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IDEA

# Functional redundancy in heterogeneous environments: implications for conservation

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**Abstract**

It has been argued that one of the best ways to conserve biological diversity is to maintain the integrity of functional processes within communities, and this can be accomplished by assessing how much ecological redundancy exists in communities. Evidence suggests, however, that the functional roles species play are subject to the influences of local environmental conditions. Species may *appear* to perform the same function (i.e. be redundant) under a restricted set of conditions, yet their functional roles may vary in naturally heterogeneous environments. Incorporating the environmental context into ecological experiments would provide a critical perspective for examining functional redundancy among species.

**Keywords**

Functional redundancy, environmental heterogeneity, species relationships, context dependency, ecological experiments.

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Much of the debate regarding the relationship between biodiversity and community function has centred on the roles that individual species have in regulating community processes (Wardle *et al.* 2000). Several hypotheses have been put forward to explain this relationship (see Johnson *et al.* 1996 for review), among which the "redundant species" hypothesis proposed by Walker (1992) may be the most consequential for conservation management. In his 1992 essay, Walker noted that "all species are not created equal" in terms of their contributions to the ecological functioning of communities. He recognized two categories of species: "drivers", whose roles in regulating community function is crucial, and "passengers", whose loss from a community leads to little change. To distinguish among these types, Walker advocates grouping species into guilds of similar functional type. Then, the degree of redundancy among species within guilds could be determined by examining the potential for species to perform the same functional processes. For example, complete functional redundancy would occur if, following the removal of one species, the remaining species increase their densities to compensate for the lost functional contribution of the removed species. Walker cautions, however, that a complicating factor in assessing redundancy is that guild members, while performing the same function, may respond quite differently to different environmental conditions (Walker *et al.* 1999).

Walker and colleagues (see McCann 2000 for review) suggest that these environmentally mediated shifts in species function are likely to be time-dependent, episodic features of guilds. We agree, but additionally propose that, because *spatial* environmental heterogeneity is a fundamental attribute of communities (Keddy 1991), species function may vary across natural gradients both *within* a community and *among* different communities. Far from being a caveat, we argue that understanding how spatial environmental heterogeneity shapes what species "do" (*sensu* Lawton 1994) may be crucial to understanding to what degree, if any, species are truly redundant.

Context dependency (*sensu* Power *et al.* 1996) refers to how species functional roles in communities can change in different parts of the environmental ranges where they occur. Gradients of temperature, light intensity, pH and other variables comprise essential axes of species' ecological niches and, as such, exert considerable influence on the physiology, behaviour and ecological performance of organisms in nature (Dunson & Travis 1991). Although environmental conditions can act as filters to determine which species will occupy a particular range of community habitats (Keddy 1991; Poff 1997), *within* those occupied ranges, some conditions will be more suitable than others for the survival, growth and reproduction of a species, i.e. its ecological performance. Such a change in species' performances across environmental gradients, then, implies that species play shifting functional roles in community organization and these roles may be mediated contemporaneously by environmental heterogeneity.

Recently, Cardinale *et al.* (2000) modelled how spatial heterogeneity interacts with temporal disturbance to modify the relationship between species diversity and ecosystem productivity. Here we focus more narrowly on spatial heterogeneity to show how the contributions made by *individual species* to overall ecosystem function can be conditioned by variation in ecological performances across natural gradients. Condition-specific performance may be critical for understanding and "diagnosing" redundancy; species may be ecologically extraneous at one point along an environmental gradient, but essential at another.

To illustrate how functional redundancy among species in communities may depend on the environmental context, imagine a guild composed of three species, A, B and C (Fig. 1). Assume these species comprise the invertebrate grazing guild in a stream community that spans a gradient of current velocity, an abiotic determinant of species performance (Hart & Finelli 1999). These grazers may be potentially redundant because they all feed on the "same thing", namely, the attached algae and associated microorganisms and detritus; thus, their fundamental niches overlap. Our community process in this example will be the rate at which algae is removed from stream substrates and converted to grazer biomass. As can be seen in Fig. 1, across the environmental gradient of current (depicted on the *x*-axis), species A, B and C all have the same *average* effect on this process (repre-sented by the dotted line). Seen in this way, the three species are redundant; however, the relative importance of each species to the community process changes dramatically as one moves across that gradient (Poff, N.L., Wellnitz, T. & Monroe J.; unpublished manuscript). Thus, while their functional roles are similar under low velocity conditions, these grazers are not functionally redundant at other points along the gradient. If we conclude these three species are redundant based on their functional contribution at low current velocity, or the average across the range, and were to remove, say, species C, then the community will lose an important functional component at the middle velocity.

Surprisingly, despite the importance spatial environmental heterogeneity may have in shaping species' functional roles, most ecological studies are conducted at some discrete point along an environmental gradient rather than at multiple points across its breadth (Huntly 1991; Keddy 1991). As a result, these studies provide limited generality for understanding how species roles may shift and can give a false view of redundancy. Indeed, environmental variation is often treated as a troublesome variable *to control* in experiments examining species functional roles and their interactions. Eliminating environmental "noise", however, artificially simplifies natural complexity and precludes a robust understanding of how species contribute to community function in naturally heterogeneous settings (Polis *et al.* 1998). More critically, tuning out environmental noise may lead conservation managers to draw false conclusions about the contribution of individual species to their communities.

In summary, if one is to empirically determine the degree to which species are redundant – conducting, for example, compensation experiments (Walker 1992; Walker *et al.* 1999) – species function must be examined at multiple points along the environmental gradients that span communities. The probability that functional redundancy is context dependent is critical for understanding the effect that species loss may have on overall community function in heterogeneous environments.

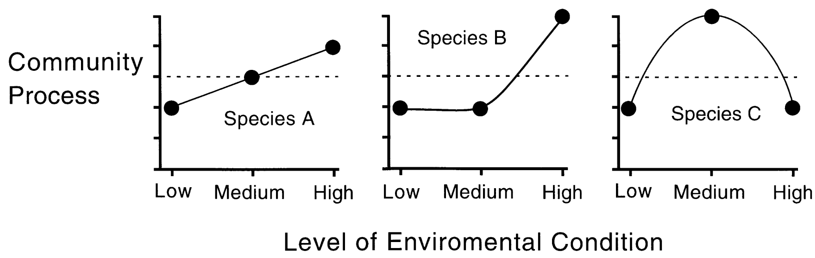


**Figure 1** Species can perform similar functions under restricted sets of conditions, yet their functional roles and fundamental niche may change substantially with the environmental context. In the figure, species A, B and C have the *same effect* on a community process (e.g. resource consumption) at the low end of an environmental gradient (e.g. low current velocity); however, the relative importance of species to this process changes dramatically as one moves across that gradient. Experiments conducted at only the low end of the gradient would reveal the three species to be "redundant", but this would not be concluded at the medium and high positions along the gradient. Similarly, an experiment that simply averaged the effect of the three species across the range of environmental conditions (dotted line) would mask the context-dependent contribution to overall community function.

Recognizing this should help guide conservation biologists in maintaining the functional integrity of natural communities.

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## BIOSKETCH

Todd Wellnitz studied aquatic ecology at the Swiss Federal Institute of Technology (ETH) and is currently a research associate at Colorado State University working with LeRoy Poff. Their collaborative work focuses on how environmental factors shape species interactions and their functional roles in aquatic communities.

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