changes. By definition, a niche encompasses all that a species requires to ensure its population viability in a given environment, as well as including its impacts on that environment (Chesson 2000). Specialist and generalist species can be characterized by differences in their niche width (Figure 1). Although a long-standing concept, niche theory still influences the fields of evolutionary and behavioral ecology (Kassen 2002; Bolnick *et al.* 2007) and could be useful for assessing the condition of ecological communities.

Specialization can be addressed in at least two ways: (1) performing laboratory-based experiments that examine the reaction norms, the expression of different genotypes across a range of environments; specialists and generalists would then be characterized according to the array of resources on which they can survive, as well as their growth rate in relation to these resources; and (2) applying habitat-suitability models (through generalized linear models, generalized additive models, or multivariate analysis), which mostly rely on explicit measurements of some niche dimensions.

In this review, we first describe how recent, fundamental developments in various subdisciplines of ecology could explain why specialist species may be more vulnerable than generalists to global changes. We then suggest that the replacement of geographically local specialists by geographically local generalists is central to the ongoing process of functional homogenization (FH), which, together with taxonomic homogenization (TH), makes up what is known as biotic homogenization (BH) (Olden *et al.* 2004). Functional homogenization is the measurement of the increase in spatial similarity of a functional variable over time. We argue that, from an ecological perspective, FH is of far more concern than TH, and that FH should not be underestimated. Studies have asserted that community ecology needs to account for functional traits in order to understand the mechanisms underlying global changes (McGill *et al.* 2006). Finally, we explore how FH processes may have consequences for ecosystem functioning and discuss the future role of FH in conservation biology. We believe that FH, because of its strong link to eco-

In a nutshell:

- Long-term persistence of specialist species is adversely affected by past and current global changes
- Generalist species have effectively replaced specialist species, causing functional homogenization at the community level
- Functional homogenization could alter ecosystem functioning and thus ecosystem goods and services
- Functional homogenization as a measurement of the loss of functional diversity could be used as a biodiversity indicator

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UMR5173 MNHN-CNRS-UPMC, Conservation des Espèces, Restauration et Suivis des Populations, Paris, France *(jclavel@mnhn.fr)*

logical theory and its widespread occurrence, is a reliable indicator of the impact of global change on biodiversity.

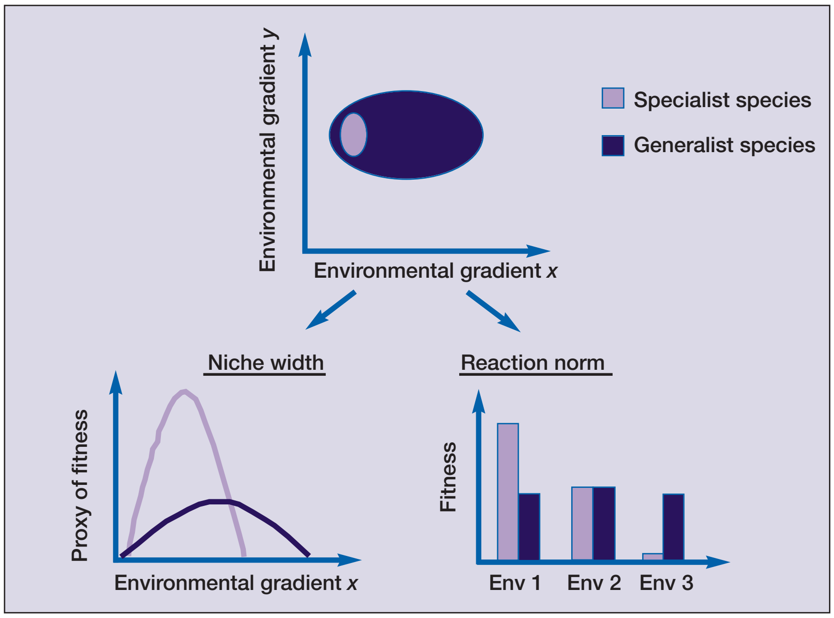

Figure 1. *Concept of the ecological niche and two different measures of it. Env = environment.*

Vulnerability of specialist species: what does theory tell us?

Specialization: a broad theoretical framework

Ecological niche theory is a synthesis of all of the interactions between a species and its environment (Hutchinson 1957; Chesson 2000). This concept therefore combines the ecological requirements of the species and its functional role in communities. The dichotomy between generalists and specialists is based on a tradeoff between the capacity to exploit a range of environmental conditions and their ability to use each one (Futuyma and Moreno 1988). For example, a field experiment on coral reef fishes (Caley and Munday 2003) showed that specialists grew faster than generalists in one or two habitats, but the generalists' growth rate was more consistent between a broader range of habitats.

In practice, specialization has long been defined as a discrete variable, depending on the biological model used. For instance, specialization has been measured in terms of host diversity in organisms such as phytophagous insects or parasites (Tripet *et al.* 2002). Continuous measurements of specialization have been developed for different taxonomic groups, including birds (Julliard *et al.* 2006), spiders (Entling *et al.* 2007), and trees (Fridley *et al.* 2007), which facilitates the study of this trait in various contexts (eg different spatial scales and different trophic levels).

Environmental variation and specialization

Environmental variation plays an important role in niche evolution. Specialization is thought to be an evolutionary response to an environment that is stable over space and time, whereas generalist strategies are more likely to be favored by organisms in heterogeneous and perturbed environments (Futuyma and Moreno 1988; Kassen 2002). In other words, specialization is more likely to occur in a relatively stable environment than in one more often subject to changes (Scheiner 2002). Depending on the environmental grain – the perception of environmental variation by organisms relative to the lifetime of an individual (Levins 1968) – different kinds of generalists will be favored. In fine-grained environments, all individuals experience environmental heterogeneity within their own life cycle, while in coarse-grained environments, individuals experience different states of the environment more indirectly, for example via gene flow to other individuals or via their progeny. Versatile generalists (ie those that exhibit reversible phenotypic responses to the prevailing environmental conditions) might be expected to evolve in fine-grained environments, whereas plastic generalists (ie those that exhibit adjustable responses early in development, but fixed phenotypes thereafter) might be expected to evolve in coarse-grained environments (Kassen 2002). In a metapopulation model, Marvier *et al.* (2004) found that habitat destruction and fragmentation favored habitat invasion by generalist species, despite the costs of reduced competitive ability.

Past and current evidence of specialist decline

Paleontology and records of specialist species

Fossil records provide an incomplete archive of the natural history of certain taxa, allowing researchers to estimate extinction rates. These data show that, over geological time, mass extinction events have been largely associated with the extinction of specialist species. Specialization in this regard is principally defined as diet specialization quantified according to morphological parameters. Survival – as estimated from fossil records – varied in a non-random way among species, and the challenge is to understand both the causes and the consequences of extinction (Jablonski 2004). Many paleontologists have pointed out that, during past mass extinction events, generalists were less prone to extinction than specialists (McKinney 1997). For example, opportunistic species and ecological generalists among the foraminifera and benthic marine invertebrates outlived other, more specialized species in the early Jurassic (Erwin 1998). By the end of the Cretaceous, more diet-specialized urchin species were extinct than their generalist urchin counterparts (Smith and Jeffery 1998). This suggests that specialization may have led to increased chances of extinction when the environment was disturbed.

Introduced species

Human activities, such as international trade, mariculture, horticulture, and recreation, have resulted in the introduction of non-indigenous species around the world, and some of these species have become invasive (Jeschke and Strayer 2005). Among introduced species, generalists are more likely to become successfully established. Seven out of eight comparative analyses show a significant relationship between establishment success and ecological specialization (in birds and fishes; Fisher and Owens 2004). This success among generalists may be the result of the higher probabilities of introduction and establishment, two crucial and interdependent stages in biological introduction.

Comparative analyses of species introductions have mainly focused on birds, and the following examples – from which two key results emerge – all consider bird species. First, populations of generalist species are, on average, more abundant than populations of specialist species (Kattan 1992) and are therefore more likely to be introduced (Blackburn and Duncan 2001); both the number of introductions and the number of introduced individuals are crucial to the success of introduced species (Veltman *et al.* 1996; Cassey *et al.* 2005). Second, because of their flexibility, generalists are often able to live in diverse habitats and are thus more likely to establish in "new" ecosystems (Cassey 2001). Wherever introduced, non-native generalists have a better chance of finding necessary resources and appropriate environmental conditions (Duncan *et al.* 2003). Genetic variability is often associated with the greater success of introduced species. Because generalist species are introduced in large numbers, they may also have greater genetic diversity, and consequently, they may be more successful in becoming established.

More generalists and fewer specialists: consequences in natural communities

Functional homogenization

Most species are declining as a result of human activities ("losing species") and are being replaced by a much smaller number of species ("winning species"). Biotic homogenization refers to the replacement of local species by other, more widespread species. In effect, this process "reshuffles" existing species distributions and reduces spatial diversity. Ecologists have long been interested in one component – TH (Elton 1958) – which describes an increased similarity in community composition with the invasion of "winning species" and the extirpation of "losing species" (Baskin 1998). However, TH is an inappropriate description of the erosion of biodiversity, because introduced or expanding species can increase species richness and confound the BH concept (Olden and Poff 2003).

A high degree of similarity between communities could be the result of two scenarios: (1) the occurrence of many of the same species or (2) the disappearance of a large number of extirpated species (Olden and Poff 2003). Beyond this BH, "winners" may also have less functional diversity, less complementary roles in the ecosystem process, than "losers". This overall reduction of ecological functional diversity is equivalent to FH. The replacement of specialist species by generalist species may provide an illustration of FH (Fisher and Owens 2004). Here, we simplify this concept, moving from the restricted context of introduction–invasion to the general context of human-perturbed ecosystems.

Three mechanisms may dictate the outcome of global change in the balance between specialist and generalist species' abundances, and therefore, FH: (1) global changes may have direct negative effects on specialists, irrespective of the presence of generalists. This happens when the fitness of a specialist is reduced to the point where it affects the local persistence of that species. For example, many European wetland species are declining because wetlands have been disappearing throughout Europe. Species adapted to that habitat are more affected because they cannot access the kinds of alternative resources that generalist species can. (2) Because they are more flexible and innovative, as discussed earlier, generalist species may have the ability to colonize new niches that have been created as a result of global change. For instance, generalist and specialist species are not similarly lagging behind climate warming because they may also have different abilities to track land-use change (Warren *et al.* 2001). (3) In many cases, global changes may have the same positive (or negative) effects on both specialists and generalists, but not to the same degree. Competition induced by these differential responses determines the relative success of generalist species. For example, unusually warm spring seasons may favor the reproductive success of all species, but may be more favorable for generalists, owing to their greater adaptability. When climatic conditions return to "normal", resampling through recruitment then favors the relatively more abundant generalists (Julliard *et al.* 2004).

Finally, combinations of these three mechanisms may further promote the success of generalists. The responses of specialist and generalist species to additional changes may differ to a greater extent if the surrounding community is already perturbed, as seen, for instance, in the greater success of introduced species in becoming established in disturbed areas (Levine *et al.* 2004) or in the presence of previously established exotic invasives (Facon *et al.* 2006).

The consequences of community changes on ecosystems

The phenomenon of FH raises numerous questions about the future of disturbed and transformed ecosystems on ecological and evolutionary time scales. Species that are highly specialized are replaced by generalist species with different or similar functions, yet the former perform less efficiently. How do changes at the community level alter ecosystem functioning and ecosystem productivity, and do ecosystem services deteriorate in such circumstances?

Early models segregated species into functional groups and assumed that species within such groups performed the same functions (Johnson *et al.* 1996). These models showed that functional characteristics, instead of diversity per se, strongly influenced ecosystem properties (Díaz *et al.* 2007). Generalist species may be considered as redundant, owing to their plasticity (Duarte *et al.* 1995), so their diversity is not fundamental to maintaining functions at the ecosystem level, as long as all functional groups are present. Some models (ie those that precisely accounted for species traits) assume that each species allows others to utilize resources differently (Tilman *et al.* 2001); some species are complementary in their patterns of niche occupation and can increase average rates of productivity. Meanwhile, environmental conditions influence the importance of complementarity for ecosystem productivity, which may be higher in resource-limited conditions (Zhang and Zhang 2006) and when, over time, the stages of ecological succession advance (Tilman *et al.* 2001). Complementary responses may therefore be directly linked with niche partitioning, and a species-rich community composed of specialist species should lead to higher resistance and better resilience than a community composed mostly of generalists.

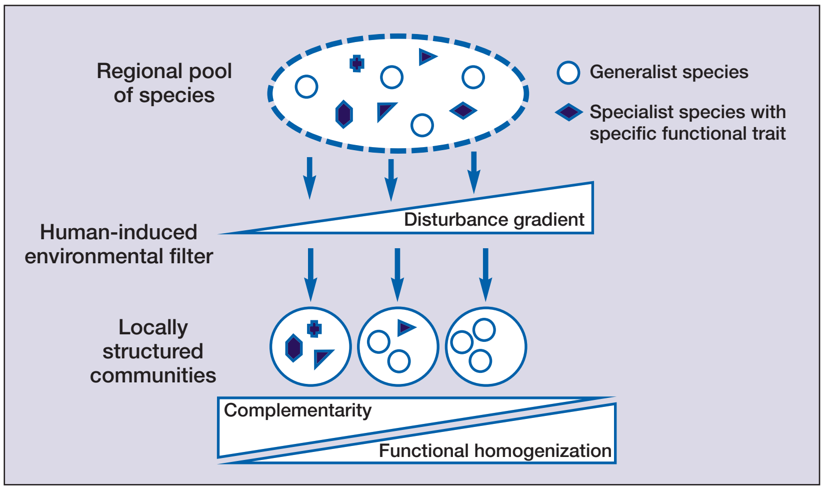

Figure 2. *Diagram describing how loss of specialists engenders loss of functional complementarity and thus functional homogenization.*

Finke and Snyder (2008) used an aphid–parasitoid wasp–radish community to demonstrate experimentally that resource exploitation improved in the presence of greater numbers of specialists, but not when generalist diversity was increased. In this case, the ecosystem function (ie parasite regulation) is better performed by specialist parasitoid communities.

Functional homogenization should increase the synchronization between connected communities facing disturbances. As a result, FH decreases the viability of the whole system, by decreasing the variability in the communities' responses to disturbance, and thereby decreasing potential landscape and regional buffering (Olden 2006). Indeed, having a range of species that respond differently to environmental perturbation can stabilize ecosystem processes (Hooper *et al.* 2005). Theoretical studies have suggested the importance of niche partitioning (Loreau and de Mazancourt 2008), although experimental examples are still lacking (Hooper *et al.* 2005). Species and communities differ in their responses to disturbance. Although a given specialist species may be more negatively affected by disturbance than a generalist species, an entire (meta)community composed of many specialized species should be relatively less affected, on account of greater niche complementarity (Figure 2).

Under suboptimal or variable conditions, and if the cost of generalization is less than the cost of coping with fluctuations, generalist species may also contribute to more efficient ecosystem functioning (Richmond *et al.* 2005). Under heterogeneous conditions, a community of generalists could outperform a community of specialists with respect to ecosystem functioning. In a global change context, the environmental tolerance of generalist species could be a determinant of ecosystem stability and may also drive the relationship between diversity and ecosystem functioning. Richmond *et al.* (2005) also questioned the impact of FH on an ecosystem over an evolutionary time scale and found that the replacement of specialists by generalists changes the equilibrium of the ecosystem. How does FH affect adaptive dynamic ecosystems? Can the system return to the initial equilibrium? Do generalists facilitate the establishment of other specialist communities, or do generalist species stabilize the ecosystem at a new equilibrium, as suggested by Richmond *et al.* (2005)? It is necessary to consider local interactions between specialists and generalists in order to study the evolutionary dynamics of local FH within the framework of adaptive dynamics theory.

■ Functional homogenization: an indicator of biodiversity loss

There has been considerable interest in the development of biodiversity loss indicators in order to meet the Convention on Biological Diversity's 2010 target. Ideally, a biodiversity indicator should accurately reflect changes in biodiversity, link such changes appropriately to specific pressures, and be rooted in sound scientific theory (Balmford *et al.* 2005). The Marine Trophic Index is an example of a functional indicator in marine ecosystems: based on food-web theory, it has proven its usefulness in summarizing the impact of fisheries exploitation on

Panel 1. Community specialization index: an indicator of functional homogenization

Julliard *et al.* (2006) have quantified the specialization of species as the coefficient of variation (standard deviation/average) of their densities among habitat classes. The species specialization index (SSI) may be useful in building a sensitive (yet simple) index of biotic homogenization at the community level. The community specialization index (CSI) could, in turn, be used to test the role played by human-induced disturbances, such as habitat fragmentation, in functional biotic homogenization.

We used data from the French Breeding Bird Survey and considered 100 common species. We investigated the response of the CSI to habitat fragmentation and quantified these pressures using a land-cover survey (CORINE Land Cover database; Figure 3). The CSI was then calculated as the weighted average of the SSI in the site *j* (weighted by the number of individuals at the *j* site).

$$CSI_j = \frac{\sum_{i=1}^{N} a_{ij}(SSI_i)}{\sum_{i=1}^{N} a_{ij}},$$

Where N was the total number of species recorded, a_{ij} the abundance of individuals of species i in plot j, and SSI_i its specialization index.

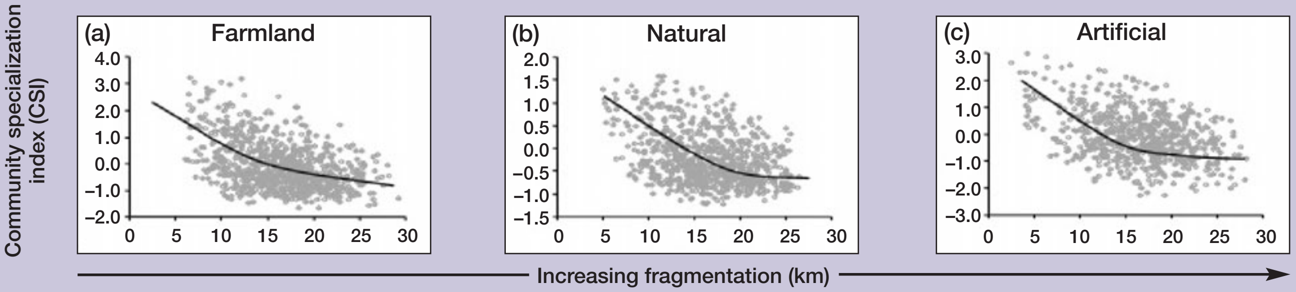

Figure 3. *Relationship between the community specialization index (CSI) and landscape fragmentation within each habitat type. We tested the relationships between the CSI and fragmentation (in kilometers) or disturbance using point counts monitored in (a) farmland (n = 5087), (b) natural (n = 3210), or (c) artificial (n = 1544) habitats. Smoothed curves were obtained with generalized additive mixed models, taking into account spatial dependence between samples.*

marine ecosystems (see Pauly *et al.* 1998). In contrast, in terrestrial ecosystems, reliable indicators able to depict changes in functional processes have not yet been proposed. The replacement of specialist species by generalist species could have severe consequences on community and ecosystem functioning. Therefore, we suggest that FH, measured as the proportion of specialist species in the community, is a good indicator because it measures the state of biodiversity, which is directly linked to drivers of global changes. We have attempted to separate FH from TH, in order to construct a robust indicator. Taxonomic homogenization is not always a synonym of diversity loss (Rooney *et al.* 2007). Likewise, similarity indices, which measure BH, are not always informative about changes in community and could suggest either an increase or a decrease in species richness (Olden 2006). To interpret these changes, researchers must identify the species that are responsible for them (Rooney *et al.* 2007).

Comparing specialization among species in communities is a promising way of studying the ecological mechanisms that drive functional diversity (Ackerly and Cornwell 2007). Calculating FH requires standardized multisite, multispecies monitoring efforts, such as citizen-science programs, which are already being implemented in many countries. For example, measurement of FH – based on how many species are present in a community, whose contributions are weighted according to continuous measurement of habitat specialization – appears to be a sensitive and interpretable measure of the impact of global change on communities (Devictor *et al.* 2008). It assumes that detectability, specialization, and sites do not co-vary. Under these conditions, the comparison could be performed relative to change over time – based on a time-series study – or relative to variation in space, based on site comparisons (with comparable sites, such as those in the same habitat; Panel 1).

■ Conclusions

The loss of biodiversity across the planet should be considered not only as a striking inventory of the poor conservation status of individual species, but also as a general biological response to global changes with various mechanisms, some of which remain to be identified. Replacement of specialist species by generalist species results in FH. Here, we have identified FH as a general process, one that is present in all ecosystems.

Because specialization is a concept anchored in ecological theory, we believe it is a powerful tool that can be used to describe and understand the responses of biodiversity to global change. The recent development of such tools, enabling the quantification of niche width, and studies incorporating the trait concept (Ackerly and Cornwell 2007) open up interesting new possibilities (eg the construction of a robust indicator of biodiversity and ecosystem functions). There is little doubt that fewer specialists are indicative of ongoing degradation. An important issue that should be addressed in the future is whether the increase in generalist species contributes to habitat degradation or whether it is the response of communities that have been subjected to perturbation. The answer to this question has profound consequences for management: should the increase in generalists be promoted or discouraged? Part of the answer relies on clarifying how the functioning of generalist communities differs from that of specialist communities. Another part of the answer depends on the fate of these generalist communities: do they represent a poor stable state of nature (in which case generalists would be seen as detrimental)? Is it a transitory state, which may return to a more specialized species assemblage once the perturbation is over, and do generalists benefit from this transition? Is it a transitory state toward novel ecosystems (ecosystems with species assemblages that have never existed before) and, again, what is the influence of generalists: facilitating the establishment of new specialist species, or becoming specialists themselves within these novel ecosystems? Further research that examines FH and its applications is crucial.

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