Community-level evolutionary processes: Linking community genetics with replicator-interactor theory

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Understanding community-level selection using Lewontin's criteria requires both community-level inheritance and community-level heritability, and in the discipline of community and ecosystem genetics, these are often conflated. While there are existing studies that show the possibility of both, these studies impose community-level inheritance as a product of the experimental design. For this reason, these experiments provide only weak support for the existence of community-level selection in nature. By contrast, treating communities as interactors (in line with Hull's replicator-interactor framework or Dawkins's idea of the "extended phenotype") provides a more plausible and empirically supportable model for the role of ecological communities in the evolutionary process.

community genetics | multilevel selection theory | replicator/interactor | extended phenotype

Evolutionary processes in multispecies assemblages have far-reaching scientific, policy, and even ethical ramifications. Symbioses such as lichens and eukaryotic cells demonstrate that new Darwinian individuals can evolve from once-separate evolutionary lineages, given "vertical inheritance" (1, 2). Such transitions are limited, however, to only a few species. Whether higher-level ecological structures comprising many species could equally be subject to natural selection remains an open question in "macrobial" (3–7) or microbial communities (8–11). The emerging field of *community and ecosystem genetics*, focused on genetic interactions in manipulated and natural environments and communities of many species of multicellular eukaryotes, specifically addresses the role of selection operating at multiple levels of organization (reviewed by Whitham et al. in 12). A novel aspect is the application of the tools of multilevel selection theory [MLST (13)] to communities without any expectation that they have undergone an evolutionary transition in individuality (2).

There is little debate about individual-level selection in a community context. Such selection can drive lineage-specific adaptation and reciprocal evolution between species (coevolution). Further, multispecies systems of genes are involved in ecosystem engineering and likely evolve according to the ecological constraints affecting individual-level fitness (14). However, do complex ecological assemblages form entities subject to evolution by natural selection at their own level, as "units of selection"? If ecological assemblages are higher-level units of selection, their collective ability to respond to their environment could be significant for surviving climate change (12, 15).

Multispecies evolutionary dynamics can often be explained by selection on individuals. So whether communities act as cohesive wholes or collections of independent populations has been debated since the 1920s (16–18). Even detecting whether populations causally influence each other's distribution and abundance is challenging, let alone whether their covariation is due to community-level selection (19–21). Statistical techniques have been developed in attempts to parse the effects of selection into individual- and higher-level components (22, 23). Another approach, common in community and ecosystem genetics, employs "community heritability" to identify whether community species composition is associated with genetic variation in a foundation species (12). Here, investigators use well-established heritability measures, which indicate the fraction of total phenotypic variation due to a species' population's genes, to assess the extent to which community traits could respond to selection.

This forms a radical extension of the "community genetics" research program first outlined by Janis Antonovics (24–27), as now communities are being treated as units of natural selection (e.g., 12). Advocates have extended heritability measures to include genetic interactions between species putatively subject to natural selection (12, 28, 29). Some interpret such extended heritability to imply that communities can also have fitness (differential survival and proliferation) and that such fitness covaries with community traits. The conceptual link between population genetic variation within a single species (from which heritability is directly measured) and the differential survival and proliferation of whole communities hinges on the premise that genetic variation within a foundation species is causally responsible for the fidelity of other species actively associating with, or avoiding, a given community during its assembly.

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We are concerned whether this causal connection can be inferred from heritability analyses and whether this approach can show that communities are units of selection themselves rather than reflecting in their composition the foundation species' "extended phenotype" (30). We begin by rationally reconstructing what community reproduction would be in nature by articulating an account of community phenotypes and community inheritance mechanisms. We aim to be charitable, providing a best-case scenario for communities as units subject to natural selection.

Mainstream formulations of evolution by natural selection (ENS) follow Richard Lewontin's "recipe" (31), which requires populations of entities that must exhibit variation, inheritance, and differential fitness. To quote Levins' and Lewontin's updated version of the recipe (32), three considerations are necessary and sufficient for ENS to occur, namely that "(i) There is variation in morphological, physiological, and behavioral traits among members of a species (the principle of variation). (ii) The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (the principle of heredity). (iii) Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness)."

For this recipe to be applied to communities, it must be "substrate neutral," so that it can be applied to multiple levels of the biological hierarchy, removing the necessity of ENS occurring within a population of a single species but requiring that something like level-specific reproduction occur (13, 33). Importantly, community genetics presently does endorse Lewontin's recipe, within a multilevel selection (MLS) setting, as the basis of community-level ENS. Whitham et al. (12), for instance, say that

> For evolution to occur at the group level, variation must occur in average group phenotype, heritability must exist such that progeny groups inherit their parent groups' traits, and selection must ensue whereby a covariance between group phenotype and group fitness allows certain group phenotypes to propagate in disproportionate numbers.

So not only must communities have phenotypic traits distinguishable from those of their lower-level constituents, some of those traits must effect differences in fitness that allow for the community to reproduce (34). We introduce a plausible description of community-level phenotypes, then reconstruct the account of community-level inheritance of these phenotypes implicit in community genetics. We then explain why we remain skeptical as to whether one can infer community selection from such heritability measures. We articulate the relationship between community inheritance and heritability, as these two concepts can be conflated. This matters: inheritance may be imposed by experimental design and, therefore, heritability measures may lack natural ecological (external) validity. We suggest that a version of David Hull's replicator-interactor framework for ENS (35) and/or Richard Dawkins's concept of the "extended phenotype" (30) better serve the purposes of community genetics (33).

Community-Level Phenotype and Lewontin's Principle of Variability

For natural community assemblages to be differentially selected, there must be a general and unified account of community-level phenotypes that can make a causal difference to the survival and/or proliferation of communities in nature, and this phenotype must vary between communities in a relevant population of communities. Experimental studies of group selection provide some guide to the different relevant higher-level properties, although most studies of group selection are conducted on single-species groups, limiting their applicability here (36).

Lean (37) categorizes community properties as follows: "the maintenance of multispecies interaction networks such as food webs (community network structures), the maintenance of compositional identity or aggregative features (emergent community properties), or the various material outputs that the joint assemblage creates (community outputs)." These are ways to describe properties at the community level, not necessarily the sort of properties that could be selected community-level phenotypes. For this, these properties must function to favor differential reproduction or (arguably) persistence of the ecological community that possesses them. Any or all of emergent properties, food webs, or ecological outputs could be properties that would allow the communities to be replicated or maintained in the face of disturbance or perturbation. If functional properties alone are considered, a proposal addressing the latter has been made in the case of holobionts (38, 39).

Equally, community properties must warrant being described as phenotypes, serving shared purposes within the community. The mere presence of community-level properties does not indicate the community is a functional collective with shared unity of purpose [i.e., Type I Agency (40)]. In having community-level properties be the result of differential selection on the genetic variation in a foundation species rather than the whole community, advocates of community and ecosystem genetics have jettisoned the requirement that there is unity of purpose between the populations in the community. The apparent higher-level adaptation of the community can be the result of the foundation species cultivating a community that will support its fitness. In the common garden experiments we are directly engaging with, there is a positive effect of foundation species variation on the species it recruits. However, this is not evidence that communities are entities capable of limiting lower-level selfishness to effect differences in community fitness (in accordance with some unity of purpose at the community level).

Experimental inquiries into purported multispecies group selection based on community phenotypes exist. Bangert and Whitham (41) consider arthropod community composition as a community phenotype, which is influenced by cottonwood genetic diversity, independently from any effects the arthropod composition has on the abiotic output of the community system. Indeed, community and ecosystem genetics considers the population size of multiple species and their genotypes as a community phenotype (12, 41). Studies of the Gaia hypothesis (42) or ecosystem evolution often consider instead community phenotypes that comprise the outputs of the assemblages

(43, 44). In the ecosystem services literature, these ecosystem outputs, which act to maintain biotic systems, are called regulatory services. When these self-reflexively maintain a community, community selection could occur due to this phenotype. It has been suggested that the birth-death dynamics of community network structures evolve by evolutionary dynamics (45).

We accept that such collective-level phenotypes could be responsible for differential community persistence and/or recurrence. In addition, of course, these phenotypes can vary community to community, even when populations of communities are circumscribed quite tightly. However, according to Lewontin's criteria, for selection to impact the distribution of such phenotypes in future "generations" of communities, they must be transmitted to whole communities as descendents by some inheritance mechanism.

Heritability, Inheritance, and Lewontin's Principle of Heredity

The principle of heredity is especially problematic for communities. Simply interacting as a whole to produce a phenotype is not sufficient. A multispecies assemblage must also have the capacity to reproduce and transmit a phenotype to offspring assemblages. This concept is further challenging to apply here because it is derived from a synthesis of two different, but related, aspects of heredity. The first is the requirement that there exists an entity-level mechanism for the transmission of a trait from parent to offspring (in accordance with "offspring resemble their parents"). The second is that some fraction of population-level phenotypic variation must be reliably transmittable to future generations as genetic effects on phenotype (in accordance with "the variation is in part heritable"). Note that these two aspects of heredity have very similar terminology, with the first referred to as "inheritance" and the second as "narrow-sense heritability." The distinction is important, as heritability of the kind routinely measured within-community genetics (i.e., associated with genetic variation within a foundation species) does not depend on the existence of an inheritance mechanism for communities. Thus, establishing that community composition is associated with genetic variation in a foundation species might be necessary (e.g., case 1 below), but it is not sufficient (e.g., case 2 below) for communities to satisfy Lewontin's principle of heredity. It is also necessary that we establish "community inheritance."

We begin with the property of inheritance, which is more challenging to apply to higher levels of biological organization (33). The intrinsic mechanisms of inheritance for lower-level reproducers like bacteria and multicellular (often sexual) organisms are widely understood, and consequently, their existence is taken for granted within Lewontin's principle of heredity (e.g., DNA replication, germ cell production and fertilization in diploid organisms need no justification). However, for higher levels of organization such as multispecies assemblages, the mechanisms for reproduction and inheritance are often speculative, if present at all. The inheritance criterion requires that there exists some causal relationship between the entities whereby those related by common descent are phenotypically more similar compared with unrelated entities—that "offspring resemble their parents" in

Lewontin's words (32). In many lower-level settings, inheritance is trivial to explain or establish (e.g., Mendelian transmission genetics for diploid organisms). However, the mere existence of lower-level genetic inheritance among the constituents of a higher-level entity is insufficient to cause, on its own, phenotypic covariance between higher-level entities (33, 38). There must exist some additional biological or experimenter-imposed mechanism to support inheritance that defines parent-offspring lineages at that level (33). Without such a mechanism, higher-level phenotypic covariance could be a consequence of individual or species-level inheritance, just as organism-level inheritance might be seen as the consequence of gene-level inheritance mechanisms (46). However, organism-level inheritance does approach 100% for asexuals and 50% for each of the parents of a sexual organism, because there are chromosomes and other apparatuses of reproduction that serve as such mechanisms or devices. Genetically encoded information will, at least some of the time, be passed directly from parent organisms to offspring organisms. What are the comparable structures or devices for communities?

In contrast to the causal relationship of inheritance between individual parents and offspring, the concept of heritability refers to a statistical property of a population. As routinely used in population genetics, heritability refers to the particular fraction of total population variation in phenotype that is due to genes (the actual partitioning of variance will be discussed below). It simply indicates that for ENS to occur, there must exist some population genetic variation associated with parent-offspring covariance. Thus, Lewontin's recipe is aligned with Fisher's Fundamental Theorem of Natural Selection, another well-known expression of ENS, which indicates that populations cannot evolve if there is no reliably transmittable (narrow-sense) genetic variance in fitness (47). For reproducers such as bacteria and multicellular organisms, the coupling of individual inheritance to the heritability of phenotypic variance within a species is largely guaranteed since genes are the material basis of both. However, the relationship is more complex when lower-level reproducers are the components of a higher-level entity and selection is on phenotypes definable only at that level. When additional levels are involved, the property of inheritance and the observation of heritability can become decoupled.

We present below two hypothetical cases to illustrate the distinction between inheritance and heritability in the community genetics context. The first case extends a classic problem to communities such that ENS cannot operate at that level because there is no genetic variance (47). The second case illustrates a unique problem for community genetics. Here, the community cannot evolve by ENS because it lacks an inheritance mechanism, despite having positive heritability in the community genetics context. These cases reveal the difficulty of interpreting the evolutionary significance of community-level heritability. Such interpretation, we will see, requires additional knowledge about the operational level of inheritance.

Hypothetical Case 1: Community-Trait Inheritance without Community Heritability. Consider a type of community that "reproduces" itself due to the collective action of the genes

in each of its constituent species. Further, the assumed mechanism is accurate because species reproduction is perfectly coordinated with community reproduction such that descendent communities have every species represented exactly as in the parent community. Such a mechanism of reproduction would yield parent-offspring lineages of communities and consequently would permit phenotypic covariance at the community level. Given a population of such communities, on average, there will be greater phenotypic resemblance among those communities that share common ancestry as compared with unrelated communities. This type of community has the property of inheritance.

Now consider that in communities of this sort, a particular community-level phenotype is due to the expression of a gene in one of the constituent species (the "focal" species). Consider that this community phenotype varies across a population of communities according to local environmental influences on gene expression, but all members of the focal species are genetically identical at the locus. Here, the community trait is passed on to descendent communities (inheritance) because the focal species is always transmitted to the next generation. However, the lack of genetic variation at the focal-species locus means that variation in this community phenotype has zero heritability. Clearly, zero heritability is not evidence that the gene has no causal contribution to the community trait. Moreover, it is also not evidence that a community would not inherit any local phenotypic influences on this trait due to niche construction. To conclude that this community phenotype cannot now respond to ENS, but that it would if sufficient genetic variation were to arise (giving rise to positive heritability), requires additional knowledge of the community inheritance mechanisms. Since natural mechanisms for community inheritance are often speculative and less precise than here, empirical estimates of community heritability are more challenging to interpret than heritability for lower-level traits.

Hypothetical Case 2: Community-Trait Heritability without Community Inheritance. Consider another type of community where there is no mechanism for community reproduction. There is, however, extensive redundancy for ecological roles among potential member species. Although species recruitment is ecologically constrained, it remains plastic in terms of species composition [e.g., there is "functional redundancy" as in (48)]. Assembly yields communities that vary in composition, but share properties determined by ecological constraints. Critically, because there is no mechanism of community inheritance, the constituent species disperse upon dissolution of communities and are recruited randomly with respect to parentage in the formation of future communities. Thus, there is no way for communities to faithfully transmit community-level traits to new communities. There will be no parent-offspring phenotypic covariance at the group level. However, due to sampling variation among ecologically redundant species during assembly [an important source of community variation, (49)], ecologically neutral variation in community traits such as species richness and evenness is expected.

Now consider the measurement of heritability for a community phenotype in this setting. Recall that within the field of community genetics, heritability is estimated by selecting a focal species so that genetic variation can be precisely circumscribed and tested for association with a community trait. If genetically divergent lineages within the focal species covary with traits sensitive to sampling variation during assembly, there would exist positive heritability for a community trait which cannot be inherited because there are no parent-offspring relationships at the community level. It is unsurprising that ecological assembly rules would dictate the association of species of similar function, but substituting such rules for evolutionary processes requiring inheritance violates the evolutionary principles on which community and ecosystem genetics rests.

Comparison of cases 1 and 2 illustrates why correct evolutionary interpretation of community heritability requires independent knowledge of any community-level inheritance mechanisms. In case 1 we require independent knowledge of community inheritance mechanisms to correctly interpret zero heritability as merely a problem of no fitness-affecting genetic variance (47). In case 2, we require independent knowledge of ecological assembly mechanisms to correctly interpret positive heritability as decoupled from the notion of community-level reproductive fitness. Case 2 highlights a unique challenge in community genetics: positive community-level heritability is not evidence of community inheritance.

Inheritance in Ecological Systems. Debate over inheritance between ecological systems goes back a long way. Many have harkened back to Fredrick Clement's vision of ecological communities being akin to organisms, with reproduction and development (16). However, more widely, most ecologists do not consider natural ecological systems as having a tightly integrated and reproduced identity (50). The difficulty is defining parent-offspring ecological lineages and describing a mechanism for sufficient parent-offspring phenotypic covariance. Either is difficult, and, as we will note, sometimes ensured only by the experimental set-up itself. We have already described (and will explore further below) one method of suggesting community inheritance, which implicitly appears in community and ecosystem genetics, that of a "community propagule." This is a member of a "foundation" or "keystone" species which, in some manner, recruits a community around it.

Ecological systems, within an area, often maintain their higher-level properties and species compositions over time. The persistence of such features may, however, be solely a result of the spatial autocorrelation between the lower-level (species) populations that comprise those ecosystems (51, 52). In such cases there is no intrinsic mechanism for ecological inheritance despite the presence of geospatial boundaries (53–55).

An inheritance mechanism of some kind might involve a lower-level community propagule causally producing a new community with the same higher-level properties as the parent system. All reproduction is subject to environmental influence, so perfect inheritance from a parent system is too stringent a criterion for such community inheritance. Instead, a propagule-based mechanism for generating new communities need only ensure that communities related by common descent are phenotypically more similar than unrelated

communities. The most suggestive examples of a propagule-like reproduction of communities are the dispersal of "foundation species," sometimes known as a "keystone species" (56). Foundation species according to Whitham et al. "define much of the structure of a community by creating locally stable conditions for other species" (12). The dispersal of a foundation species is considered to function to create a higher-level process analogous to reproduction of the lower-level entities (a higher-level process we would call, instead, re-production). Consider the case where the reproductive excess of a foundation species disperses to a new location, and this founder event is reliably followed by a process of ecological recruitment, facilitating the introduction of other populations and results in a community phenotype.

A mechanism that could lead to community re-production in this sense would be the Mendelian transmission of genes to descendent foundation species that influence how other species actively associate with, or avoid, the community during its assembly. Community genetics, specifically, presents evidence for a genetic basis of community assembly, and structure, as caused by interspecies indirect genetic effects (IIGEs) mediated by genetic variation within a foundation species (e.g., 57). This suggested mechanism of community inheritance thus depends on reliably coupling the lower-level inheritance mechanism of a foundation species to the control of higher-level ecological processes.

For IIGEs within a community to be the target of ENS, according to Lewontin's recipe, the community must have a sufficient mechanism for the reproduction and transmission of IIGEs to future generations of communities. Therefore, what is at stake here is community inheritance. We contend that community heritability, as inferred from focal-species genetic variation, is not direct evidence of community inheritance. Moreover, without some mechanism for community inheritance, such a measure of community heritability can be an inadequate predictor of community evolution via changes in IIGEs (elaborated below). Without a mechanism to accurately reproduce (rather than re-produce) the community and its phenotype, a unified adaptive response to external pressures is not possible because the IIGEs cannot be reliably transmitted to descendent communities and there is no mechanism of control over selfish species that disrupt IIGEs when they maximize their fitness. Thus, the application of Lewontin's recipe to community evolution hinges on the prior assumption that the lower-level reproduction and inheritance mechanism of a foundation species is causally responsible for a process of ecological recruitment resulting in predictable community inheritance of IIGEs. Below, we will present an alternative model for group-level selection of IIGEs that does not require strong assumptions about the existence of a reliable mechanism of community inheritance.

The reliability of the propagule-like mechanism is important. Ecological interactions are highly contingent (58). The interactions between species are often highly dependent on background conditions, such as the abiotic environment and the order of species appearance ("priority effects") (59). Consequently, inferences made about species recruitment in controlled experiments could lack validity in the wild. Another difficulty with empirically determining whether a higher-level entity is a unit of selection is the ability to provide an identity

condition for the community so as to determine what has actually been reproduced: who is the parent and who the offspring? One solution is to use the indexical community framework (e.g., 37). The reproduced community identity is described through indexing the composition to a focal population, in this case, a foundation species, and then identifying the network of populations that are causally connected to the focal population (37, 60, 61). However, higher-level ecosystem properties might be the product of multiple foundation populations. If propagule-like community reproduction required dispersal of a network of genes spread across multiple foundation species, the community propagule would then be indexed to this more complex cluster of populations (37), whose reproduction as a cluster is problematic. A further complication is the possibility of temporal variability. The composition of the index might be time dependent, with some species even leaving and rejoining a community when causal connections to the foundation species are plastic and subject to environmental modification. Clearly, identity conditions for such cases will be more challenging than for a singular foundation species. We have some difficulty, then, equating reproduction and re-production. Although we do not doubt that foundation species (one or a few) might sometimes determine what species are subsequently recruited, the principles of ecology, not evolutionary biology, are relevant here: communities are not "units of selection" (see discussion below on the principle of differential fitness).

Heritability in Community Genetics. The use of heritability scores is widespread in population genetics after being devised by R. A. Fisher (62). Broad heritability H^2 is a score between 0 and 1 representing the proportion to which variation in all genetic factors influences the variance of phenotype within a population. Through common garden experimental design, heritability measures previously used on organismal phenotypes have been extended to community phenotypes. Such experiments yield estimates of the fraction of phenotypic variation among communities (V_P) that is associated with genetic variation (V_G) within a single foundation species (e.g., 63, 64).

Broad sense heritability is standardly identified through the equation $H^2 = V_G / V_P$, where V_G is the genetic variation in phenotype and V_P is the total variation in phenotype. This includes the assumption that $V_P = V_G + V_E$, or that the phenotypic variation (V_P) is a simple sum of variation in the genes (V_G) and the environment (V_E). However, this additivity assumption can create well-documented problems when the relationship is more complex. Variation in a phenotype is more realistically represented as the result of $V_P = V_G + V_E + V_{G×E} + cov_{G×E}$, where $V_{G×E}$ represents the nonadditive interactions of genes and environment and $cov_{G×E}$ represents the degree to which genetic variation covaries with the environment experienced by the organism. Furthermore, V_G represents the sum of additive genetic effects (V_A) and interactive genetic effects such as dominance and epistasis. Critically, in the traditional setting, only the V_A are responsible for predictable phenotypic changes in response to ENS. This is the reason for the restricted form of heritability, $h^2 = V_A / V_P$, referred to as narrow-sense heritability.

Community genetics employs heritability in the broad sense. Here, heritability represents the fraction of community-level trait variation attributable to any sort of genetic variation within the foundation species. Thus, community heritability (hereafter denoted H_C^2) includes all genetic factors in a focal species, both additive and interactive, that affect a multispecies trait. The community compositional effects captured by H_C^2 are significant because the composition of a group can strongly influence individual fitness. Within multispecies groups, gene-mediated interactions come in two forms: 1) within-species indirect genetic interactions (IGEs), and 2) interspecies indirect genetic interactions (IIGEs). The latter underpin the genetic component of community-trait variation (12, 65). Thus, H_C^2 represents a significant extension of the traditional notion of broad sense heritability (H^2), which recognizes only the intragenomic interactions (dominance and epistasis). Estimates of H_C^2 for a multispecies phenotype are obtained from common garden experiments where the fraction of among-group trait variance (presumably due to variation in IIGEs) can be attributed to genetic polymorphisms within the foundation species.

In the traditional setting (diploid transmission genetics), broad sense heritability (H^2) is an inappropriate predictor of the response to ENS because sexual parents cannot reliably transmit intragenomic interactions (dominance and epistasis) to their offspring via haploid gametes. For this reason, narrow-sense heritability is used instead. Likewise, in the absence of higher-level trait transmission, H_C^2 would be an inappropriate predictor of the phenotypic response to selection. H_C^2 would become relevant to ENS, according to Lewontin's recipe, when the IIGEs responsible for a community trait are reliably transmitted between parent and offspring communities. While a positive estimate of H_C^2 from a common garden experiment is consistent with this as a possibility, it is not evidence that reproduction and dispersal of foundational species play this role over the natural scale of environmental and genetic variation (66, 67). Resemblance between community phenotypes could be due to factors outside of the variation in a foundation species. Although artificial selection experiments confirm that group-level ENS can produce significant evolution in multispecies systems, those experimental designs ensured that the IIGEs were reliably transmitted from parent to offspring collectives (4, 5, 8). It is noteworthy that these experiments validate theoretical predictions about group selection being more effective than individual selection when it can target indirect effects (68, 69). However, the capacity for natural assemblages of species to evolve as units of selection (under Lewontin's recipe) remains an outstanding question. The answer to this question does not depend on the existence of IIGEs (they have been empirically confirmed), but rather whether communities have an intrinsic capacity to transmit them to future generations.

Community Selection and Lewontin's Principle of Differential Fitness

Consider Fig. 1A, which is a multispecies version of MLST. The letters (A,B,C, ... Z) represent different species, of which organisms are members. Call these organisms "particles."

They make up "collectives" of many such particles, representing many species. The circles and ellipse are multispecies "collectives" or "communities." For convenience, only three species are shown in each, but there can be many more species present. Collectives with organisms from species A, B, and C grow larger—so that the ellipse on the left comes to harbor more particles of all species contained in the collective (A, B, and C included) than those with representation of only one of these three species. We think multispecies MLS1 and MLS2 are analogous to the uses of Heisler and Damuth (22), writing about organisms and groups within a species: "Of interest in the former case are the effects of group membership on individual fitnesses, and in the latter the tendencies for the groups themselves to go extinct or to found new groups (i.e., group fitnesses)." So in MLS1, there need be no collective or community "fitnesses" in Lewontin's sense—"different variants must leave different numbers of offspring either in immediate or remote generations." In MLS1, the phenotypic variation is indeed at the level of communities, but communities do not leave offspring communities.

Instead, as in more typical trait-group selection (70), all communities of whatever size dissolve, releasing their constituent organisms. These are then randomly recruited from a common pool to form the next generation of communities. Since there are more organisms of species A, B, and C in this pool because of their effect when together on the productivity of collectives, the second generation of collectives will have more ABC collectives than the first. The phenotypes of populations (their propensity to grow) could well be due to interactions (IIGEs) between individuals of different species, but no community in one generation would be the parent of any community in the next.

It is to the advantage of organisms in species A to associate with (or "recruit") organisms of species B and C in MLS1, and many interspecies associations will indeed qualify as IIGEs (12). If such interactions entail that the A offspring of a parent A organism wind up preferentially bound to the B offspring of that A parent's partner B (and similarly C), then we have MLS2 (Fig 1B). Collectives will reproduce at least in part (organisms of those three species, if no others) as collectives and conform to Lewontin's recipe.

In MLS1, IIGEs are only potential interactive properties experienced by the individual species, affecting individual selection within groups, as above. In MLS2, to the extent that there is vertical inheritance (collectives reproducing as collectives), IIGEs can be seen as transmittable properties of collectives. Analogously, although mitochondrial and nuclear mutations are sometimes opposed in eukaryotic cells, most of the time, there are positive interactions. This is why artificially imposed vertical group inheritance (MSL2) is such an effective means of producing a phenotypic response to selection that depends on positive IGEs or IIGEs (4, 5, 8, 68, 69).

In MLS2, the differential survival and reproduction of descendent collectives (community or collective-level fitness) will ultimately favor the reproduction of beneficial IIGEs and disfavor the reproduction of deleterious IIGEs. With MLS1, although ABC collectives differentially grow, they do not reproduce, and fitness (as Lewontin defines it) can only be attributed to organisms within species. Note that
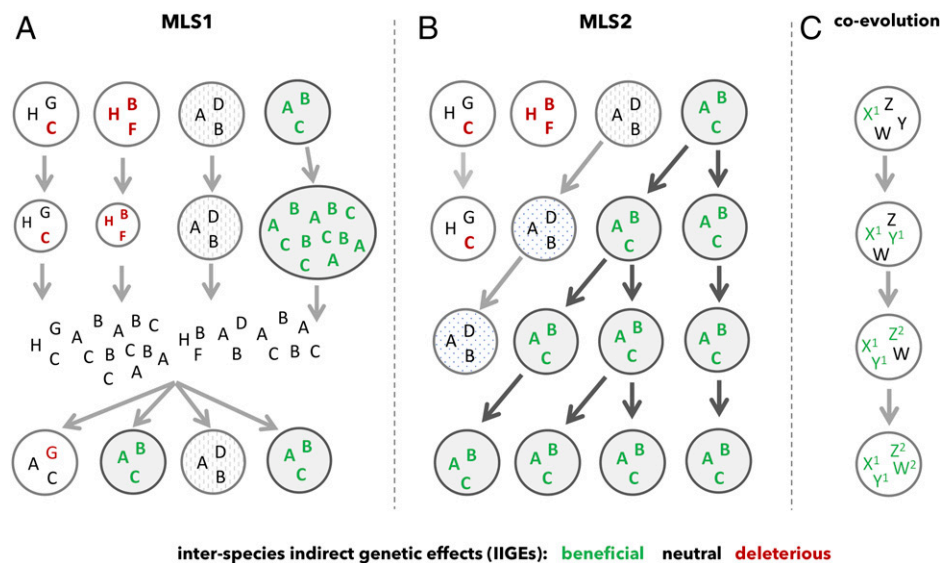
Fig. 1. Evolution of IIGEs by multilevel selection (MLS) versus organismal coevolution. Circles and ellipse represent multispecies collectives or "communities," and letters (A,B,C...) represent different species. Each letter represents a "dose" of individual organisms belonging to that species, with no necessary implication that each came from the same collective, that only the three indicated species are in the collective or that many species affect the presence of others. Interspecies genetic interactions (IIGEs) can have positive, neutral, or negative effects on individual fitness (depicted in green, black, and red, respectively). (*A*) MLS1. Mutualistic interactions between organisms of different species provide a collective benefit (e.g., cross-feeding) that manifests as greater growth (size) of the collective. An evolutionary effect is realized in future "generations" of communities through the greater numbers of individuals contributed by larger communities (e.g., those having A + B + C in green). Despite stochastic blending of many species in each "generation," the overall distribution of IIGEs evolves toward greater representation of the mutualistic interactions. (*B*) MLS2. Here, it remains an advantage for organisms of species A to interact with organisms of species B and C. Because communities are reproducing as communities, multispecies interactions can be transmitted directly to offspring communities. In this way MLS2 conforms to Lewontin's recipe. However, under MSL2, greater representation of beneficial IIGEs in future generations requires greater community-level reproductive rates. (*C*) Coevolution. Individual selection and coevolution of mutualistic IIGEs occurs within a single, enduring community. Species interact and influence each other's fitness landscape, leading to a sequence of adaptive changes in IIGEs over time (indicated by integers). Because there is no feedback to a distribution of IIGEs across a larger set or population of communities, the IIGEs cannot be the target of selection in this scenario.

while MLS1 and MLS2 represent distinct processes, a given natural collective could simultaneously express the characteristics of both to some degree.

Replacing Lewontin's Recipe with Hull's Replicator-Interactor Framework

Evidence that multispecies assemblages have the capacity to evolve as a natural unit comprised of dozens, and perhaps thousands, of species would support a major expansion of Darwinian theory, and proponents of community and ecosystem genetics are excited by the possibility, as it would provide a means of evolution for holistic adaptation otherwise inaccessible to individual-level selection. Their enthusiasm is further encouraged by experimental studies of community-level selection demonstrating that it can yield efficient and rapid evolution of holistic traits in a controlled setting (e.g., 8, 49, 71). However, in a natural setting, it is not sufficient that such traits have been shown to vary among communities and are influenced by genetically encoded interactions between species (i.e., community heritability). Their evolution by natural selection according to Lewontin's recipe can only happen if community-level IIGEs are transmitted largely intact from parent communities to offspring communities (i.e., if there is community inheritance).

In an influential commentary on an experimental paper by Swenson et al. (8) showing "heritability at the ecosystem level," Charles Goodnight (72) writes:

In the first article of the first volume of *Annual Review of Ecology and Systematics*, Lewontin points out that any level of organization that can be grouped into a population of units has the potential to *evolve by natural selection*. Evolution by natural selection has been seen in experimental studies of individual and group selection, and now Swenson *et al.* have demonstrated that *selection acting at the level of the ecosystem* can cause evolutionary change (emphases ours).

At issue, really, is the distinction between demonstrating ENS, meaning change as a consequence of that process at some level and evolving as a result of natural selection acting at the ecosystem level. We submit that the experiments reviewed by Goodnight (72) and others often cited (e.g., 49, 71) do demonstrate the former but show the latter only because MLS2-like inheritance has been imposed by the investigator. In order to allow for interactions between species to be transmitted to the next generation, the experimental design creates ecosystems with individual-like transmission dynamics that they are not known to possess under natural conditions.

For instance, Swenson et al. (8) conducted one of their ecosystem inheritance experiments as follows:

Each line consisted of 15 units and the 3 units with the highest (or lowest) value of the phenotypic trait were used as parents by combining the soil from the 3 units into a slurry that was used to inoculate the "offspring" generation of units.

It is surely unsurprising that the "offspring" so defined resemble their "parents" more than they do all parents (including those with the lowest value). What is transferred between pots with *Arabidopsis* seedlings (mass of plants is the measured phenotype) is a sample of microbes, and

when enough are transferred, the progeny communities cannot help but resemble parental communities. The experimental procedure ensures inheritance of material that, via the IIGEs preserved within the inoculum, affects *Arabidopsis* growth.

The extent to which natural ecosystems might evolve by natural selection depends on the extent to which vertical inheritance exists and dominates over natural processes, such as priority effects on ecosystem assembly, sampling variation during assembly, horizonal migration between ecosystems, and variability in the capacity of descendent system to inherit critical biotic and abiotic material produced by niche construction activities. Ecosystems in nature may behave more like horizontally acquired microbiomes, in which one lineage (often and sometimes arbitrarily designated the host or a foundation species) recruits other lineages by a combination of direct (organism-organism recognition processes) and indirect methods analogous to "ecosystem engineering."

Given that community heritability does not indicate the level at which fitness variation might be relevant to ENS, we advocate for caution in extrapolating H_C^2 from common garden experiments to natural systems. In the simple case of individual selection within a single (enduring) community, species will interact and influence each other's fitness landscape (Fig. 1C). Genetic variation within such species can be the target of individual selection, and in that case, those species would coevolve. While the IIGEs within such a community can change over time according to this process, there is no re-productive (Fig. 1A) or reproductive (Fig. 1B) feedback affecting a distribution of IIGEs across a larger set of communities, so those IIGEs cannot be the target of selection at the community level. Nevertheless, positive H_C^2 could be obtained from common garden experiments for any species-level polymorphisms that happen to be associated with some aspect of within-community composition. Here, broad sense heritability would be a poor predictor of any response to within-community ENS. A narrower sense of heritability would be more suited to this setting.

For selection to produce an evolutionary sorting of alternative systems of IIGEs, there must be some mechanism whereby fitness effects (individual level in MLS1 or community level in MLS2) can feed back to a distribution of IIGEs among groups (Fig. 1 A or B). In case of MLS2, variation in community traits captured by H_C^2 can be directly transmitted to descendent communities if the foundation species is part of the transmission "propagule." Here, since H_C^2 does summarize genetically based interactions with potential to affect differential fitness at the group level, it should be a good predictor of the evolutionary response under MLS2, if this is imposed. Alternatively, in the case of MLS1, H_C^2 can be interpreted as summarizing genetically based interactions with potential to feed back to individual-level fitness. However, since there is no community inheritance mechanism for IIGEs in MLS1, the evolutionary process depends on horizontal rather than vertical inheritance and fails to meet Lewontin's heredity criterion. Nonetheless, through effects on individual-level fitness, an evolutionary response in the genetically based interactions between species is possible via MLS1. One implication is

that sets of genes residing in different species could experience a degree of coordinated evolution [reminiscent of Dawkins's "genes-as-oarsman" analogy (46)] according to the extent that their lower-level fitness effects are additive and are compatible with a given IIGE environment. The membership and stability of gene sets having such community genome dynamics should be the focus of future community genetics investigation.

Foundation species play a role in community and ecosystem research very similar to that played by the host in "the hologenome theory of evolution" (73). Unsurprisingly, the objections to that claim (38, 74–76) focus on the problematic relationship between the re-production (rather than reproduction) of multispecies collectives and Lewontin's criteria. A solution might be realized in both settings if the standard view of ENS built around Lewontin's recipe were replaced by David Hull's replicator-interactor framework (35, 55). In Hull's conception of ENS, holistic interactions between complex entities and their environment are the causal basis of differential fitness, which is manifested as differential reproduction of lower-level replicators.

In such a framework, ephemeral entities like the ellipse in Fig. 1A illustrating MLS1 would be cast as "interactors" and could be organisms [as in Dawkins's *The Selfish Gene* (46)] but could as well be communities or ecosystems, while the cognate replicators could be genes (as in Dawkins's book) but also organisms or species whose differential reproduction is facilitated by being part of a better-growing or more persistent community or collective. Such a solution has been hinted at before and recently made more explicit (55, 77). Here, we develop this idea further by applying the replicator-interactor framework to IIGEs as an expansion of the extended phenotype concept to include multispecies MLS1. We acknowledge that multispecies interactions do occur within a single collective, and extended phenotypes can evolve by nothing more inclusive than individual selection and coevolution in this context (Fig. 1C). Under MLS1, communities evolve as interactors, having unique IIGEs as potential targets of trait-group selection. The effects of IIGEs on individual fitness feed back to their distribution among communities. According to Hull's replicator-interactor framework, this would lead to selection of beneficial IIGEs, and differential growth of communities (interactors) would cause differential survival and reproduction of those organisms (replicators) most relevant to beneficial community-level interactions. The advantage of switching to the replicator-interactor framework is that it can accommodate IIGEs that coordinate community composition without requiring all populations to have unified fitness gain. The foundation population can cultivate a community where only some of the populations have a fitness gain or even none other than itself.

The hierarchical structure of MLS models allows for a variety of evolutionary processes to operate concurrently across levels (55). Indeed, organismal coevolution is expected to occur in MLS1 whenever organism generation times permit mutation-drift-selection dynamics to play out within the lifespan of a community. When coevolution of mutualistic IIGEs does occur within a community (Fig. 1C) and this in turn causes an increase in the frequency of the genetic environment in which the individual genes are favored (Fig. 1A), further evolution of mutualistic IIGEs

could be accelerated (54). A side effect of within-community coevolution could be the evolution of genetic mechanisms whereby species having mutualistic IIGEs "assemble" more frequently than expected by random. Evolution of such assembly mechanisms implies a more complex version of MSL1, showing assembly bias. The latter can be viewed as an analog to the linkage disequilibrium parameter in classical evolutionary genetics, as it sets the degree to which mutualistic IIGEs might occur in excess of pure blending as depicted in Fig. 1*A*. However, coevolution does not affect every gene in every species, which might limit the opportunity of otherwise neutral species-level assembly mechanisms to hitchhike to fixation in concert with community-level selection for mutualistic IIGEs.

Interestingly, the extended phenotype was originally the core framework of community genetics (25, 28), and we suggest that a return to this framework, expanded to include Hull's replicator-interactor formulation, may be a more successful conceptual framing for community and ecosystem genetics. Community-level vertical inheritance would no longer be a necessary condition for the evolution of community-level mutualism (as underpinned by IIGEs). Interactive properties, like IIGEs, become a target of selection when communities that embody them function as interactors, regardless of whether such interactions can be passed intact to future generations of communities. Of course, some degree of vertical inheritance would very likely enhance the effectiveness of selection operating at the level of interactor, but the only necessary condition is that some component of fitness is unique to the community as an interactor. In sum, we suggest that accounts of evolution in a community context are not well served by an exclusive commitment to Lewontin's recipe-based formulation of ENS (i.e., MLS2-thinking). Hull's replicator-interactor framework is more inclusive by admitting interactors as potential targets of selection concurrent with evolutionary processes operating at a variety of other levels. Because the communities of interest here are not expected to make the evolutionary transition to individuality, it works to the advantage of community and ecosystem genetics that differential fitness of either genes or organisms (as replicators) can explain the evolution of community traits (i.e., MLS1-thinking).

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