**HOW TANGLED IS THE BANK? EFFECTIVE COMMUNITY DIVERSITY AND ECOLOGICALLY-DEPENDENT OPPORTUNITY FOR SELECTION**

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ABSTRACT

Community genetics investigates the influence genetic variation within species has on ecological interactions among species. It is generally thought that the utility of a community genetics approach diminishes as species diversity increases because interspecific interactions become too diffuse to measure. To determine when genetic variation in one species is likely to have evolutionary consequences for other species, we introduce a method to identify the relative contribution of within and among species interactions to the total opportunity for selection. Our method provides a means for estimating the *effective community diversity* (*DE*), a quantitative measure of the number of species that influence total selection on traits involved in interspecific interactions within any given community. We report three key findings: First, we show how the total opportunity for selection on a trait can be partitioned among ecological contexts of interspecific interactions and used to quantify effective community diversity, *DE*. Second, we show that *DE* is reduced by strong or frequent interactions involving foundation species; i.e., relatively few species can “drive” a community. Third, heritable variation in traits of foundation species involved in interspecific interactions will explain a significant fraction of the observed variation in the fitness of interacting, non-foundation species. The important conceptual advance and practical implication of defining a species’ effective community diversity is that the genetic analyses of relative few species may tell us much about the structure and evolution of much larger communities. Thus, even in a species-rich community, strong and/or frequent interactions between species can greatly reduce the effective diversity of the community. We conclude that a community genetics approach is evolutionarily and ecologically important whenever the effective community size for interacting species is small.

Key Words- community genetics, foundation species, effective community size, diffuse selection, interspecific indirect genetic effects.

“*It is interesting to contemplate a tangled bank…” – Darwin (1859)*

Antonovics (1992) identified “community genetics” as the analysis of evolutionary genetic processes that occur among interacting populations within a community, e.g., a formal contemplation of what Darwin (1859) may have called, “a tangled bank.” Community genetics represents the union of community ecology with population and quantitative genetics and emphasizes how genetic variation that exists within species may influence interactions that occur among species. Ehrlich and Raven’s (1964) classic work on the coevolutionary trajectories of plants and butterflies concluded that pairwise coevolution could be the starting point for studies of community evolution. Indeed, integrating species interactions and evolutionary change is central to the study of community genetics, and is now considered a major frontier in biology (Thompson et al. 2001; Whitham et al. 2006; Shuster et al. 2006; Wade 2007). Two distinct approaches currently address this community genetics frontier. One emphasizes the consequences of genetic variation in a focal species for the abundance of dependent species. The other takes the reverse approach by emphasizing how ecological and genetic variation of the dependent community can feed back to affect the evolution of the focal species.

Application of the first approach of community genetics shows that plant genetic variation can predict variation in the composition of dependent communities (e.g., arthropods, soil microbes) at both local (e.g., Fritz and Price 1988; Maddox and Root 1990; Floate and Whitham 1995; Dickson and Whitham 1996; Dungey et al. 2000; Hochwender and Fritz 2004; Wimp et al. 2004, 2005; Johnson and Agrawal 2005; Crutsinger et al. 2006; Shuster et al. 2006; Crawford et al. 2007; Schweitzer et al. 2008; Sthultz et al. 2009) and regional levels (Bangert et al. 2005, 2008; Barbour et al. 2009). Such foundation species are especially important as they structure a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (Dayton 1972; Ellison et al. 2005). Thus, the genetic-based impacts of these species are especially important to quantify and understand as they are by definition “community drivers”. Although we focus on these foundation species for simplicity, it is important to emphasize that non-foundation species can also affect dependent communities; indeed, because their effects are presumed to be small much less research has been devoted to such species (e.g., Johnson and Agrawal 2005). Herbivore population dynamics have also been experimentally shown to be dependent on plant genotype (Underwood and Rausher 2000; Stireman et al. 2005; Evans et al. 2008). While these community genetics studies do not explicitly show the mechanisms that lead to covariance between plant genes and its associated community, they suggest that genetically-based (i.e., heritable) traits of one species can have diffuse fitness consequences for many other species (Bailey et al. 2006; Wooley et al. 2010). In other words, the ecological pattern of the community depends on the evolutionary (genetic) context of the plant or other foundation species (Whitham et al. 2006, 2008; Wade 2007).

The second approach complements the first by emphasizing that trait evolution within a plant species can depend on the ecological context of interacting herbivorous insect species. Stated differently, selection on traits is diffuse rather than pairwise, and depends on the fitness consequences of genetically-based interactions among multiple community members (Janzen 1980; Strauss et al 2005). Since Janzen (1980) coined the term, “diffuse coevolution”, a growing body of empirical (Simms and Rausher 1989; Hougen-Eitzman and Rausher 1994; Iwao and Rausher 1997; Juenger and Bergelson 1998; Stinchcombe and Rausher 2001; Agrawal 2004) and theoretical work (Rausher 1992, 1996; Strauss et al. 2005) indicates that the covariance of relative fitness with trait values (a selection gradient) may also depend on the presence or absence of multiple species. This context-dependent selection has obvious implications for trait evolution by natural selection. While much of the work on community genetics has been performed on plant-herbivore interactions, proponents of a community genetics perspective suggest that it can be applied to other types of interactions in community ecology, i.e., to predator-prey (Yoshida et al. 2003;), competition, host-parasite (Inouye and Stinchcombe 2001), biodiversity, stability (Crutsinger et al. 2006; Keith et al. 2010) and even ecosystem processes such as nutrient cycling (Whitham et al. 2003; Wade 2003; Schweitzer et al. 2004, 2008).

A growing body of research indicates that community genetics is generally applicable to many aspects of community and ecosystem ecology (Bailey et al. 2009), and there is conceptual understanding that genetic variation should be incorporated into ecological dynamics under some, but not all, ecological scenarios or contexts. Morin (2003) suggested that community genetics may not be as important in highly diverse systems when species interact with a greater diversity of selective agents. Morin’s statement suggests that the importance of genetic variation for species interactions is a continuum where at one end of the community genetics spectrum, genetic variation is very important and at another, it is of no importance. As Strauss et al. (2005) emphasizes, populations of different species impose selection upon one another through traits. So, the likelihood that heritable trait variation in one species causes variation in the fitness of another (i.e., causing ecological and potentially evolutionary responses) depends not only on the existence of the pair-wise interaction but also on its contribution relative to all the other sources of selection. In other words, the importance of community genetics depends on how tangled the bank is.

We present a quantitative framework for considering selection caused by interactions between two or more species. To accomplish this goal, we: (1) assess the frequency of interactions among species as well as (2) the consequences of these interactions from a fitness standpoint, then (3) identify the relative contribution of selection acting within and among species to the total opportunity for selection acting within a community context and finally, (4) introduce “effective community diversity” as a measure of the diversity of selective agents one species faces. This approach has been introduced to understand the consequence for trait evolution of indirect genetic effects (IGEs) through interactions between individuals of the same species (Moore et al 1997; Wolf et al. 1998, 2001; Agrawal et al. 2001). The common thread between IGEs on trait evolution within species and trait evolution in a community context is that variation in fitness consequences of interactions has a genetic basis. Here, we expand the scope of IGEs from a social setting of individuals within species, to a community consisting of populations of individuals in multiple species, that is, to include *interspecific* indirect genetic effects, or IIGEs (Shuster et al. 2006). This approach provides a theoretical framework for measuring selection intensity within a community genetic context. Furthermore, it provides us with a quantitative method for evaluating the relative role of community genetics in communities that are species-rich versus those that are species-depauperate and/or those that are driven by foundation species (e.g., Ellison et al. 2005) versus those that are not.

THEORY – QUANTIFYING THE TANGLE

Community genetics can be thought of as the study of how heritable trait variation in one species causes natural selection to act on one or more other species. While it is not usually stated explicitly, the field of ecology could be synonymous with the study of the sources of natural selection. Community ecology would thus be the study of selection (the change in reproduction or survival) that comes from interactions among species. Furthermore, the strength of ecological selection is a function of the rate of interaction (often depicted with a mass action term) and the consequence of the interaction (often referred to as ** in Lotka-Volterra equations). For community genetics to be important, fitness response to interspecific interactions must vary between individuals and this variation must be explained by heritable variation in trait values, i.e., heritable variation in **.

To show how the likelihood of genetic variation in one species can influence the abundance of another, we first assume that the effect of genetic variation of one species on another is proportional to its selective influence. Strauss et al. (2005) points out, however, that the selective consequence of interactions between two species may be mediated by a third, so there is likely to be variation in the consequences of direct interactions that arise from variance in ecological contexts. In order to determine the total effect of species *j* on species *i*, one must account for all contexts in which species *i* and *j* interact and determine the net contribution to selection between each species.

Specifically, the effects one species has on another is nested within all ecological contexts in which the two species co-occur. If there are *n* species in a community, then the potential number of contexts for selection on species *i* is equal to 2n, and the number of these contexts that involve species *i* and *j* is equal to 2n-1. Under an assumption that interactions occur according to mass action, the probability that any community context *k* occurs involving species *i*,*Cik*,is simply equal to the product of the frequencies, *pi*, of the species present in that context, such that:

, (1)

where *xik* is equal to 1 if species *i* is present in context *k* and 0 if it is not. Summing C*ik* across all 2n contexts should equal 1. If interactions do not occur due to mass action, C*ik* would be estimated directly from observation of all contexts involving species *i*. For illustration we will assume interactions based on mass action.

To illustrate the theoretical context, consider four distinct types of ecological communities (Fig. 1). There are 10 species in each community but the frequency of the 10 species and structure of their interactions vary among the communities. In the “symmetrical” community (Fig. 1a), all possible interspecific interactions are present and equal in frequency. In a “variable” community (Fig. 1b), all interspecific interactions are present but species interactions vary in their frequency. In a community heavily influenced by a foundation species (Fig. 1c), all pairwise interspecific interactions are present but one species’ interactions is stronger than all others. Lastly, in a “sparse” community (Fig. 1d), there are 2 to 5 interspecific interactions (links) per species and the strength of these interactions vary (see Supplementary material for table of values).

FIG 1

Now consider that within each of the 10 species, there are differences between individuals in trait values that are important for fitness outcomes of interactions with the other species in these networks. In other words, for an individual of species *i*, there is a trait value that maximizes its fitness when interacting with individuals from a set of species *j*’s within each ecological context *k* (from equation 1)*.*  Moreover, species *i*'s maximizing trait value will depend on the particular individuals of each species *j*.

We recognize two main sources of fitness variation for species *i*: genetic variance within species *i* and fitness variance caused by different ecological contexts. The latter source of fitness variation represents a “tangled bank” of trait optima caused by ecological variation. Community genetics thus represents the extent that genetic variance within any one species contributes “tangledness” to the ecological bank. To formally quantify how tangled species *i*'s bank is and what contributes to the tangle, we quantify and partition species *i*'s opportunity for selection.

Estimates of the "opportunity for selection," provide an empirical estimate of selection intensity. Crow (1958; 1962) noted that the variance in fitness, *VW*, divided by the squared average fitness, *W*2, equals the variance in relative fitness, *Vw*, thus providing an upper boundary on the change in mean fitness itself, as well as on the standardized change in the mean value of all other phenotypic traits. The ratio, *VW*/*W*2= *Vw*, describes the “opportunity” for selection because not all fitness variation within a selection episode is heritable, and because by chance, an imperfect relationship exists between the actual variance in fitness, *VW*, and the expected covariance between phenotype (*z*) and relative fitness (*wz*), Cov(*z*, *wz*). Crow’s (1958) approach was extended by Wade (1979, 1995) to understand the sex-difference in the opportunity for selection. This sex difference in selection intensity determines whether and to what degree selection will cause the sexes to diverge in character. The total variance in relative fitness is informative because its value limits the potential strength of phenotypic selection on a suite of traits (Crow 1958, 1962; Wade 1979, 1995; Wade and Arnold 1980; Shuster and Wade 2003). We further extend Shuster and Wade’s approach to sexual selection to examine contributions to selection arising from different ecological contexts.

*Contribution to the tangled bank*

Assuming selection on a single trait *z* in species *i*, there is an optimum trait value for each context *k*, *k*, such that selection on trait z of species *i* in context *k, sik*:

 (2)

where  and  are the mean and variance of trait *z* in species *i* and ** is the selection intensity. For simplicity and ease of analysis, we assume that *k* arises from additive interactions of species *j*’s interacting with species *i*, such that , where *xjk* is equal to 1 if species j is found in context *k* and 0 if it is not; *zj* is the trait value of species *j* and *ji* is a scalar that converts units of species *j*’s trait into units of species *i*'s trait. The first term inside the parentheses of equation 2 represents evolutionary load while the second represents demographic load (Lande and Shannon 1996, Ronce and Kirkpatrick 2001). The fitness result for individuals of species *i* in context *k, rik*, is , where *ri* is intrinsic fitness. Thus, mean fitness for an individual within a panmictic population of species *i,* , is the sum of the selection intensities, *sik*, weighted by the likelihood of each ecological context, *Cik*, such that:

 (3)

The variance in fitness arising from different ecological contexts is simply the sum of squared deviations from mean fitness for context *k* weighted by the likelihood of context *k* occurring:

, (4)

and thus the total opportunity for selection on a single trait z in species i, as a result of selection in its individual as well as in its ecological context is the variance divided by the mean squared:

. (5)

This represents species *i*’s tangled bank of selection and the larger its ecological opportunity for selection, the more tangled its bank.

We can partition the total opportunity for selection into the contributions made by each ecological context and then determine the net contribution to selection from each species from its inclusion in each of *2n-1* contexts. Context *k’*s contribution to total opportunity for selection is simply its squared deviation from mean fitness divided by mean fitness squared:

. equation (6)

To partition the total opportunity for selection into contributions between two species, *j* with *i*, *Iij*, we determine the average contribution to the opportunity selection coming from each context *k* involving species *i* and *j, Cijk* . Thus *Iij* is simply*:*

, equation (7)

where , x*ijk* = 1 and *Iijk* = . Thus the relative contribution of species *j* to species *i*’s opportunity for selection, *ij*, is:

. equation (8)

Using the relative contribution to opportunity for selection, we can calculate the effective diversity perceived by species *i, DE,i*:

. equation (9)

Analogous to Simpson’s species diversity index (also the calculation for allelic diversity), a species’ effective diversity quantifies the relevant number of species that each species perceives from a total selection point of view. Therefore, each species within a community has its own perception of diversity or community size. While equation 5 measures the overall tangledness of the ecological bank, equation 9 quantifies the number of species contributing to it.

The consequence of genetic variation in one species for fitness variation in another (community genetics) is proportional to the relative contribution of species *j* to species *i*’s opportunity for selection, *ij*. In other words, we can quantify the covariance of fitness in species *i* with genetic variation in a trait of species *j*, *SGij* , as

 equation (10)

where is broad-sense heritability of trait *z* in species *j*, the total genetic proportion of variation in the ecologically relevant trait *z* of species *j*.

The theory presented builds from previous work by Shuster et al. (2006) in which they presented a quantitative definition of broad-sense community heritability,. It is worth repeating their definition to provide context of the theory here. “Community heritability should be proportional to the product of the broad sense heritability of the tree trait, **, used to identify genetically similar communities and the intensity of community-level selection, , relative to total selection in each ecological context, (*+En*). Thus, from equation 1 in Shuster et al. [2006],

, equation (11)

where  is broad-sense heritability of tree trait **, and  summarizes the intensity of the fitness consequences of genetic interactions between each arthropod species and its host plant.” Here, we have quantified the second term of the product on the right-hand side of the equation, such that is analogous to, defined in equation 8.

*Methods*:

We apply the theory above to quantify the covariance of species *i'*s fitness with trait values of species *j* and determine whether heritable differences in the trait values of species *j* are likely to alter the fitness of species *i* (c.f., equation 10), i.e., to determine when a community genetics perspective is necessary. To address this objective, we use the four community types presented above answer the following question: *How does variation among species’ effective community diversity affect the covariance of fitness in species j with traits of species i?* Using the four community structures, we calculated the marginal fitness response in all species to changes in trait values. To do this, we modified the trait value of one species *i* with19 discrete steps and measured the change in fitness in each species in the community arising from all 2*n-1* community contexts. We used Matlab (ver. 7.3.0; Mathworks, Inc., Natick, MA) for our analysis. The analysis will provide the covariance matrix of each species *j*’s fitness with trait value of each species i, *cov(rj, zi)*, and thus the interspecific indirect genetic effect is simply the broad-sense heritability of trait *zj* times *cov(rj, zi)*.

*Results and Discussion*

Our results show that as the interspecific variation in selection increases, effective community diversity decreases from the total richness of species in the community (see Figs. 2, 3) and that the genetic variation in one species is more likely to influence the fitness of another (see Fig. 4). Species in the symmetric interactions community all perceive the full diversity of species in the community and have the largest effective community diversity. Variation in strength and frequency of interactions reduce effective community diversity. Foundation species that provide the major sources of interspecific selection reduce effective community diversity even further. Few and varying interactions further reduce effective community diversity.

FIG 2

We also found that a species’ effective community diversity (*DE,i*) is negatively correlated with the maximum covariance between its fitness and the trait value of an interacting species (Fig. 3), and generally, as the number of interactions decline or as variation in selection among species increases, each species’ effective community diversity decreases. In particular, when compared to species that are not foundation species, trait variation within a foundation species *i* has a much greater influence on its interacting community, as measured by the average fitness of interacting species *j’s* (Fig. 4).

The important conceptual advance and practical implication of defining a species’ effective community diversity is that the genetic analyses of relative few species may tell us much about the structure and evolution of much larger communities. This perspective may allow us to understand how communities with vastly different species richness may or may not fundamentally differ in the number of species that define and structure these communities. Furthermore, it is likely that even where one sees hundreds of species in a community, the *effective community diversity* of each species is much lower than the total number of species present (Fig. 2). Many species simply do not interact with sufficient frequency or adequate intensity to affect the outcome of total selection acting within the community. In contrast, interactions among foundation species such as beaver (*Castor canadensis*) and riparian cottonwood trees (*Populus* spp.), can determine whether habitat type is riparian or dry grassland (Chadde and Kay 1991) thereby defining the community and imposing disproportionate selection upon a large number of species. While100s if not 1000s of species that may exist in such circumstances, the overwhelming influence of foundation species reduces the effective community diversity to a much smaller, functional number.

FIG 3

*The importance of a community genetics perspective*

If community genetics is important when few species impose disproportionate affects on many other species (Fig. 4), it is important to ask if few interactions are rare or common in ecological systems. Dunne et al. (2002) reviewed the topology of 15 aquatic food webs from various environments (5 ponds, 5 terrestrial, 2 streams, and 3 estuaries) and showed that species vary in their overall connectivity and number of links per species (one can think of links per species as a species’ perception of richness). They observed that 25-40% of species in these food webs have 3 or fewer direct connections and the average links per species is much lower than the total number of species. When viewing food web diagrams, we encourage the reader to consider the number of links (i.e., the richness of interactions) coming from each species because there are likely to be few. Species certainly don’t directly interact with all other species. These observations indicate that many species are likely to have low effective community diversity. In these cases, genetic variation in a few species, especially foundation species, could affect the evolutionary and ecological dynamics among many other species in these communities.

FIG 4

Because foundation species likely have the largest selective influence on the other species (Fig. 4), they reduce the effective community diversity of all other species (Figs 2 and 3). Heritable variation in one species will likely cause fitness or ecological variation in another when it is the dominant ecological selective force. Although few studies have experimentally examined the strength of genetic-based links between a foundation species and a dependent community, they can be surprisingly strong and require few steps. For example, Dickson and Whitham (1996) explored how the interaction between aphid resistant and susceptible cottonwood trees affected a much larger community. They found that susceptible trees supported 31% greater species richness and 26% greater relative abundances than resistant trees (Dickson and Whitham 1996). Because this analysis included 42 arthropod taxa from 35 families and 14 orders (herbivores, predators, and parasites), this represents a clear case of greater biodiversity being associated with susceptibility. They then removed the aphid from susceptible trees to see if the genetic-based interaction of the aphids with the tree was responsible for the community differences or if independent of the aphids, the genetic differences between tree phenotypes acted directly on the community. They found that with the removal of the aphids, the communities of susceptible trees were very similar to resistant trees arguing that interspecific, indirect genetic effects (IIGEs) between two foundation species (i.e., tree and aphid) defined a much larger community. Studies by Keith et al. (2010) also show that the same aphid has a stabilizing effect on the arthropod community such that trees with aphids have more similar communities year-after-year than resistant trees without aphids, and that community stability can be quantified as a heritable plant trait mediated by the presence of aphids. In addition to arthropods, Dickson and Whitham (1996) also found that a fungal parasite and avian predators were affected by the presence of aphids. See also Crawford et al. (2007) for similar findings using a removal experiment with gall makers on goldenrod.

In contrast to the previous two examples, Sthultz et al. (2009) found just the opposite effect; scale susceptible and resistant pines supported very different mycorrhizal communities (21 taxa in two divisions), but with the 20 yr removal of scale insects from susceptible trees that had recovered from scale attack, the mycorrhizal community was still the same as control susceptible trees that had lost most of their foliage. Thus, in the first case, two links defined the community in which plant genetics interacted through an herbivore to define the community. In the second case, only one link was required; plant genetics defined the mycorrhizal community independent of scale insects. Such examples support our models in which IIGE among species need not be diffuse or complex; and that effective community diversity, *DE* can be a very small subset of the whole community.

Scenarios also exist in which potentially strong genetic interactions among species have little impact on the outcome of selection within communities because the species rarely interact. For example, Hubbell’s (2001) neutral theory describes the dynamics of tropical forests, wherein high species diversity makes the frequency of interactions between individuals of any two species very low. In this situation, the fitness consequence of interspecific interactions could be high, but the frequency of particular interactions within the community is so low that the effect of any one species on another is close to zero. Thus, while effective community diversity within a trophic level could be high the system is effectively neutral with respect to evolution in a community context. Under such circumstances, genetic variation in one species is likely of little consequence for the evolutionary and ecological dynamics of another.

While Hubbell’s theory does not address interactions between trophic levels , it is possible that frequent and strong interactions between species of different trophic levels could cause the effective community diversity to be low across trophic levels, e.g., plant-pollinator interactions. Because many such trophic interactions occur (e.g., plant-herbivore, predator-prey, parasite-host, plant-fungal), it is important that future studies critically examine the relative contribution of these important interactions on effective community diversity. Importantly, to confirm either neutral or non-neutral hypotheses in a community context, it is important to experimentally confirm either case as was done with the experimental removal of species as in (Dickson and Whitham 1996; Crawford et al. 2007; Sthultz et al. 2009).

By illustrating the importance of selection and genetic variation for ecological dynamics, community genetics provides a predictive ecological and evolutionary continuum from Ehrlich and Raven’s observations of coevolution to Hubbell’s neutral theory. When, as Hubbell suggests, interactions between species are many and too diffuse for interactions between any two species to predict the change in community structure over time, then genetic variation within any one species also is of no importance for those interactions (dashed line in Fig. 4). By contrast, in strict pairwise coevolution, one species accounts for all the ecological selection of another and vice-versa; their effective community diversities are one,the effective community for one species is represented by the other, and heritable variation in each species is of great importance. The connection of these theories resides in the proportion of one species’ total ecological selection that is comprised by another. Thus, if interspecific interactions (i.e., ecological selection) are important for predicting community structure, then heritable variation in traits that cause ecological selection is also likely to be important. As species’ effective community diversity increases from one towards infinity, we move from an ecological, selection-driven world to a neutral, drift-driven world.

Network theory considers similar relationships among species (refs and possible additional review of this area). While this approach does consider the relative “centrality” of particular species in terms of the number of connections that exist between it and other members of the community, it does not provide a means for assessing how centrality or the lack of it may influence the intensity of selection responsible for shaping community organization. Community genetics seeks to describe forces that influence community organization within an evolutionary context. Our approach for estimating effective community diversity, *DE*, examines how genetic variation in within species influences the fitness consequences of interspecific interactions in other species, and weight their overall effect by their relative frequency and intensity. Our approach thus provides a method for understanding community organization that is as empirically straightforward as network theory, and is consistent with community genetics theory (or some shit like that).

*Conservation implications*

The concept of effective community diversity may have important conservation implications. When a community is largely characterized and ecologically dominated by a few species, then genetic variation within these foundation species and their interactions may be crucial to the conservation of the rest of the community. Because these types of species effectively drive effective community diversity down, genetic variation within these species represents niche variation for dependent species (Fig. 5).

This approach differs from other conservation genetics approaches that emphasize the conservation of genetic diversity in rare and endangered species, and have resulted in concepts such as MVP, the minimum viable population needed to maintain a species (Schaffer 1981). Our findings derived from effective community diversity, *DE*, argue that it is important to consider the minimum viable interacting population size (MVIP – Whitham et al. 2003) that represents the size of a population needed to maintain the genetic diversity at levels required by *other* dependent and interacting species. Thus, the minimum viable population (MVP) sizes for conserving the target species are probably much smaller than what is required to conserve other community members that might be dependent upon those interactions for their survival. An understanding of community genetics and effective community diversity should broaden conservation goals because genetic variation is linked not just to single-species survival, but also to patterns of interactions among species (see also McIntyre and Whitham 2003; Booth and Grime 2003; Wimp et al. 2004, Bangert et al. 2005; 2008; Evans et al. 2009).

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**Tables**

Table 1. List and definition of terms used in the theory.

|  |  |
| --- | --- |
| *Term* | *Definition* |
| *pi* | Frequency of species *i* in the community |
| *Cik* | Probability that any community context *k* occurs involving species *i* |
| *sik* | Selection on a trait of species *i* in ecological context *k* |
| *k* | Optimum trait value for each context *k* |
| ** | Selection intensity |
|  | Mean of trait *z* in species *i* |
|  | Variance of trait *z* in species *i* |
| *ji* | A scalar that converts units of species *j*’s trait into units of species *i*'s trait |
| *rik* | Fitness for individuals of species *i* in context *k* |
|  | The total opportunity for selection on a single trait z in species i, as a result of selection in its individual as well as in its ecological context |
|  | The relative contribution of species *j* to species *i*’s opportunity for selection |
| *DE,i* | The effective diversity perceived by species *i* |
|  | Broad-sense heritability of trait *z* in species *j* |
| *SGij* | The covariance of fitness in species *i* with genetic variation in a trait of species *j* |

**Figure Legends**

Figure 1. Four communities with identical number of species that vary in the structure of interactions. A is a “symmetric” community in which all pair-wise interactions are identical in strength and frequency, B is a “varying” community in pair-wise interactions vary among species, C is a community in which a foundation species defines community interactions. D is a “sparse” community where not all species interact and the interactions vary. The width of the line is an indication of selective influence that comes from interactions between two species. We define selection as the product of the frequency of interaction and the consequence of the interaction.

Figure 2. Variation in strength and number of interactions reduces species’ effective community diversity.

Figure 3. The maximum covariance between species i's fitness and species j's trait value declines as its effective community diversity (*DE*) increases. The maximum covariance represents the species *j* that has the largest selective effect on species *i* of the *n* species in the community. As the variation in strength of interspecific interactions increases, effective community diversity decreases further from the total number of species in the community and genetic variation in one species is more likely to influence the fitness of another.

Figure 4. Trait changes in foundation species have much stronger effect on species’average fitness than non-foundation species. Thus, community consequences of heritable trait variation are more likely to be detected in foundation species and with species that have low effective diversity than species with non-foundation species that have high effective diversity.



Figure 1.



Figure 2.



Figure 3.



Figure 4.