Evolution in metacommunities

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A metacommunity can be defined as a set of communities that are linked by migration, and extinction and recolonization. In metacommunities, evolution can occur not only by processes that occur within communities such as drift and individual selection, but also by among-community processes, such as divergent selection owing to random differences among communities in species composition, and group and community-level selection. The effect of these among-community-level processes depends on the pattern of migration among communities. Migrating units may be individuals (migrant pool model), groups of individuals (single-species propagule pool model) or multi-species associations (multi-species propagule pool model). The most interesting case is the multi-species propagule pool model. Although this pattern of migration may a priori seem rare, it becomes more plausible in small well-defined 'communities' such as symbiotic associations between two or a few species. Theoretical models and experimental studies show that community selection is potentially an effective evolutionary force. Such evolution can occur either through genetic changes within species or through changes in the species composition of the communities. Although laboratory studies show that community selection can be important, little is known about how important it is in natural populations.

Keywords: metacommunity; indirect genetic effects; epistasis; multi-level selection; community evolution; coevolution

1. INTRODUCTION

The evolution of communities is generally considered to occur by processes of individual selection acting within the individual community. From this perspective, community evolution can occur by the gain and loss of species, and by genetic changes occurring within species. Such evolutionary changes are limited to changes occurring as a result of individual selection, and any adaptation that occurs can only be adaptation of the individual to its environment. When a community is spatially subdivided, that is, it is a 'metacommunity', a much richer range of evolutionary forces becomes possible [1].

Evolution within a single community can only proceed by selection among units within that community. Thus, the primary evolutionary change of interest will be classical coevolution. Such coevolution occurs when there are reciprocal selective pressures on traits in separate species [2], a process that, at least for individual selection, is well understood (e.g. [3]). In this coevolutionary process, the selection that is being exerted on one species is a function of the character state of its 'partner' species; however, this partner species is effectively a part of the environment. Although the partner species is part of the environment, it is of course true that it will evolve over time; thus both species will be evolving to the continually changing environment provided by their partner species. Thus, processes that have been described as 'coevolutionary arms races' can occur. When a community is divided into isolated 'sub-communities' to form a metacommunity, coevolution can occur through processes that are qualitatively distinct from the simple pairwise individual selection described by Janzen [2].

2. FACTORS AFFECTING METACOMMUNITY EVOLUTION

In a metacommunity, there are three factors I will discuss that may affect metacommunity evolution. First, the subdivision of the community into smaller communities will mean that not all communities will have identical species compositions, and that evolution can proceed by changing the presence and absence or the abundance of individual species, irrespective of genetic changes that may occur within the individual species. Second, the species that are present in a community will have smaller population sizes, and there will be opportunities for them to differentiate among communities either by genetic drift, or by selection in communities that differ in their composition. Finally, with a subdivided community, there is the potential for multi-level selection, both at the single-species group level and at the whole community level. These different processes are not independent; for example, shifts in the species present in a community will change the population sizes of the other species, and the selection pressures acting in the communities; thus, changes in community composition can potentially affect the within-species differentiation...
of populations through selection and drift. Similarly, changes in genetic differentiation and species composition will change the nature and response to multi-level selection.

These three factors are tied together by a fourth factor, and that is how communities are founded. To introduce this it is convenient first to consider single-species groups. Wade [4] made a distinction between populations founded via a ‘migrant pool’ model and a ‘propagule pool’ model. In the migrant pool model, individuals migrate out of their natal population and then group randomly to form new populations. In contrast, in the propagule pool model, groups of individuals migrate from the natal population and together found a new population. The difference between these two models is telling. In the migrant pool model, migration is a homogenizing force that tends to reduce variance. By randomly sampling from a set of natal populations any genetic differences that arose among those populations is reduced by the migration process. In contrast, in the propagule pool model, because groups of founders migrate from a single natal population to found a new population, genetic differences among populations are preserved, and because the founder propagules are a small subset of the natal population they may even enhance the differentiation of populations [4].

Moving this model to the community level, there are two levels at which ‘propagules’ can be recognized. As with the single-species populations, individual migrants or propagules may migrate to found new communities. In addition, propagules may consist of single species migrating independently of other species (single-species propagule pool), or they may consist of multi-species assemblages (multi-species propagule pools; figure 1). As with the single-species migration structure, the pattern of migration of communities can profoundly affect the response to selection. The importance of this distinction between single-species propagule pools and multi-species propagule pools will be discussed below.

The potential for multi-species propagule pools depends on the type of community being considered. At one extreme, there are large communities, such as forest communities consisting of many species of trees, shrubs, vertebrates, arthropods and other organisms. Such communities are unlikely in the extreme to migrate together to found a new community. In the middle may be communities such as the arthropod communities on trees [5]. In most cases, these communities probably are colonized by migrant pools and single-species propagule pools; however, there is the potential that community colonization by a multiple-species propagule can occur. For example, a multi-species propagule could result from a phoretic species riding on its host. Finally at the opposite extreme are communities that show adaptations that specifically promote the movement of propagules of intact communities. Examples of this include lichens that have isidia or soridia, small packets of fungal hyphae and algal cells that are wind dispersed [6], Atta ant queens that carry packets of symbiotic fungi that they use to found their new colony [7], and

Figure 1. Three models of migration. (a) Migrant pool—individuals migrate independently to found the next generation. Each ‘offspring’ community is the result of mixing of individuals and species from many ‘parental’ communities. (b) Single-species propagule pool—groups of the same species migrate to found new populations. Within each offspring community, the constituent species each come from one community (or a few communities), but the different species come from different communities. (c) Multi-species propagule pool—groups of two or more species migrate to form new populations. The entire offspring community or a multi-species subset of the offspring community comes from a single parental community.
burying beetles that carry with them phoretic mites [8]. Finally, real communities may well be founded by a mixture of migration patterns, with some species migrating in as individuals (migrant pools), others coming in as single-species propagules, and still others arriving as multi-species propagules.

3. EVOLUTION IN METACOMMUNITIES

Once communities are formed, evolution in a metacommunity can occur by selection and drift acting within individual communities, but it can also occur through a process unique to the metacommunity structure. Selection and drift acting within communities should proceed following the standard population genetics theory. In brief, genetic drift and potentially random extinctions will randomly change the genetic structure and the species structure of each community. Selection acting on individual-level fitness differences will then act within the framework of this individual community. In addition, it is important to recognize that the random forces of drift and random extinction, and colonization will cause the different communities to vary in the specific species present in each community, and in the genetic makeup of those species. As a result, to the extent that individual selection results in adaptation to the specific details of the community in which a population is found, selection will act differently in different communities, and drive increased community divergence.

If migration levels are high, species may adapt to the weighted average of the community types rather than to the individual communities. As a consequence, a species may adapt relatively rapidly to common community types, but only vary slowly to rare community types. This will be particularly interesting if there is a negative genetic correlation between the fitnesses in the different community types. This is a situation that is similar to the evolution of phenotypic plasticity models explored by Via & Lande [9]. In this case, a species potentially may fail to adapt to the rarer community types because of the negative genetic correlation. As an example, consider that a predator may not be able to adapt to a particular prey species if the prey species occupies only a few communities, even if that prey species is abundant where it does occur. Thus, the prey species may avoid being the focus of predator adaptation by being globally rare, even if it is locally abundant.

No models are available demonstrating that interactions among species can lead to selectively driven diversification among communities, although a similar effect is seen in the diversification of single-species populations when there is gene interaction (dominance or epistasis). In a series of models [10,11] I defined the local average effect of an allele to be the subpopulation-specific average effect of an allele on the phenotype of an individual measured as a deviation from the metapopulation mean. Note that this differs from the standard concept of average effect [12] in that an allele has only a single average effect, but may have different local average effects in each subpopulation of a metapopulation. In these models, I demonstrated that when there were only additive effects the local average effect of an allele (adjusted for the population mean) was constant; however, when there was gene interaction it was no longer constant. This means that alleles that have a positive effect on the phenotype in one subpopulation may have a negative effect in other subpopulations. As a result, even if selection is acting in the same manner in all subpopulations, when there is gene interaction it can become a diversifying force causing demes to differentiate genetically.

A similar effect will be seen in a metacommunity. If there are indirect genetic effects [13,14] between species this will have the potential to change the local average effects of alleles in one species based on the presence or absence of other species in the community, or because of different genetic strains of other interacting species. If communities are established by a migrant pool or a single-species propagule pool then these indirect genetic effects will behave as environmental effects. This is because migrants leaving one community and entering a new community will experience a new multi-species genetic environment. Thus, the interspecies’ indirect effects will be experienced as a genotypic effect by environment interaction. By contrast, if migration occurs as a result of multi-species propagule pools then the propagules have the potential to carry the interspecies indirect genetic effects with them. In this case, because interacting species move together between communities, the interaction is transferred with the propagule, and the interaction can move from being a part of the environment to being a heritable component of variation.

When this variation among communities is coupled with extinction and recolonization [15] or differential migration among communities [16], it is possible that community-level selection can occur [17–20]. Following a definition consistent with contextual analysis, community selection occurs when the fitness of an individual is a function of community membership ([21], see also [22–25]). Alternatively, following Wade [26], community selection may be defined as the differential survival and/or reproduction of communities. These two definitions are consistent with each other; however, the contextual analysis definition is both more general and more controversial.

There have been two experimental studies of the response to community selection, one by Goodnight [17,18] examining the response to selection in two-species communities of the flour beetles *Tribolium castaneum* and *Tribolium confusum*, and the second by Swenson et al. [19,27], examining the response of communities of water and soil micro-organisms to selection on community-level traits. Importantly, the *Tribolium* experiments focused on communities with fixed species compositions, and thus only genetic changes could occur, whereas the micro-organism communities used in the experiments of Swenson et al. were diverse communities in which the response to selection appeared to occur primarily through changes in community composition. Both of these sets of experiments used a multi-species propagule pool. By contrast, Wilson [20] theoretically examined community evolution with a migrant pool.
4. EVOLUTION WITH FIXED SPECIES COMPOSITION

Goodnight's [17,18] selection experiment using Tribolium illustrates several important features of community-level selection [1]. In this experiment, there were eight different treatments, each with two replicates, for a total of 16 independent selection treatments. Each selection treatment was a metacommunity consisting of 10 two-species communities, and the 'communities' consisted of two species of Tribolium flour beetles, T. castaneum and T. confusum. These two species are fierce competitors, and the environmental conditions were set so that the two species were almost equal in competitive ability [28]. In continuous culture, one of the two species would have driven the other to extinction; however, competitive exclusion was prevented by transferring 16 individuals of each species to the next generation.

In each community, four traits were measured. These were population size in T. castaneum, population size in T. confusum, emigration rate in T. castaneum and emigration rate in T. confusum. Each of the independent selection treatments consisted of community selection either up or down for one of the four traits. Note that although these are traits measured on the individual species, because these two species are strong competitors all of these traits have the potential to be influenced by heritable factors in both species.

Selection was performed by measuring the four traits, ranking the 10 communities in a metacommunity by the value of the trait under selection in that treatment, and choosing the five most extreme communities to be found in the next generation. Each of the surviving communities founded two communities in the next generation using a multi-species propagule pool model.

The main result of this study was that community selection was effective. A significant response to selection was seen for all four traits (e.g. figure 2). This alone was important because community selection has much in common with group selection, which has often been considered to be less effective than individual selection (e.g. [29], but see [4]). There were a number of other interesting results from this experiment as well.

First, a number of correlated responses to selection were observed. These included both within species, and more significantly, between species correlated responses to selection. For example, selecting on population size in T. confusum led not only to an increase in T. confusum population size, but also to an increase in T. castaneum emigration rate (figure 3). These interspecies correlated responses can only occur if there are between-species indirect genetic effects. That is, a response to selection, in a species such as these without cultural inheritance, will necessarily involve changes in gene frequency in the individual species. An interspecies correlated response to selection implies that at a minimum a genetic change in one species is affecting traits in both species. This provides direct evidence that community selection can act on interspecies indirect genetic effects [14].

Second, in a follow up study to the selection experiment, I examined the genetic basis of the observed responses to selection [18]. To do this I took the intact communities from the selection experiments and subjected them to three different treatments. The first treatment was simply the intact community with both species present. In the second treatment, I set up single-species populations from the two-species communities, and in the final treatment, I set
up two-species communities; however, only one of the species was from the selection treatment, with the second species having come from a naive test strain (figure 4). The intact communities confirmed that all of the traits showed a significant response to selection (assay A). By contrast, the response to selection was not observable in any of the single-species populations (assay B). This indicates that the ecological or genetic structure of the community was required for the responses to selection to be observed. From this assay alone it is not possible to tell whether the lack of response to selection is because of an evolved interaction, or because there is a genotype by environment interaction such that the responses to selection are only observed in the intact community. The reconstructed communities (assay C) were important because they restored the ecological setting of the communities, but nevertheless disrupted the genetic setting of the selected communities. In this assay, an interesting divergence of results was observed. In the treatments in which there was selection on emigration rate, the response to selection was restored in the reconstructed communities. This indicates that much, if not all, of the genetic basis for the response to selection was in the species selected, and was only expressed in the community setting. By contrast, in the treatments in which there was selection for population size, the response to selection completely disappeared in the reconstructed communities. This indicates that the response to population size resided entirely in the interaction between the two species, and that the selected strains of both species needed to be present for the response to selection to be expressed.

It is interesting to compare this with another study on similar, but unselected, communities. In this study, Goodnight & Craig [30] examined the effects of coexistence on competitive outcome. They compared the competitive outcome of communities that had been allowed to coexist for 18 generations by individual selection with communities that had been maintained for the 18 generations as separate single-species populations and had been placed in two-species communities for the first time. We found that there was substantial genetic variation among communities, and that the communities would respond rapidly to community-level selection, but that there was no detectable difference between the coexistence and the single-species communities. This study indicates, that in agreement with other studies [31,32], there is no evidence that competitive ability can evolve by individual selection. However, there is substantial evidence that community selection would be successful in changing competitive outcome.

The conclusion that community selection, but not individual selection, can modify competitive outcome makes sense if it is recognized that competition is an interaction between individuals. As a consequence, there is a strong potential for interspecies genetic interactions (interspecies epistasis) and indirect genetic effects that affect competitive ability to be high. In his classic work on what are now called indirect genetic effects Griffing [33], considering only single-species populations, demonstrated that individual selection could not act directly on indirect genetic effects; however, group selection was able to act on indirect effects. As a consequence, for traits involving substantial interactions among individuals, individual selection would typically be ineffective or even counterproductive, whereas group selection could act on these interactions and would therefore be far more effective. In a similar manner it makes sense that, consistent with the lack or response to coexistence, selection within communities could not act on interspecies indirect effects and epistasis, whereas community selection could act on these interactions, and would lead to a response to community selection.

5. EVOLUTION THROUGH SPECIES REPLACEMENTS IN METACOMMUNITIES

In the experiments described above, the number and identity of the species were fixed, and any evolutionary change occurred as a result of genetic changes within the species. It is also possible for evolution to occur through changes in the species present in the communities. Wilson [20] developed a model in which metacommunities diverge and evolve as a result of changes in species present in the communities. Wilson examined a situation in which sub-communities within the metacommunity were established by randomly sampling a fixed number of individuals from a pool of 10 species. Because of the random sampling, the sub-communities consisted of a subset of the 10 species with the initial population density for each species also being random. In some simulations, all 10 species were forced into each community by assuming that there was a minimum background density maintained by continual low-level migration. Species interactions were initially modelled using Lotka–Volterra competition equations involving competitive interactions among all of the species within the community weighted by their frequency. In a second set of simulations, the simple
two-species interaction coefficients were replaced by three species interaction coefficients. Thus, for example, the interaction term $\alpha_{ijh}$ was defined as the effect of species $j$ on species $i$ in the presence of species $h$ (see [20] for the details of this model). The final interaction between a pair of species ($\alpha_{ij}$, the effect of species $j$ on species $i$) was taken as the weighted average of the three way interactions taken across all of the species present in the community. An important result of this model was that the initial founding conditions of the sub-communities strongly affected the within-community dynamics, and the same set of interaction coefficients could develop communities that shared no species in common. It is apparent that in these simple models there were multiple stable communities, and which species set a community evolved towards depended on the initial founding conditions. This becomes particularly apparent because, as mentioned above, in many of the simulations all species were forced to be present at a minimal frequency. Thus, the different community compositions evolved in spite of the fact that all species were present at some level in all communities.

Wilson [20] also examined the potential for community-level selection by examining the effects of multiple iterations of random community formation and dispersal back into a global migrant pool. In the simulation he identified a focal species, and made the probability of extinction of the sub-community a function of the frequency of the focal species in the community. He found that when he exerted this selection pressure, the frequency of the focal species rapidly declined, and that the global frequencies of the other species adjusted such that there was a high probability that communities that suppressed the focal species would be formed.

This model is important in that it illustrates that community evolution can occur strictly by species replacements with no genetic changes taking place within the species themselves. Important, in the simulations in which the community-level selection was applied he found that this higher level selection force could lead to adaptive evolution in the form of changes in global species abundances that favoured communities that suppressed the focal species that was disrupting the community.

In a separate study, Swenson et al. [19,27] experimentally examined a situation that was analogous to that modelled by Wilson. Their study reports on two independent experiments; however, the first experiment examining the evolution of soil communities illustrates the results adequately. In this study, the sub-communities were obtained by sampling soil from a forest and using sterilized water to extract a representative biotic community from the soil. Each sub-community consisted of a single pot of sterilized soil inoculated with soil extract, and 50 surface-sterilized Arabidopsis seeds. The trait selected was the above-ground biomass of Arabidopsis (figure 5). Each generation, after assessing the above-ground plant biomass in the up treatment, the three pots with the highest (or lowest in the down treatment) above-ground biomass were selected, and the soil from these pots was combined and used to inoculate sterilized soil used in the next generation. The plants for each generation were drawn from a constant stock population. Thus, the plants were genetically constant, and any response was due to changes in the soil community composition.

As with all multi-level selection experiments [34], there was a rapid response to selection. Unfortunately, soil communities are difficult to measure, and Swenson et al. [19] were not able to measure the species composition of the soil communities, but they were able to demonstrate that the soil nutrients in the up and down lines were significantly different, with the up line having higher levels of potassium, zinc and phosphorus than the down line. Even without the species composition data, their results are consistent with the Wilson model. That is, it is very probable that the response to selection that they observed took place primarily by species replacements, although genetic changes within species cannot be ruled out.

6. CONCLUSIONS

These laboratory studies and models of community evolution make several important points. Most important is to recognize that the members of a community interact, and because of these interactions, the effects of genetic changes may be seen in species other than the species in which the genetic changes occurred. The consequences of these indirect effects will depend on the level at which the selection is acting, and on the manner in which new communities are founded. We can recognize three possible levels of selection: individual selection, single-species group selection and multi-species group selection, and three forms of migration: migrant pool, single-species propagule pool and multi-species propagule pool. This results in nine possible combinations of selection and migration pattern. It is excessive to discuss all nine of these possibilities; however, it is worth contrasting several of the possibilities.

First, it is instructive to contrast individual selection and migrant pool migration with community selection and a multi-species propagule pool migration. If selection is acting at the individual level, and communities are founded by migrant pool migration then indirect genetic effects and genetically based interactions will be the evolutionary equivalent of environmental effects. As Griffing [33] has pointed out, in many cases these indirect effects will be negatively correlated with the direct effects. In other words, in many cases, a response to individual selection in one species will have negative fitness consequences for other interacting species, and quite probably for the community as a whole. Thus, we can expect that in many cases pure individual selection will be disruptive to community function and cohesiveness. By contrast, community selection acts on the community as a whole. Not surprisingly, it can act on all of the genetic effects and interactions that are internal to the community [35]. If, furthermore, communities are founded by multi-species propagule pool migration, then these interactions will be transferred intact between generations. Thus, we should expect community-level selection to favour a balance of direct and indirect effects that maximizes the overall fitness of the community.

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If selection is acting solely at the level of the individual, then it is interesting to contrast the migrant pool with the multi-species propagule pool migration. From the perspective of community evolution, this is most interesting from the perspective of coevolution. If migration is based on a migrant pool (or single-species propagule pool), classical reciprocal individual-based coevolution can potentially occur, but such coevolution will be one species adapting to the metacommunity average for the interacting species. If migration takes the form of a multi-species propagule pool, the same, generally, negative effects of individual selection on community would be expected. However, the multi-species propagule pool should allow coevolution between pairs of specific strains of interacting species, rather than to the average of the competitive pair to occur. Goodnight [36] looked for, but was unable to detect, this kind of coevolution in competing strains of *T. confusum* and *T. castaneum*. Although this one experiment failed to detect such coevolution, the possibility that it can occur cannot be ruled out.

At the opposite extreme it is useful to compare the effects of community selection under a migrant pool (or single-species propagule pool) model with the response under a multi-species propagule pool model of migration. Community selection, can act on any genetic effects that are within the community. Goodnight [18] showed that in his two species *Tribolium* system, migration and population size were qualitatively different in how they responded to community selection. In the case of migration, the response to selection was observed not only in the intact communities, but also in the reconstructed communities. In these reconstructed communities only the selected strain of the species expressing the trait was present, with the competing species being a standard laboratory strain. This suggests that migration would have responded to selection under any of the three migration models. That is, even if the community is broken up, each generation community selection will still be effective at changing the migration rate. By contrast, Goodnight [18] only observed a response to selection for population size in

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Figure 5. Results of Swenson et al. [19] ecosystem selection experiments expressed as deviations from the overall means. (a) Difference between above-ground biomass of *Arabidopsis thaliana* grown in soils selected for high and low biomass with 6.0 g inoculum. (b) Difference in above-ground biomass with 0.06 g inoculum. Open upward-pointing triangles are communities selected for high value of the trait, solid downward-pointing triangles are communities selected for low values of the trait. Stars indicate significant differences. (Reprinted from [19]).
the intact communities. This indicates that the response to selection resides in a genetic interaction between the two species, and that the response to community selection would be far greater when the two species migrate together in a multi-species propagule pool than in either a migrant pool or in a single-species propagule pool. Thus, in the migrant pool form of migration, community evolution should be limited to adaptations that are due to genetic changes that are entirely within a single species. On the other hand, a multi-species propagule pool will allow multi-species genetic interactions to evolve in which interacting genes affecting community-level fitness are distributed across two or more species. It is this sort of distributed response to community selection that contributed to the response to population size in Goodnight’s [18] study.

Although less is known about evolution through species replacements, it is reasonable to suspect that the same general issues arise. As an adaptive process, community evolution by species replacements can only occur through community-level selection. Pure individual selection and single-species group selection are forces that act within species, and species replacements are necessarily a multi-species process. Nevertheless, the distinction between the migrant pool and the single- and multi-species propagule pools will influence the evolutionary process. Particularly relevant here is Wilson’s [20] simulation in which community-level selection was imposed that favoured reducing the frequency of a focal species. In this simulation, Wilson observed adaptive changes in community composition that suppressed the frequency of the focal species. It is tempting to speculate that this process might have been faster had he used a multi-species propagule pool model of migration rather than a migrant pool model, the reasoning being that sets of species that were particularly good at suppressing the focal species would migrate together in the multi-species propagule pool. This may have allowed the evolution of favourable multi-species interactions in a way that would not have been possible with the migrant pool.

Much remains to be done examining the metacommunity genetics, and selection and evolution at the community level. There have been only two sets of experiments [17–19,27] examining community-level selection, and only one model of community selection [20]. These experiments and models have established that evolution by community selection can be an effective force in the laboratory. What is needed is some sense as to how strong community-level selection is in natural populations. Specific experimental protocols for studying community selection in natural populations have not been described; however, methods, such as contextual analysis (e.g. [37–40]), that have been developed for studying single-species group selection in natural populations, should be readily adaptable to studying community selection. As important is examining the heritability of community-level traits. This will be complicated by the difficulty of defining how the heritability of such traits should be measured, but an understanding of the mechanisms by which communities are founded would go a long way towards addressing this problem. It will not be an easy task to study community selection in nature; however, the question of how important it is in evolution is an empirical one that can only be answered by empirical studies of natural populations.

REFERENCES


