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CONCEPTUAL SYNTHESIS IN COMMUNITY ECOLOGY

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ABSTRACT

Community ecology is often perceived as a mess given the seemingly vast number of processes that can underlie the many patterns of interest, and the apparent uniqueness of each study system. However, at the most general level, patterns in the composition and diversity of species (the subject matter of community ecology) are influenced by only four classes of process: selection, drift, speciation, and dispersal. Selection represents deterministic fitness differences among species; drift represents stochastic changes in species abundance; speciation creates new species; and dispersal is the movement of organisms across space. All theoretical and conceptual models in community ecology can be understood with respect to their emphasis on these four processes. Empirical evidence exists for all four and many of their interactions, with a predominance of studies on selection. Organizing the material of community ecology according to this framework can clarify the essential similarities and differences among the many conceptual and theoretical approaches to the discipline, and can allow articulation of a very general theory of community dynamics: Species are added to communities via speciation and dispersal, and these species' relative abundances are then shaped by drift and selection, as well as ongoing dispersal, to drive community dynamics.

INTRODUCTION

Community ecology is the study of patterns in the diversity, abundance, and composition of species in communities, and the processes underlying these patterns. It is a difficult subject to grasp in its entirety, with the patterns of interest seemingly contingent on every last detail of environment and species interactions, and an unsettling morass of theoretical models that take wide variety of forms. Fifteen years ago, Palmer (1994) identified 120 different hypotheses to explain the maintenance of species diversity, and the list would no doubt be longer today. However, despite the overwhelmingly large number of mechanisms thought to underpin patterns in ecological communities, all such mechanisms involve only four distinct kinds of process: selection, drift, speciation, and dispersal.

Many biologists will recognize these four processes as close analogues of the “big four” in population genetics: selection, drift, mutation, and gene flow. Many ecologists, however, might be skeptical that such a simple organizational scheme is applicable to the more complex subject of community ecology. Population genetics, despite being faced with essentially the

47 same problem as community ecology – understanding the composition and diversity of alleles in
48 populations – is an easier subject to grasp, and I submit that the reason is not because of any
49 fundamental difference in the complexity of the subject matter, but because of the coherence and
50 simplicity of its theoretical foundation. Every detail of the complex interactions between species
51 and their environments studied by ecologists can also be important agents of natural selection,
52 but it is quite useful to begin by recognizing just that: such interactions mostly fall under the
53 single conceptual umbrella of selection. Add the relatively simpler processes of drift, gene flow,
54 and mutation to the mix, and you have The Modern Evolutionary Synthesis, which remains a
55 robust, general, and widely accepted theoretical foundation for population genetics and
56 microevolution, notwithstanding arguments about whether it fully encompasses all facets of
57 modern evolutionary biology (Pigliucci 2007).

58 The perspective that synthesis in community ecology can be achieved by organizing
59 processes into the four categories of selection, drift, speciation, and dispersal, flows directly out
60 of a sequence of conceptual developments in community ecology over the last half century. In
61 the 1950s and 60s, G. Evelyn Hutchinson and Robert MacArthur ushered in an era of community
62 ecology in which the discourse was dominated by the deterministic outcome of local interactions
63 between functionally distinct species and their environments, i.e., selection. Initial developments
64 of mathematical theory in community ecology occurred decades earlier (e.g., Lotka 1925), but by
65 all accounts the 1960s marked the period during which theoretical development in community
66 ecology flourished (Kingsland 1995; Cooper 2003). The importance of selective processes in
67 local communities ruled the day, and the vast body of theoretical and empirical research in this
68 vein has been dubbed “traditional community ecology” (Lawton 1999; see also Brown 1995).

69 In response to the emphasis on local-scale selective processes almost to the exclusion of
70 other factors, Ricklefs (1987) and others (Brown 1995; chapters in Ricklefs and Schluter 1993)
71 argued for and successfully sparked a shift in emphasis in community ecology to a more
72 inclusive approach, explicitly recognizing the importance of processes occurring at broader
73 spatial and temporal scales for understanding local-scale patterns. One key contribution here
74 was to recognize that the composition and diversity of species, even at a local scale, depend
75 fundamentally on the composition and diversity of the regional pool of species, which in turn
76 depends on the process of speciation. Just as mutation is the ultimate source of genetic variation,
77 so speciation is the ultimate source of the species that make up ecological communities.

78 The next key addition to the mix was ecological drift. Ecologists have long recognized
79 that changes in the composition and diversity of species can have an important stochastic
80 element (e.g., Chesson and Warner 1981). However, it wasn't until Hubbell (2001) imported the
81 neutral theory of population genetics into ecology that drift was incorporated into theory as much
82 more than noise in an otherwise deterministic world. Pure ecological drift happens when
83 individuals of different species are demographically identical, which is exceedingly unlikely.
84 However, drift need not be the only active process in order to be an important process, and in
85 many groups of species that show only modest functional differentiation drift may indeed be
86 quite important (McPeck and Gomulkiewicz 2005). The fact that neutral theory was imported
87 into ecology essentially unchanged from population genetics, suggests the possibility of a
88 broader synthesis of processes in both population genetics and community ecology, neutral and
89 otherwise (Vellend and Geber 2005; Hu et al. 2006; Vellend and Orrock 2009).

90 The final key process is dispersal, the ecological equivalent of gene flow in population
91 genetics. Dispersal has been incorporated into ecological theories of all kinds over the past 50
92 years, but in recent years it has been brought to the fore in the form of the metacommunity

93 concept (Holyoak et al. 2005), which is explicitly concerned with the role of dispersal among
 94 local communities in influencing community patterns at multiple scales. The movement of
 95 organisms across space can have a variety of important consequences in communities.

96 For each of the latter three processes – speciation, drift, and dispersal – conceptual
 97 developments were motivated by a perceived lack of emphasis in the literature on the importance
 98 of the process under question. Selection, in the form of deterministic interactions among species
 99 and between species and their environments, was always recognized as important. With the
 100 additions of speciation, drift, and dispersal, we now have a logically complete set of process
 101 categories within which all other more specific processes can be placed. I believe that
 102 organizing the overwhelming number of specific ecological theories for communities under this
 103 scheme can help achieve at least two important goals. First, the essential similarities and
 104 differences between different ecological models can be clarified in fairly straightforward terms,
 105 thereby making the full set of them easier to understand, apply, and teach to students. Second,
 106 we can articulate a very general theory of community dynamics, which may on the surface sound
 107 obvious and too generalized to make any specific predictions, but may nonetheless serve the
 108 same critical function as foundational theory in population genetics.

109 Before proceeding, it is important to emphasize that I am not arguing that the parallels
 110 between processes or models in population genetics and community ecology are perfect. For
 111 example, selection among individuals across species can be manifested in ways that are rare or
 112 absent within species (e.g., trophic or parasitic interactions), and speciation is a far more
 113 complicated process than mutation. The list could go on. Rather, my argument is that we can
 114 define a similar set of four logically distinct processes in community ecology to provide a
 115 coherent conceptual framework for the discipline.

116 The rest of this paper is structured as follows. I first specify more precisely the
 117 motivation for conceptually organizing the material in community ecology, and provide
 118 operational definitions of important terms. I then illustrate – with separate sections on theory
 119 and data – how the subject matter of community ecology can be presented using the proposed
 120 organizational framework, describing how selection, drift, speciation and dispersal influence
 121 communities. I then touch on some of the general patterns that community ecologists have
 122 traditionally been interested in, and how pattern is connected with process. Finally, I compare
 123 the framework presented here with other conceptual frameworks in community ecology.

124 COMMUNITY ECOLOGY IS A MESS

125 Based largely on empirical results, Lawton (1999) famously called community ecology
 126 “a mess”, and ascribed the mess to the inherent contingency of ecological patterns on the details
 127 of how the underlying processes or rules act: “the rules are contingent in so many ways ... as to
 128 make the search for patterns unworkable” (Lawton 1999). One source of motivation for the
 129 present paper is that even theoretical community ecology can be considered a mess for much the
 130 same reason: each and every twist added to theoretical models seems to matter, making an
 131 overarching treatment of the subject very difficult. Consider the number of different models that
 132 can be constructed from the simple Lotka-Volterra formulation of interactions between two
 133 species, layering on realistic complexities one by one. First, there are at least three qualitatively
 134 distinct kinds of interaction (competition, predation, mutualism). For each of these we can have
 135 either an implicit accounting of basal resources (as in the Lotka-Volterra model) or we can add
 136 an explicit accounting in one particular way. That gives six different models so far. We can then
 137 add spatial heterogeneity or not ($\times 2$), temporal heterogeneity or not ($\times 2$), stochasticity or not
 138 ($\times 2$), immigration or not ($\times 2$), at least three kinds of functional relationship between species

139 (e.g., predator functional responses, $\times 3$), age/size structure or not ($\times 2$), a third species or not
 140 ($\times 2$), and three ways the new species interacts with one of the existing species ($\times 3$ for the models
 141 with a third species). Having barely scratched the surface of potentially important factors, we
 142 have 2304 different models. Many of them would likely yield the same predictions, but after
 143 consolidation I suspect there still might be hundreds that differ in ecologically important ways.
 144 As Lawton (1999) put it, “the necessary contingent theory looks unworkably complicated”.

145 One important manifestation of this mess is that textbook treatments of community
 146 ecology and their associated university courses – that is, the vehicles by which the subject matter
 147 is learned by students – have a structure whose logic is not easy to discern. Section or chapter
 148 topics typically fall loosely under one or more of the following headings: community patterns,
 149 competition, predation (plus other enemy-resource interactions), niches, food webs, and issues of
 150 space and time (e.g., Putman 1994; Morin 1999; Ricklefs and Miller 1999). This is a confusing
 151 list because it includes unlike entities: patterns, processes (competition, predation), concepts
 152 (niches, food webs), objects of study (food webs), or a consideration that is always important to
 153 think about (space and time) (Vellend and Orrock 2009). In contrast, books and courses in
 154 population genetics (e.g., Hartl and Clark 1997) follow a structure that is easier to follow, with a
 155 consistent focus on the four processes of selection, drift, gene flow and mutation, and how these
 156 individually or jointly determine patterns of genetic variation. In my opinion, ecology textbooks
 157 and courses reflect fairly well the way that practicing community ecologists have self-organized
 158 around particular research topics or themes, but I am not convinced that this is the best way to
 159 organize the subject matter for facilitating synthetic and integrated understanding by students and
 160 practitioners alike. As elaborated below, selection, drift, speciation, and dispersal may not be of
 161 equal importance in understanding ecological patterns, but they fully represent the logically
 162 distinct categories of important processes in community ecology.

163 A THEORY OF WHAT IS POSSIBLE

164 Amazingly, the foundation of theoretical population genetics was built in the near
 165 complete absence of data on patterns of genetic variation in natural populations – the very
 166 subject matter of the discipline (Provine 1971). Perhaps for this reason, at least in part, a
 167 theoretical foundation was built to describe a logically complete range of the basic *possible*
 168 processes that could cause evolutionary change, rather than a theory skewed towards an
 169 emphasis on those processes that are *actually* important in nature. The latter is an empirical
 170 rather than theoretical issue. In contrast, long before the existence of ecological theory, patterns
 171 in nature were well known to any keen observer. Allen and Hoekstra (1992, p. 1) describe
 172 ecology as a discipline “whose material study is part of everyday encounters: birds, bees, trees,
 173 and rivers”. They go on to argue, albeit in a somewhat different context, that “It is, however, a
 174 mistake to imagine that this familiarity makes ecology an easy pursuit...the very familiarity of
 175 ecological objects presents the difficulties”. I argue that the everyday familiarity with ecological
 176 patterns pushed ecological theory down the path of emphasizing particular viewpoints on the
 177 processes that are *actually* most important in nature, rather than a logically complete set of
 178 *possible* processes that must play at least some role in community dynamics. The emphasis in
 179 ecology has been on pattern before process (Roughgarden 2009; Vellend and Orrock 2009).
 180 Using the structure of population-genetic theory as a guide, with details altered where necessary
 181 for communities, the following presents an organizational scheme for community ecology,
 182 within which all specific models and frameworks can be described.

DEFINITIONS

183
 184 Table 1 provides operational definitions of key terms used in this paper. With respect to
 185 the definition of a community, there has been considerable debate in ecology concerning the
 186 degree to which ecological communities are sufficiently coherent entities to be considered
 187 appropriate objects of study (reviewed in Ricklefs 2008). The definition of community used here
 188 – *a group of organisms representing multiple species living in a specified place and time* –
 189 bypasses this issue, recognizing that properties of communities are of central interest in ecology
 190 regardless of their coherence and integrity. This definition of community also implicitly
 191 embraces all scales of space and time. Studying communities in 1m² plots or across entire
 192 continents requires different methods, and the relative importance of different processes likely
 193 varies across scales, but we are often interested in understanding the same kinds of patterns (e.g.,
 194 diversity, composition) at these different scales. This represents an expansion of the purview of
 195 community ecology beyond its traditional focus on relatively small scales, without applying a
 196 new name to the discipline (e.g., studies in “macroecology” of species diversity are considered
 197 part of community ecology here).

THE FOUR PROCESSES OF COMMUNITY ECOLOGY: THEORY

SELECTION

199
 200 Use of the term selection to describe deterministic fitness differences among individuals
 201 of different species (Table 1) requires some explanation as it is not yet commonplace in ecology
 202 (but see Loreau and Hector 2001; Norberg et al. 2001; Shipley et al. 2006; Bell 2008). Although
 203 the term selection is used in biology most often with respect to evolutionary dynamics within
 204 species, the definition of selection in no way restricts its application as such. Selection occurs
 205 when individuals in a population vary in some respect, and when different variants reproduce or
 206 replicate themselves at different rates (Darwin 1859; Bell 2008; Nowak 2006). In its most
 207 generalized form, the concept of selection (and even evolutionary change more broadly), can be
 208 applied “based only on the assumption of a population of things that leave descendants and have
 209 measurable phenotypes” (Rice 2008).

210 Applying the concept of selection to species in a community, rather than to alleles in a
 211 species’ population, requires two changes to the frame of reference. First, rather than invoking
 212 selection at any higher level than the individual organism, we simply define the “population” as
 213 containing individuals of multiple species; we call this population a community. Second, the
 214 “phenotype” of interest, which may be under selection, is most often just the species identity.
 215 The species identity is a categorical phenotype, assumed to have perfect heritability, except when
 216 speciation occurs, after which new species identities are assigned (just as mutation changes the
 217 identity of an allele). The same way that selection may favor allele *A* over allele *a* within a
 218 species’ population, selection may favor species *X* over species *Y* in a community. It is
 219 important to note that while the concept of selection in communities is easier to envision for
 220 species on the same trophic level than for species on different trophic levels, the difference is one
 221 of degree and not of kind. For example, a lynx and a hare are very different organisms, but
 222 selection still favors hares when lynx are declining, and it favors lynx when hares are abundant
 223 (Krebs et al. 2001).

224 Rather than focus only on species identities, it is also possible to define each species by
 225 one or more traits (e.g., beak depth, leaf thickness; McGill et al. 2006), and to then apply tools
 226 from quantitative genetics at the community level (e.g., Norberg et al. 2001; Shipley et al. 2006).
 227 This opens the door to simultaneous consideration of selection both within and among species.
 228 However, to simplify the discussion and focus attention most sharply at the community level, I

229 henceforth address selection in communities by assuming that individuals of a given species
230 have the exact same “phenotype” (e.g., the species identity). Relaxing this assumption forms the
231 basis of a very active area of research (e.g., Hughes et al. 2008), but before doing so it is
232 necessary to first establish the basic building blocks of community ecology with species as the
233 fundamental category of accounting in the assessment of community-level phenomena.

234 In a community context, there are three relevant forms of selection: (1) constant, (2)
235 frequency- or density-dependent, and (3) spatially- or temporally-variable selection. Constant
236 selection is simple: if relative fitness is constant in space and time, independent of species’
237 densities, but variable across species, the species with the highest fitness will exclude all others
238 (Figure 1A). Other forms of selection are more complicated.

239 Frequency- or density-dependent selection is central to the vast majority of theoretical
240 models with species interactions in community ecology. For simplicity, I will only use the term
241 density-dependent, given that most ecological models include densities rather than frequencies –
242 a key distinction from the tradition in population genetics (Lewontin 2004). If community size is
243 constant, density and frequency are equal (as in Figure 1 for simplicity of presentation).
244 Density-dependent selection occurs when individual fitness in a given species depends at least in
245 part on that species’ density, and the densities of other species. For two species, negative
246 density-dependent selection favors species when they are at low density, and is thus capable of
247 maintaining stable coexistence (Figure 1B). Positive frequency-dependent selection favors
248 species at high density, and thus cannot maintain stable coexistence (Figure 1C). Selection can
249 also depend on species densities in more complex ways, possibly allowing more than one stable
250 state at which coexistence is maintained (Figure 1D), or creating repeated oscillations in
251 interacting species’ abundances (Morin 1999). A major challenge in ecology is presented by the
252 nearly limitless variety of configurations the full set of intra- and inter-specific density
253 dependencies can take in a species-rich community.

254 The nature of density-dependent selection between pairs of species depends on the
255 qualitative ecological relationship between them (e.g., competition, predation, mutualism,
256 disease, etc.), and the quantitative form of this relationship. With more than two species, indirect
257 interactions can arise whereby fitness in one species depends on the density of a second species
258 not because of a direct interaction, but because each of the two species interacts directly with a
259 third (Strauss 1991). Even the nature of the direct interaction between two species can be
260 influenced by other species, amplifying even further the number of ways a community can be
261 configured. A massive edifice of theoretical research has addressed the community
262 consequences of different forms of density-dependent interactions among species (Morin 1999).
263 From a given set of initial conditions, any outcome ranging from the exclusion of all but one
264 species, the indefinite coexistence of all species, complex temporal fluctuations, or entirely
265 different equilibrium patterns depending on initial conditions, is possible.

266 Selection, whether constant or density-dependent, may vary across space or time, with
267 potentially important consequences for community dynamics. Most importantly, the behavior of
268 such models can deviate qualitatively from spatiotemporally invariant models when the relative
269 fitnesses of different species switch in different places or times, thereby possibly allowing
270 coexistence of species that would otherwise not be possible (Levene 1953; Chesson 2000). More
271 generally, species coexistence always depends on trade-offs of some kind, with different species
272 having fitness advantages under different sets of conditions specified by some combination of
273 the abiotic environment and the densities of the species themselves (Chesson 2000).

DRIFT

274
275 Because birth, death, and offspring production are inherently stochastic processes,
276 changes in any community with a finite number of individuals will also have a stochastic
277 component. This is ecological drift. If individual-level demographic parameters are identical
278 across all individuals in a closed community, drift is the only driver of community dynamics
279 (i.e., there are no deterministic changes in abundance, Figure 1E), and eventually all but one
280 species will drift to extinction. The probability of each species reaching mono-dominance is
281 equal to its initial frequency, and the rate at which this is achieved is negatively related to
282 community size (Figure 2). As such, declines in community size (i.e., disturbance) may increase
283 the importance of drift. Importantly, drift need not act alone to have an important impact on
284 community dynamics. The interaction of drift with speciation and dispersal (Hubbell 2001) will
285 be described in subsequent sections; here I address the interaction of drift and selection.

286 If selection is relatively strong and community size large, selection will override any
287 effects of drift. But if selection is relatively weak and community size small, drift can override
288 the effects of selection. Between these two extremes, selection makes some community
289 outcomes more likely than others, but does not guarantee any particular outcome (Nowak 2006).
290 For example, even with constant selection favoring one of two species, there is some probability
291 that the species with higher fitness will drift to extinction (Figure 2).

SPECIATION

293 Most treatments of community ecology inherently exclude from their purview the
294 question of how the species in an area arose in the first place, leaving such questions to the fields
295 of biogeography and macroevolution (Ricklefs 1987; Brown 1995). From the perspective of
296 understanding how species interactions play out in homogeneous small-scale localities, this is
297 entirely defensible, because the origin of the local species pool does not matter, just that the
298 species are present locally and with a given set of traits. But to compare community patterns
299 across different regions, and even across environmental gradients at quite local scales, it may be
300 important to incorporate the biogeographic and macroevolutionary context in which the species
301 pool originated (Ricklefs 1987; Ricklefs and Schluter 1993; Pärtel 2002). We can no more
302 afford to exclude speciation from community ecology than we can afford to exclude mutation
303 from population genetics, even if speciation is far more complex a process.

304 I deliberately focus on speciation, rather than embracing extinction under this umbrella as
305 well, because with an expanded spatial and temporal scope of community ecology (see
306 DEFINITIONS section above), extinction is best considered as an outcome of selection and drift
307 rather than a distinct process in and of itself. When the last individual of a species dies, the
308 species is extinct, and while the decline to extinction may have many specific causes, they must
309 either be deterministic (selection) or stochastic (drift). Even major geological events (e.g.,
310 glaciation) are distinguished from more subtle environmental changes (e.g., slight acidification
311 of a lake) as agents of selection by the rate, magnitude, and spatial scale of change, rather than a
312 qualitatively distinct influence on communities. Such environmental changes may also alter the
313 effects of drift via changes in community size.

314 I focus here on some of the simplest ways speciation has been incorporated into
315 theoretical community models, and also some empirically-motivated conceptual models. At
316 large spatial scales, such as entire continents, the rate of speciation can enter mathematical
317 models directly as a key determinant of community dynamics. For example, Hubbell (2001)
318 considered a neutral community of fixed size in which speciation rate is constant, with the rate of
319 extinction due to drift increasing with the number of species because with more species, each

320 species' population must be smaller. Alternatively, MacArthur (1969) posited that both
 321 speciation and extinction rates increase with the number of species, but with the increase
 322 decelerating for speciation and accelerating for extinction, thus resulting in an equilibrium
 323 number of species in the region. These models correspond to drift-speciation balance and
 324 selection-speciation balance, respectively, and in both cases a greater rate of speciation leads to a
 325 larger species pool, all else being equal. In a model of multiple local communities connected by
 326 dispersal along an environmental gradient, McPeck (2007) found that the nature of the speciation
 327 process influenced local species diversity: greater ecological similarity between new and existing
 328 species extended times to extinction, thereby elevating local species diversity at any given time.
 329 More conceptual (rather than mathematical) models address the consequences of variation in the
 330 rate at which species are produced that are adapted to particular conditions (e.g., regionally
 331 common or rare abiotic conditions). The term "species pool hypothesis" has been used to
 332 describe this type of conceptual model (Taylor et al. 1990). Via its effects on the regional
 333 species pool, speciation then indirectly becomes a potentially important determinant of
 334 community dynamics and patterns even at a local scale where the rate of speciation is negligible
 335 relative to other processes (e.g., Ricklefs and Schluter 1993; Pärtel 2002).

336 DISPERSAL

337 Dispersal involves the movement of organisms across space, and thus its influence on
 338 community dynamics depends on the size and composition of communities where the dispersers
 339 come from and where they arrive (Holyoak et al. 2005). As such, the community consequences
 340 of dispersal can only be addressed in relation to the action and results of other processes –
 341 selection and drift in particular. Construction of theoretical community models addressing the
 342 role of dispersal usually specify whether organisms are distributed continuously across space, or
 343 in discrete patches. The latter will be adopted here for the sake of simplicity and clarity.

344 With respect to the relative sizes of the source and recipient communities for dispersers,
 345 two kinds of model represent the ends of a continuum. Mainland-island models assume one-way
 346 dispersal from a source community of effectively infinite size (the mainland) to one or more
 347 smaller, discrete local communities (the islands, or localities). These models assume that
 348 community dynamics in small localities are sufficiently rapid relative to the mainland that the
 349 composition of the pool of dispersers is effectively constant. In contrast, island models assume a
 350 network of small local communities linked by dispersal among them, with no distinct mainland.
 351 Such networks of local communities may be called "metacommunities" (Holyoak et al. 2005).

352 Dispersal can interact with drift and speciation. In a mainland-island model with local
 353 drift but no speciation or selection, dispersal increases local species richness and causes local
 354 community composition to converge on that of the mainland. For a given level of dispersal, the
 355 number of new species introduced per unit time will decrease as local species richness increases
 356 because fewer and fewer of the dispersers will represent new species in the locality. With fixed
 357 local community size, greater species richness necessitates smaller population size per species,
 358 so the rate of species' extinction increases with species richness, at some point equaling the rate
 359 of species introduction and thus determining an equilibrium number of species whose identities
 360 nonetheless change through time. This is the simplest form of the theory of island biogeography
 361 (MacArthur and Wilson 1967). In an island model with local drift but no speciation or selection,
 362 dispersal increases local diversity by countering drift, and causes the similarity in composition
 363 among localities to increase (Wright 1940). Without input via speciation or dispersal from a
 364 separate metacommunity, all but one species will nonetheless ultimately drift to extinction. In a
 365 model with drift, speciation, and dispersal, but no selection, all community patterns are

366 determined by the size of the local communities, the size of the entire metacommunity, and the
 367 rates of speciation and dispersal (Hubbell 2001).

368 Not surprisingly, the range of outcomes when dispersal interacts with selection is vast.
 369 The nature of selection among species in one locality can take many different forms, and
 370 dispersal implies multiple localities, each of which may represent a unique selective
 371 environment. The consequences of dispersal depend on these details. Also, in addition to the
 372 many kinds of trade-offs in different models of pure selection, dispersal ability itself may vary
 373 among species, possibly with a trade-off involving other aspects of fitness. Enumerating all
 374 possible ways that dispersal can interact with selection and drift is well beyond the scope of the
 375 present paper. Three generalized examples provide a flavor of how selection and dispersal can
 376 interact. First, if selection via competition or predation causes a species to go locally extinct,
 377 that species may nonetheless persist regionally (along with its competitor/predator) if it has a
 378 superior ability to disperse to “open” sites, where either the superior competitor has gone extinct
 379 for other reasons or where the predator went extinct due to an absence of prey (Caswell 1978;
 380 Tilman 1994). Second, if selection favors different species in different patches, dispersal can
 381 nonetheless maintain persistent local populations of species even in patches where they are at a
 382 fitness disadvantage (Levene 1953). If species vary in their mean fitness across patches, then
 383 very high dispersal will allow the species with highest average fitness to exclude all others.
 384 Finally, in a mainland-island context, dispersal to the island determines the species pool in a way
 385 closely analogous to the role of speciation on continents.

386 RELATING EXISTING THEORIES TO THE FOUR PROCESSES

387 Four processes (or any four items) can be considered singly or in combination in 15
 388 different ways: each of the four alone, six pairwise combinations, four trios, and all four
 389 together. However, it is impossible to build a theoretical community model with only speciation
 390 and/or dispersal without specifying the fate of new species or dispersers with respect to selection
 391 or drift. Thus, the four processes can form the basis of theoretical models in 12 different ways.

392 Table 2 relates many of the influential and familiar theories, models, and conceptual
 393 frameworks in community ecology to their emphasis on selection, drift, speciation, and dispersal.
 394 Briefly, the idea of species “niches” (Chase and Leibold 2003) is essentially synonymous with
 395 selection, and many models of species interactions represent different manifestations of
 396 selection. Adding demographic stochasticity to selection-based models represents a combination
 397 of drift and selection (e.g., Tilman 2004), as do models proposed under the rubric of a niche-
 398 neutral reconciliation (e.g., Shipley et al. 2006; Adler et al. 2007). The species-pool hypothesis
 399 (Taylor et al. 1990), and the broader conceptual framework based on the interaction between
 400 local and regional processes (Ricklefs and Schluter 1993), represent the interaction between
 401 speciation and selection, and to some degree dispersal. Classic island biogeography theory
 402 (MacArthur and Wilson 1967) represents a balance between drift and dispersal, and the full
 403 version of Hubbell’s (2001) neutral theory represents the combined influence of drift, dispersal
 404 and speciation. Metacommunity theory (Holyoak et al. 2005), and the many specific models
 405 under this umbrella such as those involving colonization-competition tradeoffs or “mass effects”,
 406 emphasize dispersal first and foremost, and how dispersal interactions with selection and drift.

407 THE FOUR PROCESSES OF COMMUNITY ECOLOGY: DATA

408 A vast empirical literature addresses the processes underlying the dynamics of ecological
 409 communities. The purpose of this section is to illustrate the kinds of evidence available from lab
 410 experiments, field experiments, and observations of nature, that speak to the importance of
 411 various forms of selection, drift, speciation, and dispersal in communities.

SELECTION

412
413 Most communities appear to be characterized by unique combinations of selective
414 factors, and case studies of selection in ecological communities number in the thousands
415 (Diamond and Case 1986; Putman 1994; Lawton 1999; Morin 1999). Important factors that
416 underlie the influence of selection on community patterns include species' responses to the
417 abiotic environment, the disturbance regime, the types of direct interactions between organisms
418 (competition, predation, parasitism, herbivory, mutualism, etc.), the functional or behavioural
419 responses of organisms to different densities of interacting species, the degree of specialization
420 in interspecific interactions, the number and types of limiting resources (e.g., renewable or non-
421 renewable), and the presence and nature of indirect interactions among species (Putman 1994;
422 Ricklefs and Miller 1999; Morin 1999). The following handful of examples focus mostly on
423 competition and trophic interactions to illustrate the basic types of selection (Figure 1) and the
424 range of outcomes of selection in local communities, such as the exclusion of some species by
425 others, stable coexistence of species, complex fluctuations in abundance over time, or alternation
426 between different stable states. I focus on studies in which the outcome of selective processes is
427 measured as changes in species' abundances or diversity, rather than responses in focal species
428 such as individual growth rates or body size, which are often measured under the assumption that
429 they may have consequences at the community level (e.g., Van Zandt and Agrawal 2004).

430 Species can exclude each other. While selection in any real situation is unlikely to be
431 constant across all species' densities (Figure 1A), one species may be at an advantage across the
432 full range of possible densities. Lab experiments have demonstrated competitive exclusion
433 between species of paramecium (Gause 1934), phytoplankton (Tilman 1977), and flour beetles
434 (Park 1948), among many others, as well as the exclusion of prey species by a predator (Gause
435 1934; Huffaker 1957). Field experiments similarly have revealed competitive exclusion, for
436 example between barnacle species at particular tidal depths (Connell 1961), or plant species
437 under particular resource conditions (Tilman 1982, 1988). In many cases of competitive
438 exclusion, the winner in competition depends on environmental conditions, establishing the
439 possibility (in lab experiments) or existence (in field studies) of spatially-variable selection.
440 Many species distribution patterns have been interpreted as evidence of competitive exclusion
441 between functionally similar species (e.g., Diamond 1975), although it is very difficult to
442 confidently infer process from pattern in such cases (Strong et al. 1984). Regardless of the
443 strength of direct interspecific competition, environmental change in the past (e.g., glacial
444 cycles) has acted as an agent of selection among species, favoring some, and causing others to
445 decline, sometimes to the point of extinction (McKinney 1997; Williams et al. 2004).

446 Competing species often exist in stable combinations via negative density dependent
447 selection. With multiple limiting resources and two phytoplankton species, Tilman (1977) found
448 that one species (*Asterionella formosa*) was a superior competitor for the resource most limiting
449 to the other species (Si) and vice versa (*Cyclotella meneghiniana*, and P), resulting in stable
450 coexistence via negative density-dependent selection at intermediate Si/P ratios. Coexistence
451 among grassland plant species via the same mechanism has been found in field experiments as
452 well (Tilman 1988). A trade-off between competitive ability and colonization ability can create
453 negative density dependent selection contributing to the coexistence of protozoans and rotifers in
454 lab microcosms (Cadotte et al. 2006), although field evidence for this mechanism is more
455 ambiguous (e.g., Levine and Rees 2002). Temporally variable selection via environmental
456 fluctuations can lead to stable coexistence of diatoms under variable temperatures in the lab
457 (Descamps-Julien and Gonzalez 2005), and appears to be a likely explanation for fluctuations

458 and coexistence of grassland plants in variable climatic conditions in Kansas (Adler et al. 2006).
 459 Patterns of species composition are often closely correlated with environmental conditions, with
 460 spatially-variable selection almost certainly playing an important role (Whittaker 1977).

461 Trophic interactions among species can lead to coexistence with fluctuations over time
 462 via complex forms of density dependent selection. Predators and their prey can coexist over the
 463 long term with regular cycles, both in lab microcosms such as those with different species of
 464 mites (Huffaker 1957) or rotifers and algae (Fussman et al. 2000), as well as in field populations
 465 such as snowshoe hares and lynx in the boreal forest (Krebs et al. 2001). Density dependent
 466 species interactions can also lead to complex chaotic dynamics with species persistence in
 467 aquatic laboratory food webs (Benincà et al. 2008).

468 Positive and negative density dependent selection over different ranges of species'
 469 densities can lead to switches between multiple states with respect to community composition.
 470 Changes in the initial abundances of species in aquatic microcosms can lead to very different and
 471 seemingly stable final species compositions (Drake 1991), a result that has been found in a
 472 variety of lab and field experiments (Schröder et al. 2005). In natural non-experimental systems,
 473 a change in the abiotic environment can act as a selective force changing species composition,
 474 which in some cases may not be reversible just by returning the environmental condition to its
 475 original state (Scheffer et al. 2002). In lakes, for example, nutrient input can push species
 476 composition towards a new stable state that is not reversible without reducing nutrients to much
 477 lower levels than the level at which the initial change took place (Dent et al. 2002).

478 The range of detailed mechanisms underlying the influence of selection on communities
 479 is vast. In a nutshell, almost any kind of selective interaction between species can be found in
 480 some community on earth, or recreated in the laboratory. Likewise, many case studies have been
 481 able to reject hypotheses based on particular forms of selection, although such "rejections"
 482 typically apply only to the system under study, rather than representing a general refutation of a
 483 hypothesis. Ecologists working in different kinds of communities have traditionally emphasized
 484 the importance of particular processes (e.g., competition among terrestrial plants vs. trophic
 485 interactions among aquatic animals), although it is not clear whether these reflect real differences
 486 among communities or logistic constraints to studying different processes in different systems.

487 DRIFT

488 Testing for ecological drift among species presents considerable empirical challenges.
 489 First, pure ecological drift without any selection seems unlikely given the myriad differences
 490 between species. Second, while selection is relatively easy to detect as a consistent fitness
 491 difference between species across observational or experimental units, the unexplained variance
 492 across such units can not automatically be attributed to drift. This is because of the entirely
 493 plausible possibility that much of the unexplained variance is due to minor differences in
 494 uncontrolled factors such as environmental parameters. One can always dream up a
 495 deterministic explanation for apparent randomness. Indeed the discussion sections of many
 496 ecological papers implicitly attribute low values of r^2 to unmeasured but deterministic factors,
 497 rarely entertaining the possibility that the unexplained variation is truly random – that is, due to
 498 ecological drift. Nonetheless, in a world of finite size, drift is a fact of life, and indeed there are
 499 many empirical studies in which a compelling case can be made that drift is an important process
 500 underlying community dynamics.

501 Experiments by Thomas Park and colleagues with *Tribolium* flour beetles demonstrated a
 502 competitive advantage of one or another species depending on conditions of temperature and
 503 humidity, but they also discovered conditions under which the outcome was indeterminate (Park

1948; Mertz et al. 1976). Sometimes *T. castaneum* wins, sometimes *T. confusum* wins, despite seemingly identical conditions across replicate microcosms. It has been suggested that differences in the genetic composition of populations can provide a selective explanation for the seemingly indeterminate results (Lerner and Dempster 1962), but ultimately it appears that under particular conditions the two species are sufficiently close to competitive equivalency that ecological drift indeed plays an important role in the outcome of competition (Mertz et al. 1976). More recently, density-manipulation experiments with *Enallagma* damselflies strongly suggested ecological equivalence between two species, with no obvious advantage to either species at low relative abundance, but strong sensitivity of demography to total density across the two species (Siepielski et al. 2009).

I know of few other examples where conclusive evidence has been found that drift plays a dominant role in community dynamics, but a number of studies have reported seeming competitive equivalence between species under particular conditions, in organisms ranging from vascular plants (Goldberg and Werner 1983) to salamanders (Fauth et al. 1990). Hubbell (2001; 2005) has vigorously advanced the hypothesis that many tropical tree species are effectively ecological equivalents, with their community dynamics determined by drift and dispersal in the short term, along with speciation in the long term. Some tropical tree species show clear evidence of ecological differences in traits such as a trade-off between survival vs. growth rate in gaps (Hubbell 2005) and environment-dependent fitness (John et al. 2007), suggesting an important role for selection in community dynamics. However, there still remain hundreds of co-occurring species of any particular ecological “type”, suggesting a potentially important role for drift, even though it is clearly not the only important process in tropical forests. In many data sets, species composition is strongly related to environmental conditions (indicative of selection), but a variation in the compositional similarity between sites is also related to spatial proximity independent of environment – an indirect indication of drift (Cottenie 2005). For species engaged in trophic interactions, the concept of pure neutrality does not apply, although changes in predator and prey abundances almost certainly have an important stochastic component in many cases (Chesson 1978).

SPECIATION

Speciation is obviously an important determinant of the number and types of species found in large regions such as entire continents, as well as on isolated islands (MacArthur 1969; Losos and Schluter 2000; Ricklefs 2008). Although the distinction of discrete spatial scales is largely arbitrary (Ricklefs and Schluter 1993), the present discussion can be focused by addressing circumstances under which speciation has an important influence on community patterns at comparatively small scales.

Speciation appears to be critical to understanding at least two kinds of species diversity pattern. First, why do equal-sized areas under very similar environmental conditions but in different geographical regions contain different numbers of species? These have been dubbed “diversity anomalies” (Ricklefs 2008). For example, across a range of scales, equal-area portions of eastern Asia contain about twice the number of plant species as in eastern North America, despite similar environmental conditions and strong taxonomic affiliations between the two regions (Ricklefs et al. 2004). Increased opportunity for speciation in eastern Asia due to greater physiographic heterogeneity appears to be an important contributor to this pattern (Qian and Ricklefs 2000). More generally, many studies report linear increases in local species richness with increasing regional species richness (Srivastava 1999), suggesting an important

549 influence on local diversity of processes that determine the regional species pool, including
550 speciation, as well as dispersal.

551 The second kind of species diversity pattern for which speciation can be a key underlying
552 process is the relationship between species diversity and local environmental gradients (Ricklefs
553 2004). Such patterns are widespread (Rosenzweig 1995), and an important consideration in the
554 assessment of underlying processes is that the species in lower diversity areas may not just be a
555 subset of the species in higher diversity areas. For example, while the number of species per unit
556 area may change with elevation up a mountainside, there are also different sets of species living
557 at the base and the top of the mountain (Whittaker 1977). If we take the regional species pool as
558 a given and assume that all species have been able to reach different areas, selection must be an
559 important process underlying the composition-environment relationship. However, why should
560 we find different *numbers* of species at different elevations, or levels of productivity? For
561 productivity gradients in plants, one selection-based explanation is that high productivity fosters
562 dominance by fast-growing species, thereby limiting species diversity under such conditions
563 (Grime 1973). But again, why should there be relatively few species capable of exploiting high
564 productivity conditions, or more generally any particular set of conditions (Aarssen and Schamp
565 2002)?

566 One potentially important part of the answer is that different sets of environmental
567 conditions have been represented to variable degrees over time, such that speciation has
568 produced many species that are adapted to common, widespread conditions, and many fewer that
569 are adapted to rarer conditions (Taylor et al. 1990). For example, in regions where relatively
570 high soil pH has predominated, plant species diversity tends to be positively correlated with pH,
571 while in regions where relatively low soil pH has predominated the opposite is true (Pärtel 2002).
572 Even if different habitats have been equally available over time, current species richness might
573 be greatest in conditions under which a particular group of organisms initially evolved, and
574 therefore where diversity has had more time to accumulate via speciation. For example, Wiens
575 et al. (2007) found similar rates of diversification at different elevations for a clade of tropical
576 salamanders, but that mid-elevation habitats were colonized earliest in the evolution of the clade,
577 thus helping explain a mid-elevation peak in species richness patterns. In sum, although
578 selection is a key determinant of compositional change along gradients, speciation is likely a
579 critical process contributing to many diversity-environment relationships (Ricklefs 2004).

580 DISPERSAL

581 Dispersal can have manifold consequences for community patterns at multiple spatial
582 scales. First, much like speciation, dispersal is a key contributor to the regional species pool, and
583 therefore the various community consequences that entails (Ricklefs and Schluter 1993).

584 From the point of view of a local habitat, a common empirical result is that increasing
585 dispersal into the locality increases species diversity. For areas undergoing primary succession,
586 such as following volcanic eruption of Krakatau, dispersal is required for a community to be
587 established and for diversity to increase (Whittaker et al. 1989). Experimental dispersal via seed
588 addition into established plant communities in the field often results in increased species
589 diversity (Turnbull et al. 2000), and proximity of an island or habitat patch to potential sources of
590 dispersers often correlates positively with local species diversity in a wide range of organisms
591 (e.g., MacArthur and Wilson 1967). For amphibians in a network of ponds, increased
592 connectivity positively influenced species turnover, suggesting that dispersal can affect not only
593 species composition and diversity, but also their temporal rates of change (Werner et al. 2007a).

594 Since species vary in their propensity for dispersal, the proximity of a locality to potential
595 source habitats can also influence species composition, with distant localities containing a
596 preponderance of good dispersers (e.g., Kadmon and Pulliam 1993). With variation in local
597 species composition created by dispersal, either related to locality isolation or stochastic
598 variation, density-dependent selection via species interactions can then magnify local variation in
599 species composition further, as in freshwater communities of zooplankton and their insect or fish
600 predators (Shurin 2001).

601 Dispersal can interact with selection or drift to influence community patterns at the
602 regional scale as well as the local scale. In an experimental metacommunity of protozoans and
603 rotifers, local species richness was maximal at intermediate rates of dispersal (Cadotte 2006a).
604 The shift from low to moderate dispersal increases the rate of addition of new species to
605 localities and allows competitively inferior species to find temporary refuges, whereas the shift
606 from moderate to high dispersal allows superior competitors to dominate across the
607 metacommunity. In the same experiment, compositional variability among localities was
608 maintained to the greatest degree with low to moderate dispersal, thus maximizing richness
609 across the entire metacommunity (Cadotte 2006a). A meta-analysis of similar experiments
610 found local diversity generally to be maximized at intermediate dispersal rates in animal
611 communities, but at the highest dispersal rates in plants, with either a negative effect or no effect
612 of dispersal rate on regional diversity (Cadotte 2006b). For the pond amphibians mentioned
613 above, species turnover was strongly influenced by both connectivity and environmental factors,
614 suggesting an important interaction between dispersal and selection (Werner et al. 2007a,b).

615 The body of research on the community consequences of dispersal and its interactions
616 with selection is still comparatively small. As with selection, it seems likely that any
617 theoretically plausible effect of dispersal on community dynamics will be found in some
618 experimental or natural community, while at the same time many hypotheses concerning the
619 consequences of dispersal will be “rejected” in particular systems.

620 GENERAL PATTERNS AND THE PATTERN-PROCESS RELATIONSHIP

621 In this paper I have argued for a conceptual organization of community ecology based on
622 the recognition of four fundamental classes of process. However, research directions in
623 community ecology have seldom begun by starting from first principles and asking what patterns
624 in nature we expect to see based on the action of elementary processes. More often, patterns are
625 observed in nature, after which explanations are sought. Patterns that have received considerable
626 attention include the distribution of species' relative abundances; the relationship between
627 species diversity and area, latitude, elevation, productivity, disturbance, or spatial heterogeneity;
628 the relationship between local and regional species diversity; patterns in the connectance and
629 other properties of food webs; and temporal changes in species composition during succession
630 (Diamond and Case 1986; Rosenzweig 1995; Morin 1999; Ricklefs and Miller 1999).

631 A major source of debate in community ecology is the fact that most such patterns have
632 multiple explanations. As such, finding a particular pattern in a given system often reveals very
633 little about the important processes at work in that system. Species-area relationships provide an
634 illustrative example. According to the theory of island biogeography, large islands contain larger
635 populations of component species, so the rate of extinction due to drift is lower than on smaller
636 islands, thus leading to a greater number of species on large vs. small islands (MacArthur and
637 Wilson 1967). It is also possible that larger islands provide a bigger target for dispersing
638 organisms, such that the rate of immigration, and therefore species richness, is greater on large
639 than small islands (Gilpin and Diamond 1976). The environmental heterogeneity of an island

640 also tends to scale positively with island area, such that spatially-variable selection allows more
 641 species to coexist on large than small islands (Whittaker and Fernandez-Palacios 2007). Finally,
 642 opportunities for speciation may be greater on large than small islands, thereby contributing to
 643 positive species-area relationships (Losos and Schluter 2000). Thus, drift, dispersal, selection
 644 and speciation can all explain or contribute to the species-area relationship. Similar arguments
 645 pertain to other common community patterns.

646 As such, perhaps the greatest challenge in community ecology is drawing the link
 647 between process and pattern. Community ecologists have, in fact, risen impressively to this
 648 challenge, by developing a suite of experimental and observational methods to tease apart the
 649 workings of particular communities in particular places, often providing critical guidance to
 650 applied management efforts (Simberloff 2004). It is, therefore, fairly straightforward to study
 651 processes at relatively small scales, or to document broad-scale community patterns. The “mess”
 652 stems from our inability to make general statements about process-pattern connections (Lawton
 653 1999; Simberloff 2004). Thus, there is a kind of black box in community ecology, within which
 654 are the innumerable ways to get from process to pattern (Figure 3), and it is disconcerting to
 655 many that when we peer into the box, what we see seems to be fundamentally system specific.
 656 Lawton (1999) takes this as a lesson that local experimental studies are no longer a fruitful
 657 avenue for pursuing generalities in ecology. Alternatively, it could be taken as a lesson that
 658 seeking generalities of the form “pattern X has a broadly-applicable explanation in simple theory
 659 Y” or “process Q is always the key to understanding community patterns” is bound to fail in
 660 community ecology. Generalities of the form “community patterns can be understood as the
 661 outcome of interacting processes A, B and C” seem more likely to hold. This paper is about
 662 defining the ABC’s of community ecology in the simplest possible, logically complete way.

663 EXISTING ORGANIZATIONAL FRAMEWORKS IN COMMUNITY ECOLOGY

664 A number of different frameworks have been put forth aimed at the conceptual
 665 organization of community ecology, or at least major parts of community ecology, with which
 666 the present framework can be compared. Ecology has a long history of debates centered around
 667 whether or not populations and communities reach some kind of equilibrium state – i.e., a
 668 “balance of nature” (Kingsland 1995). The conceptual framework presented here is silent on this
 669 issue – and indeed any issue regarding what has most often actually happened in nature – but is
 670 focused on conceptually organizing the processes that can influence what happens in
 671 communities whether at equilibrium or not.

672 At least three fairly recent conceptual frameworks are popular in the contemporary
 673 literature: equalizing vs. stabilizing mechanisms of coexistence (Chesson 2000), local vs.
 674 regional controls on community structure (Ricklefs and Schluter 1993), and the metacommunity
 675 concept (Holyoak et al. 2005). With respect to models of species coexistence, Chesson (2000)
 676 recognized two fundamental classes of mechanism – those that equalize fitness differences
 677 thereby slowing competitive exclusion (and possibly enhancing drift), and those that stabilize
 678 coexistence via negative density dependent selection. This framework is reflected in many of the
 679 recent efforts at synthesis under the rubric of niche-neutral reconciliation (e.g., Shipley et al.
 680 2006, Adler et al. 2007), and has proven very useful, but its domain is restricted to competitive
 681 coexistence and is focused almost entirely on local selection and drift.

682 The emphasis on historical and regional processes (Ricklefs and Schluter 1993) was
 683 developed to underscore the importance of processes occurring at broader spatial and temporal
 684 scales than is typically considered in traditional community ecology – namely speciation and
 685 long-range dispersal. The framework presented here shares much in common with the

686 perspective of Ricklefs and Schluter (1993). The graphical representation of their perspective
687 shows regional diversity determined by input via “biotal interchange” and “species production”
688 and output via “mass extinction”; local diversity is determined by input via “habitat selection”
689 and output via “stochastic extinction”, “competitive exclusion”, and “predatory exclusion”
690 (Figure 30.1 in Ricklefs and Schluter 1993). This perspective is quite similar to a common type
691 of graphical model showing a local community as the outcome of a series of filters, including
692 dispersal, the abiotic environment, and biotic interactions (e.g., Morin 1999). The conceptual
693 framework presented here takes these a step further by recognizing four distinct classes of
694 process, within which all others fall, which allows for a more comprehensive and logically
695 complete framework. For example, biotal interchange and habitat selection (as used by Ricklefs
696 and Schluter) both fall under dispersal, and competition and predation are only two of many
697 deterministic factors that can exclude species, all of which fall under selection.

698 The metacommunity framework explicitly encompasses drift, selection, and dispersal
699 (Holyoak et al. 2005). Speciation is not explicitly excluded, but is for the most part absent from
700 this framework. Within the metacommunity framework, four perspectives are recognized:
701 neutrality, patch dynamics, species sorting, and mass effects. These correspond loosely to
702 theoretical constructs or formalisms around which practicing ecologists have self-organized, but
703 in my opinion they do not represent fundamental, logically distinct classes of ecological process.
704 Mass effects, for example, include species sorting, and patch dynamics models can be neutral.
705 The metacommunity perspective also excludes from its purview community dynamics that do
706 not involve dispersal as a key component. For these reasons, the present framework is distinct
707 from the metacommunity perspective, although metacommunity models fit comfortably within it.

708 In addition to these three conceptual frameworks specifically focused on community
709 ecology, two highly influential theoretical frameworks that cut across sub-fields of biology, with
710 some connections to community ecology, are worth mentioning: the metabolic theory of ecology
711 (Brown et al. 2004) and ecological stoichiometry (Sterner and Elser 2002). In simple terms,
712 these two approaches explore the consequences of considering organisms essentially as physical
713 entities that process energy optimally given their size (metabolic theory), or that interact with
714 their environment based largely on their chemical composition (stoichiometry). In my opinion,
715 these frameworks are most powerful in aiding the understanding the functioning of individual
716 organisms or of the fluxes of energy and chemicals in whole ecosystems. The contributions of
717 these frameworks to community ecology, such as predictions concerning the effect of
718 temperature on species diversity (metabolic theory) or of plant-herbivore interactions
719 (stoichiometry), fall comfortably within the present framework, usually as mechanisms
720 underlying selection.

721 IMPLICATIONS

722 The first goal of this paper was to organize the material of community ecology in a
723 logically consistent way to clarify the similarities and differences among different conceptual
724 constructs in the discipline. One motivation was the common criticism that ecologists tend to
725 repeatedly reinvent the wheel: we claim ideas as new that are only subtly distinct, or not distinct
726 at all, from ideas put forth long ago (Lawton 1991; Graham and Dayton 2002; Belovsky et al.
727 2004). There are likely many reasons for this, but one important reason, at least in community
728 ecology, may be the lack of a coherent framework within which particular perspectives or
729 theories can be described and related. As such, a plethora of terms, each of which sounds new
730 and different, is often used to communicate much the same thing, such as niche processes,
731 species interactions, or species sorting to describe selection. It matters not whether selection is

732 the best term for deterministic fitness differences among species, but it is critical to recognize
733 that different mechanisms underlying selection, such as competition or predation, share more in
734 common with one another than either does with drift, dispersal or speciation.

735 Recognizing how different theoretical traditions in community ecology relate to one
736 another based on fundamental, logically distinct categories of process can potentially prevent
737 students from concluding from a Web of Science search that research on species sorting or
738 metacommunities goes back no more than 15-20 years. We might also make more modest, and I
739 believe realistic, assessments of the degree to which popular areas of research represent truly
740 new paradigms or (more likely) incremental advances on previous work. Placing ecological
741 ideas in their full historical context can curtail wheel reinvention and thus help to advance and
742 expand ecological understanding in the long term (Graham and Dayton 2002).

743 My hope is that the present framework will be useful to practicing community ecologists
744 as a way to place their research in a process-based context. I also think that this conceptual
745 framework can potentially be of great use in teaching and communicating the subject matter of
746 community ecology to a broader audience. As argued in the introduction, the traditional
747 presentation of community ecology can be confusing because the common threads among topics
748 such as food webs, competitive coexistence, and island biogeography are quite difficult to
749 discern. The essential similarities and differences among these theoretical traditions can be seen
750 quite clearly in the present framework (Table 2). The core subject matter in community ecology
751 need not change, but I believe there can be great benefit to shifting the emphasis away from an
752 organizational structure based on how researchers have carved out useful lines of inquiry, to one
753 based on the fundamental processes that underlie community dynamics and patterns.

754 The second goal of this paper was to articulate a general theory of community ecology.
755 Such a theory might seem so generalized as to be of little use, but the utility of the Modern
756 Synthesis in evolutionary biology – warts and all (Pigliucci 2007) – suggests otherwise. In
757 essence, the Modern Synthesis can be summarized as positing that genetic variation is created in
758 populations via mutation and immigration, and then shaped by drift and natural selection to drive
759 evolutionary change (Kutschera and Niklas 2004). The fact that the all-important mechanism of
760 heredity was essentially unknown until the rediscovery of Mendel made the construction of the
761 Modern Synthesis a profound scientific achievement in a way that cannot be matched in
762 community ecology, where the important rule of heredity is decidedly facile: elephants give rise
763 to elephants and daffodils to daffodils. However, on its own, the Modern Synthesis makes no
764 predictions about exactly how processes will interact to determine evolutionary change in any
765 particular situation, but simply establishes the fundamental set of processes that may be at work.

766 We can likewise articulate a very general theory of community ecology: *Species are*
767 *added to communities via speciation and dispersal, and these species' relative abundances are*
768 *then shaped by drift and selection, as well as ongoing dispersal, to drive community dynamics*
769 (Figure 4). The precise way in which these processes interact to determine community dynamics
770 varies tremendously from case to case, just as the processes that determine evolutionary change
771 interact in ways that vary tremendously from case to case. Stating a general theory of
772 community ecology in this way echoes the perspective of Ricklefs and Schluter (1993), and I
773 believe that recognizing this perspective as the community-ecological counterpart to the
774 evolutionary Modern Synthesis highlights an important sense in which community ecology
775 already has a general theoretical framework that is every bit as robust as that in population
776 genetics. The oft-cited recalcitrance of community ecology to generally applicable theory (e.g.,
777 Lawton 1999) seems like a fair assessment if the goal is to be able to make general predictions

778 about how particular processes have actually shaped real ecological communities. If the goal is
 779 to make general statements about the fundamental processes that can underlie community
 780 dynamics, and possible ways in which these can interact, community ecology appears to be in
 781 excellent shape.

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1008
1009TABLE 1
Definitions of terms.

Term	Definition
<i>Community</i>	A group of organisms representing multiple species living in a specified place and time
<i>Community ecology</i>	The study of patterns in the diversity, abundance, and composition of species in communities, and the processes underlying these patterns
<i>Community dynamics</i>	Change over time in the relative abundances of species in a specified area, including extinctions and species additions via dispersal or speciation
<i>Species composition</i>	For a given community, a state defined by the abundances of all species
<i>Species' relative abundance</i>	The proportion of all organisms in a given area that are of a given species; equivalent to species' frequency.
<i>Species' density</i>	The number of organisms of a given species per unit of space
<i>Community size</i>	The total number of organisms in a community
<i>Coexistence</i>	The indefinite persistence of a specified set of species in a specified area
<i>Absolute fitness</i>	The quantity of offspring produced by an individual organism per unit time, including survival of the organism itself
<i>Relative fitness</i>	The absolute fitness of a given organism divided by the mean absolute fitness across all individuals in the community
<i>Species' fitness (absolute or relative)</i>	The mean fitness (absolute or relative) across all individuals of a given species in the community; for absolute fitness, this is equivalent to the species' per capita population growth rate
<i>Selection</i>	A deterministic fitness difference between individuals of different species
<i>Drift</i>	Random changes in species' relative abundances
<i>Neutrality</i>	A state in which all individual organisms share identical demographic properties
<i>Speciation</i>	The creation of new species
<i>Dispersal</i>	The movement of organisms across space

TABLE 2

Twelve combinations of selection, drift, speciation and dispersal, and how existing ecological theories relate to these combinations.

	Selection	Drift	Speciation	Dispersal	Theories and models	Representative references
1	x				Niche models of all kinds (resource competition, predator-prey, food webs, etc.)	Tilman (1982); Chase & Leibold (2003)
2		x			Neutral theory I (demographic stochasticity)	Hubbell (2001)
3	x	x			Niche-neutral models (any niche model with demographic stochasticity)	Tilman (2004); Adler et al. (2007)
4	x		x		Historical/regional ecology I (species pool theory; diversity on gradients; speciation-selection balance)	MacArthur (1969); Ricklefs (1987)
5		x	x		Neutral model II - non-spatial	Hubbell (2001)
6	x			x	Metacommunities - deterministic (spatial mass effects, spatial food webs)	Holyoak et al. (2005)
7		x		x	Neutral model III (Island biogeography)	MacArthur & Wilson (1967); Hubbell (2001)
8	x	x	x		Historical/regional ecology II	Ricklefs (1987)
9	x		x	x	Historical/regional ecology III	Ricklefs (1987)
10		x	x	x	Neutral model IV – spatial	Hubbell (2001)
11	x	x		x	Metacommunities - stochastic (colonization-competition tradeoffs, stochastic versions of 6)	Holyoak et al. (2005)
12	x	x	x	x	The theory of ecological communities	This paper

1 **Figure captions**

2 **FIGURE 1. EXPECTED DYNAMICS AND EQUILIBRIA BETWEEN TWO SPECIES**

3 Examples for species A and B in a community of constant size are shown under (A)
4 constant selection favoring species A, (B) negative frequency-dependent selection, (C) positive
5 frequency-dependent selection, (D) complex frequency-dependent selection, and (E) no
6 selection. Solid and open circles indicate stable and unstable equilibria, respectively. Dotted
7 lines indicate the difference between the fitness of species A and species B. Arrows indicate the
8 change in species' frequencies. These figures are modeled after Nowak (2006). Note that when
9 species densities (rather than only frequencies) are of central interest, as in most models of
10 trophic interactions, each species density would need to be represented by a separate axis rather
11 than along a single axis, as in these simplified examples.

12

13 **FIGURE 2. FREQUENCY DYNAMICS OF TWO SPECIES UNDER DRIFT AND SELECTION.**

14 Dynamics are shown for two species A and B with non-overlapping generations in 10
15 simulated communities of constant size J with (A) no fitness differential and $J = 500$, (B) no
16 fitness differential and $J = 50$, (C) a 5% fitness advantage to species A and $J = 500$, and (D) a 5%
17 fitness advantage to species A and $J = 50$.

18

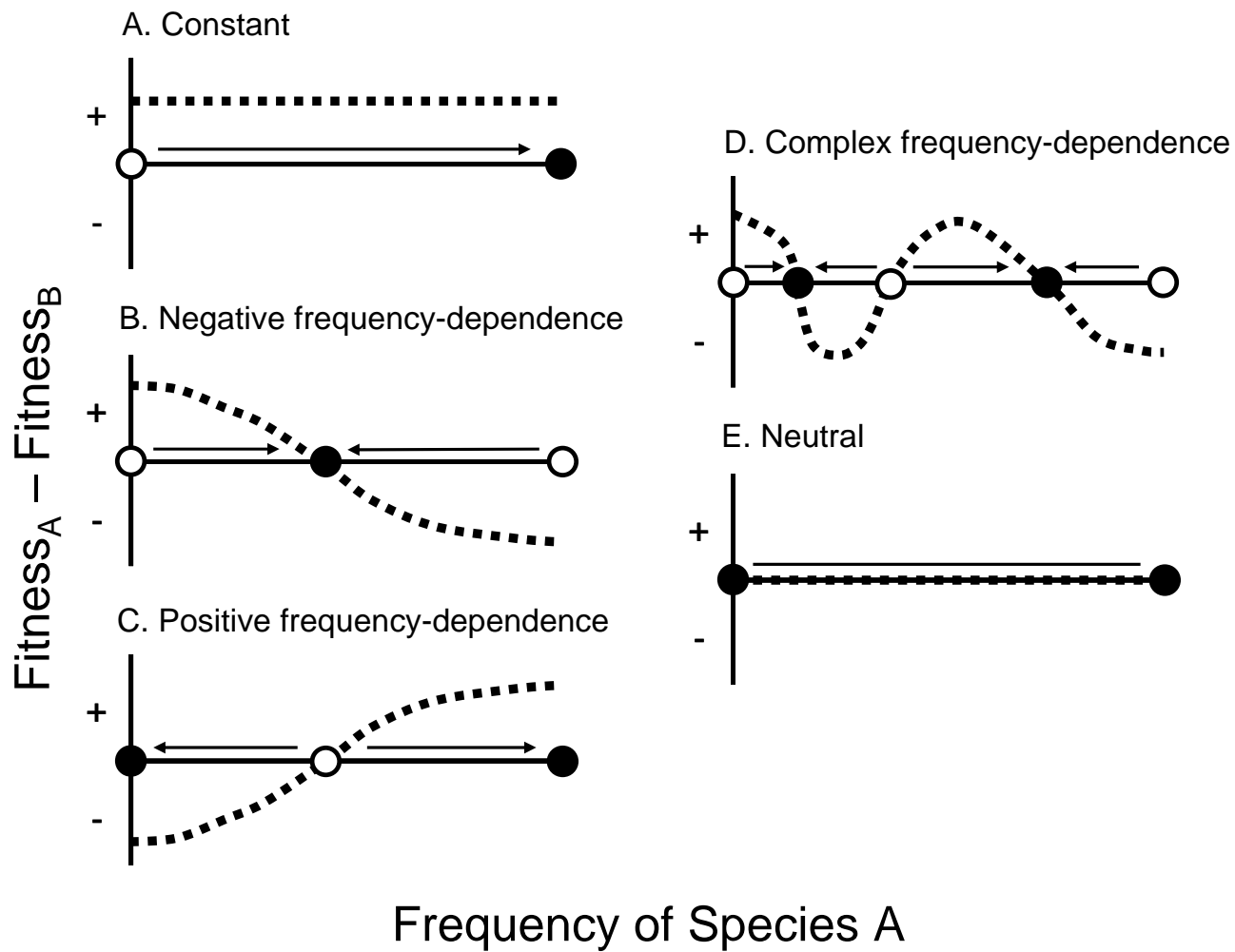
19 **FIGURE 3. THE BLACK BOX OF COMMUNITY ECOLOGY.**

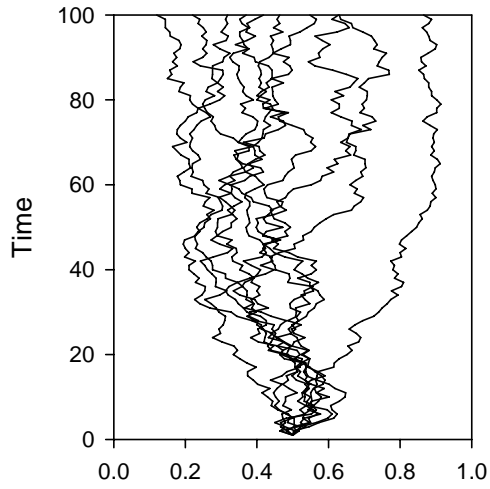
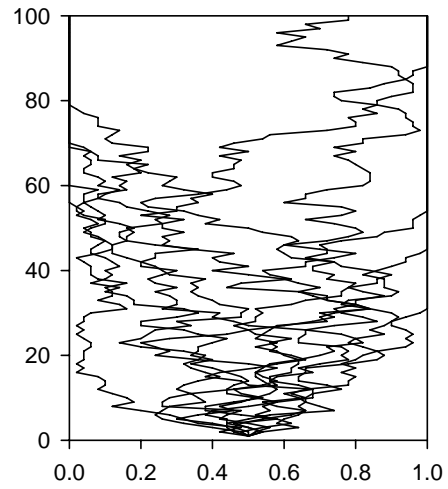
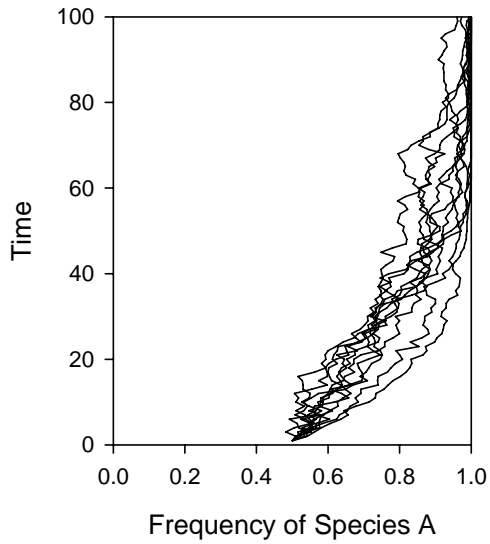
20

21 **FIGURE 4. THE THEORY OF COMMUNITY ECOLOGY.**

22 Selection, drift, speciation, and dispersal interact to determine community dynamics
23 across spatial scales. The delineation of discrete spatial scales is arbitrary, and used only for
24 clarity of presentation. Figure modified from Vellend and Orrock (2009).

25
26



A. Pure drift, $J = 500$ B. Pure drift, $J = 50$ C. $s = 0.05$, $J = 500$ D. $s = 0.05$, $J = 50$ 