



UNIVERSITY OF LEEDS

This is a repository copy of *Conceptualizing communities as natural entities: a philosophical argument with basic and applied implications*.

White Rose Research Online URL for this paper:
<http://eprints.whiterose.ac.uk/122380/>

Version: Accepted Version

Article:

Steen, DA, Barrett, K, Clarke, E orcid.org/0000-0003-1839-6405 et al. (1 more author) (2017) Conceptualizing communities as natural entities: a philosophical argument with basic and applied implications. *Biology and Philosophy*, 32 (6). pp. 1019-1034. ISSN 0169-3867

<https://doi.org/10.1007/s10539-017-9589-8>

© Springer Science+Business Media B.V. 2017. This is an author produced version of a paper published in *Biology & Philosophy*. The final publication is available at Springer via <https://doi.org/10.1007/s10539-017-9589-8>. Uploaded in accordance with the publisher's self-archiving policy.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>

1 Abstract. Recent work has suggested that conservation efforts such as restoration ecology
2 and invasive species eradication are largely value-driven pursuits. Concurrently, changes
3 to global climate are forcing ecologists to consider if and how collections of species will
4 migrate, and whether or not we should be assisting such movements. Herein, we propose
5 a philosophical framework which addresses these issues by utilizing ecological and
6 evolutionary interrelationships to delineate individual ecological communities.
7 Specifically, our Evolutionary Community Concept (ECC) recognizes unique collections
8 of species that interact and have co-evolved in a given geographic area. We argue this
9 concept has implications for a number of contemporary global conservation issues.
10 Specifically, our framework allows us to establish a biological and science-driven context
11 for making decisions regarding the restoration of systems and the removal of exotic
12 species. The ECC also has implications for how we view shifts in species assemblages
13 due to climate change and it advances our understanding of various ecological concepts,
14 such as resilience.

15

16 Keywords: climate change, community, invasive species, resilience, reference condition,
17 restoration

18

19 **Introduction**

20 Ecological restoration focuses either on the repair of “damage caused by humans
21 to the diversity and dynamics of indigenous ecosystems” (Jackson et al. 1995) or on the
22 recovery of those ecosystems (SER 2004). However, recent work has questioned the
23 relative roles of scientific, ethical and aesthetic principles in establishing the value of

24 such ecosystems and the consequential prioritization of management actions (Higgs
25 1997). For example, Davis and Slobodkin (2004) argue that communities have no
26 “...intrinsic evolutionary or ecological purpose...” and therefore it is not valid to,
27 “...invoke any ecological (or evolutionary) rationale to establish particular restoration
28 goals.” The argument has also been made that attempting to restore communities is a
29 value-driven pursuit based more on human judgments than on ecological structure and
30 processes (Choi 2007). Others recognized the role of value-driven goals in restoration
31 while suggesting that ecological restoration has a foundation with empirical support
32 (Winterhalder et al. 2004).

33 While philosophers debate whether restoration of ecological communities is
34 justified, the practice is occurring on large scales; we suggest this disparity is encouraged
35 by a lack of prior clarity about what the relevant entities are, what criteria are used to
36 delineate them, and why. Although the concept of a community is frequently invoked as
37 the relevant target of restoration, there has been little examination into how to
38 differentiate among communities or identify them as ecological entities. Given the
39 relevance of a community concept to current ecological and conservation-oriented
40 problems the need for introspection is clear (Simberloff 2004).

41 The effective restoration of communities is hindered by a lack of consistency
42 regarding what a community is; numerous definitions have been developed (McCoy and
43 Shrader-Frechette 1992, Mikkelson 1997). For example, definitions include those that
44 stress dominant species (e.g., Ricklefs 1990), interactions (e.g., Wilbur 1972, Holt 1977),
45 or statistical properties (Field et al. 1982; Clarke 1993; Leaper et al. 2014). Some
46 researchers have presented more refined definitions (e.g., Looijen and Andel 1999) to

47 enhance precision for addressing ecological questions while others have argued that a
48 very general definition for what constitutes a community will suffice for most studies
49 (Fauth et al. 1996, McGill 2010). The existence of multiple definitions of a community
50 can probably be attributed to the complexity of these systems, which tends to preclude
51 development of general laws (Lawton 1999). In any case, given a relative inability to
52 define a community it should not be particularly surprising that some have suggested they
53 are of little importance (Ricklefs 2008).

54 Restoration efforts often presuppose an implicit concept of the target of
55 restoration, typically a community or species assemblage within a given area. However,
56 one consequence of the ambiguity surrounding restoration targets and a lack of
57 consistency regarding community definitions is that we risk managing damaged
58 ecosystems so that they move toward conditions that represent a reconstructed system
59 with missing or novel parts. At the same time, rapidly changing climates and landscapes
60 limit our ability to achieve restoration targets based largely on historical conditions (e.g.,
61 Jachowski et al. 2015); however we suggest below that the evolutionary interactions
62 existing within communities contain information that can help guide the formation of
63 restoration targets. We provide an explicit characterization and justification of this
64 concept, which we will call the Evolutionary Community Concept (ECC).

65

66 **What is an Evolutionary Community?**

67 We propose that an Evolutionary Community is conceptualized as a unique assemblage
68 of species, which occurs in a given geographic area and is connected by interspecific and
69 abiotic interactions that have evolved over time. As the name suggests, our concept

70 foregrounds evolutionary considerations. In generating this concept we favor ultimate
71 over proximate approaches to community ecology (Losos 1996). Proximate approaches
72 concern themselves with, "the processes occurring within communities and the effect
73 those processes have on community structure" (Losos 1996). However, the species
74 present in a given area are not solely influenced by current forces and may be a function
75 of the evolution of a particular lineage in a given area (Helmus et al. 2007, Cavender-
76 Bares et al. 2009). Ultimate approaches to community ecology, which acknowledge that
77 evolutionary lineages are likely to be spatially constrained, come closer to helping us
78 conceptualize communities as something more than just a collection of arbitrary species.
79 Such an approach is defined by Losos as, "involv[ing] study of why communities have
80 particular organization and why differences exist between communities [emphasis ours]"
81 (Losos 1996).

82

83 **Evolutionary Communities are Natural Entities**

84 Natural entities are widely recognized as those objects or systems that exist as
85 entities without regard to human actions or beliefs (Eldredge 1985, Lo 1999, Castree
86 2004, Katz 2009). An extensive literature has developed around the argument that
87 biological species are a particular type of natural entity – an individual (Hennig 1966,
88 Ghiselin 1987, Hull 1976, Wiley 1980, Holsinger 1984, Mishler and Brandon 1987,
89 Ereshefsky 1992, Baum 1998, Coleman and Wiley 2001, Mayden 2002, Rieppel 2007,
90 Reydon 2009). A similarly useful framework was provided more recently regarding areas
91 of endemism (Crother and Murray 2011). Communities differ from areas of endemism
92 because they cannot be identified from a single species and they are not hierarchical (i.e.,

93 larger communities do not necessarily contain smaller ones). Further, communities are
94 not characterized by endemic species on any scale and do not require them to be
95 identified as a unique individual. Finally, the structure and composition of communities
96 are influenced by interspecific, as well as abiotic, interactions (Fontaine et al. 2011) that
97 have coevolved over time, which may or may not be true for areas of endemism. We do
98 not make the claim that ecological communities are individuals in a metaphysical sense;
99 however, we believe the established framework is useful for developing an understanding
100 of ecological communities as natural entities.

101

102 **A framework for identifying communities as natural entities**

103 **Boundaries**

104 Eldredge (1985 p. 162) states that, “some ecologists...take strong issue with the
105 suggestion that communities can be construed as individuals. The problem seems to come
106 from the apparent lack of definitive boundedness to such entities.” Evolutionary
107 Communities, like species, have fuzzy boundaries in space and time. Nevertheless,
108 Evolutionary Communities, we argue, are like species in being natural ecological entities
109 that exist independent of anthropogenic naming conventions. Their spatial and temporal
110 boundaries are determined by natural evolutionary processes, rather than by us and it is
111 the gradualness of evolution that explains the fuzziness of those boundaries (Clarke &
112 Okasha 2013). Previous concepts suggesting that communities are natural entities (e.g.,
113 Clements 1916) may have been evaluated unfairly by imposing an expectation that
114 temporal and spatial boundaries between communities should necessarily be sharp.
115 Although it is possible to delineate a discrete boundary surrounding an assemblage by

116 stipulating a threshold for a particular variable (such as the density of a given species or
117 interaction) (e.g., Highton 1989), such thresholds will always be arbitrary (Frost and
118 Hillis 1990). Even organismal boundaries admit fuzziness when we consider, for
119 example, strands of hair. Allowing a certain degree of fuzziness when delineating
120 boundaries is not a concession to our limitations at identifying their extent but rather a
121 more accurate characterization of the entity in question (Baum 1998).

122 Evolutionary Communities, like organisms and like species, can be fuzzily
123 bounded. However, we can determine approximate spatial bounds according to
124 biogeographical patterns in species richness and composition. For example, an area's
125 biological uniqueness may be inferred after using null models to demonstrate that
126 observed patterns differ from random expectations (e.g., the mid-domain effect;
127 Wollenberg et al. 2008, Kozak and Wiens 2010). It is necessary to have some a priori
128 designation of the spatial boundaries of areas so that patterns of species richness may be
129 compared for these analyses; operationally, areas may be defined by a grid system (e.g.,
130 Hawkins and Diniz-Filho 2002), political boundaries (e.g., Means and Simberloff 1987),
131 or elevation (e.g., McCain 2004). Species composition may allow us to distinguish
132 between areas with similar species richness patterns. If a group of species occurs in
133 sympatry more frequently than expected (e.g., as defined by null models; Gotelli 2000),
134 this suggests the area is subject to ecological or evolutionary forces resulting in a
135 particular species assemblage. If these same species occur together more frequently in a
136 given geographical area than they do in other geographic areas, these areas may be
137 considered discrete. In addition to co-occurrence analyses, parsimony analysis of
138 endemism (Morrone 1994) is a method of identifying areas with unique species

139 compositions and analyses may be performed to determine areas of endemism that cluster
140 significantly frequently (Huang et al. 2008), a feature that may aid in development of
141 hypotheses for the historical origin of communities.

142 Like species, Evolutionary Communities will also have fuzzy temporal bounds.
143 Over time, extirpation and colonization may shift species composition patterns such that
144 they cease to be different from nearby geographic areas. Species that were part of a
145 community may alter or cease interactions with other species in a way that is outside the
146 bounds of the distribution by which they were previously characterized. Conversely, at
147 some point in time, random species assemblages in a given area can become non-random
148 and different from other areas. Species within such areas would likely begin interacting
149 and shaping the evolutionary trajectories of one another. So, although it is operationally
150 difficult to pinpoint precise beginnings or ends, it is theoretically plausible that one could
151 assign temporal boundaries to a unique group of species within a spatial area (Figure 1A).
152 Species concepts such as the Phylogenetic Species Concept (Cracraft 1983, 1987) may
153 provide an analogous solution toward resolving the temporal beginning and end of a
154 community.

155 The temporal bounds of an Evolutionary Community will be determined by
156 several causes, including anthropogenic climate change or succession (Gleason 1926;
157 Figure 1B, C) and biogeography (Wiley 1988). Individual phylogenies of species are
158 influenced by vicariance and dispersal events, and these individual phylogenies may
159 ultimately influence community assembly (Webb et al. 2002; Figure 1D). It is also the
160 case that such biogeographic events may act directly on the incipient community, rather
161 than being propagated through species. For example, the creation of a river, or separation

162 of tectonic plates could split a community, a divergence of ecological significance
163 resulting in a rather sharp boundary. Similarly, the removal of geographic barriers will
164 allow two communities to converge.

165 It follows from the ECC that a given area will possess multiple communities over
166 geological and ecological time as changing climates, autogenic, and allogenic processes
167 alter habitat suitability for a given suite of species. Because species and interactions will
168 be replaced over time, succession will also result in multiple communities. Nevertheless,
169 the scale of relevance to most ecological studies suggests communities can change to
170 some degree through time yet retain their identity. Individual organisms may undergo
171 relatively drastic changes over the course of their lives – such as in the case of a tadpole
172 developing into a frog or a caterpillar into a butterfly – while retaining their identity (Hull
173 1976). Similarly, Evolutionary Communities will change, for example as when
174 populations of competitors, or of predator and prey, fluctuate in abundance. Fluctuations
175 in the frequency, duration, or intensity of natural disturbance may also occur. If
176 organisms and species can change, within certain limits, and stay the same individual,
177 then Evolutionary Communities can too. So long as the unique coevolved assemblage of
178 species and their associated interactions are extant and functional, an Evolutionary
179 Community remains the same individual.

180 **An Ostensive Definition**

181 Evolutionary Communities, like species, lack essential intrinsic properties. For
182 example, no list of intrinsic properties can be considered as necessary and sufficient for
183 qualifying as a tiger, because tigers evolve continuously and without limit (Hull 1994).
184 There is no characteristic whose appearance would make a tiger's cub into a member of a

185 new species (Sober 1994). New species come into being gradually, over lengthy
186 timescales, as a consequence of speciation events which break down the cohesive forces
187 which hold the members of a species together. Likewise, Evolutionary Communities may
188 not be defined by any list of member species or other structural or functional
189 characteristics. They are bounded only by discontinuities in the form or pattern of
190 interactions amongst their parts – though it may be up to us to set thresholds for these
191 discontinuities.

192 As noted above, certain species will co-occur together within a given area more
193 often than expected by chance and more often than they co-occur together elsewhere.
194 These species are often considered specialists of a given habitat with limited geographic
195 distributions. Indicator species analysis (Dufrêne and Legendre 1997) may be a useful
196 means of identifying characteristic species of a given area. Such species help diagnose
197 communities based on their presence in a manner to analogous to genes providing
198 guidance for the diagnosis of species. For example, at the scale of a forest stand, the
199 presence of longleaf pine (*Pinus palustris*), gopher tortoises (*Gopherus polyphemus*), red-
200 cockaded woodpeckers (*Picoides borealis*), and wiregrass (*Aristida* sp.) in a given area is
201 sufficient to identify that the assemblage is unique to the Coastal Plain of the
202 Southeastern United States. In sum, we can define communities ostensibly by observing
203 characteristic species in a certain place at a certain point of time and documenting a
204 history of interactions that shaped the evolution of these species. The presence or absence
205 of any one of these species is not sufficient to consider the community extinct, just as the
206 presence or absence of a single gene would not cause of us to re-evaluate the status of

207 most species. Nevertheless, at some point of loss or gain of species and their interactions
208 community identity would change.

209 We must revisit the issue of scale. If our area of interest was planet Earth and we
210 wished to compare the species assemblage of Earth to neighboring planets, then every
211 species is an indicator of Earth. As the focal scale decreases, widespread species will
212 begin to stop playing a role in what makes a given area unique. For example, the gopher
213 tortoise is an indicator of Earth, the continent of North America, the Coastal Plain of
214 southeastern United States, and the longleaf pine forest, but not the pitcher plant bogs that
215 may occur within longleaf pine forests. Beyond the scale of the longleaf pine forest, the
216 gopher tortoise is not useful for differentiating between areas.

217 This matter of scale may shed some light on controversial subjects in ecology.
218 Neutral theory (Hubbell 2001) suggests communities may be comprised of assemblages
219 of organisms arising from forces independent of species interactions. Similarly, Gleason
220 (1927) argued that the structure of a particular assemblage is due largely to pioneering
221 species; these species become established due to their dispersal abilities, rather than
222 because they belong to any discrete entity. These ideas, at least on small temporal and
223 spatial scales, appear to run counter to some of community ecology's most basic
224 underpinnings (Chase and Leibold 2003). We suggest that examining an assemblage at an
225 inappropriate scale may encourage misleading interpretation. Continuing our longleaf
226 pine forest example, quantifying species composition within forest stands of a few
227 hectares each may reveal that the species within each stand appear random. However, at a
228 larger scale, the species characteristic of longleaf pine forests are different than those that

229 appear in a ponderosa pine (*Pinus ponderosa*) forest, or in the Sonoran desert. At this
230 scale, species assemblages are not random, they are distinct.

231 **Community Cohesion**

232 The parts that make up Evolutionary Communities are heterogeneous, rather than
233 conforming to a common type, but are bound into a single entity by virtue of historical
234 causal connections. Organisms are bound into a common species thanks to reproductive
235 and ecological interactions. What processes cause an assemblage of species cohere into a
236 community? We argue that the parts of Evolutionary Communities are bound together by
237 interspecific interactions in a shared biotic and abiotic environment, which promote co-
238 evolution and community structure and dynamics (Johnson and Stinchcombe 2007). For
239 example, longleaf pine trees are conduits for lightning strikes that ignite a highly
240 flammable understory, often including dropped longleaf pine needles (Platt et al. 1988).
241 The resulting ground fires are necessary for reproduction of other species (e.g., wiregrass;
242 Mulligan and Kirkman 2002) and maintain habitat suitable for others (e.g., gopher
243 tortoises, Yager et al. 2007). Gopher tortoises, through the process of burrow creation,
244 provide structure important to other species (e.g., Jackson and Miltrey 1989, Kinlaw and
245 Grasmueck, 2012). The establishment of one or more of the species listed above
246 facilitated the persistence of additional species. In addition, a change, such as gradual
247 climate change that alters the abiotic conditions in a given area, will likely reduce habitat
248 suitability for one or more species. Due to the influence of interspecific interactions,
249 many species within the unique assemblage are likely to respond cohesively.

250 If we recognize an Evolutionary Community as a natural entity, for example, the
251 longleaf pine forest community, there cannot be another longleaf pine forest community.

252 This does not preclude the possibility that the long leaf pine community has many parts
253 that are separated in time and space, as long as we assume that these parts are linked via
254 current ecological interactions (e.g., via dispersal events), or through their historical
255 evolutionary interactions. As an analogy, populations of the same species frequently
256 occur in different and isolated areas. Similarly, there can be many members of an
257 ecological community that are naturally isolated, such as pitcher plant bogs or Carolina
258 bays, or were once continuous but have now been fragmented by anthropogenic
259 influences, such as the longleaf pine forest.

260

261 **Applications of the Evolutionary Community Concept**

262 **Exotic Species**

263 Perhaps the most relevant application of the ECC concerns exotic species (i.e., a
264 species living outside its native range, Hunter 1996) and particularly those exotic species
265 that become invasive (e.g., Fritts and Rodda 1998). Invasive species management is often
266 driven by a desire to rid a particular area of species deemed damaging to the native
267 species or communities (e.g., brown tree snakes, *Boiga irregularis*, in Guam) but this
268 type of management has been criticized as potentially xenophobic or based primarily on
269 ethics (e.g., Brown and Sax 2005). This criticism is likely encouraged by the fact that
270 identification of communities has heretofore been subjective (Simberloff et al. 2003) and
271 did not sufficiently differentiate between species considered native versus those that are
272 considered introduced (e.g., Fauth et al. 1996). However, if communities are spatially and
273 temporally bounded and consist of a unique assemblage of species and their associated
274 interactions, then exotic species threaten their continuity. Removal of invasive species

275 can be justified not because they are ugly or non-traditional, but only because their
276 interactions with the other members of the community are not part of the evolutionary
277 history of that community. This fact alone may not be viewed by many as sufficient to
278 justify removal of exotic species. Finding such a justification is not our purpose; instead,
279 we aim to expand the theoretical context around which such debates take place.

280 Because humans influence the planet on a scale larger than any other single
281 species (Vitousek et al. 1997), it is reasonable to categorize human activity as distinct
282 from other biotic processes. Species physically moved by humans or whose movements
283 were facilitated through infrastructure, such as imported decorative plants, invertebrates
284 within ballast water, or escaped pets, are not components of the native communities they
285 were introduced into. The proximate cause of invasion by many species is clearly direct
286 human intervention and their presence in an area is not due to the community's unique
287 evolutionary lineage. Because exotic species may result in the functional extirpation of a
288 native species, as well as the functional extinction of interactions between native species
289 (e.g., Ricciardi and Simberloff 2009), they may result in the demise of the original
290 community. Consequently, under the ECC, efforts to eradicate exotic species are
291 consistent with a desire to maintain a community's identity while assisted migration
292 efforts (McLachlan et al. 2007) are not if they result in a species interacting with other
293 species different from those it evolved alongside.

294 Some have argued that the presence of exotic species in a given area may have
295 conservation benefits (Schlapefer et al. 2011), by providing ecosystem services or when
296 exotic species fill the role of extinct organisms. For example, coyotes have colonized
297 the eastern coast of the United States and largely fill the niche of extirpated wolf

298 populations (Tingley et al. 2009). In this case, although co-evolution was not a factor in
299 an exotic species' role within a community, its role is indistinguishable from those that
300 arise from co-evolutionary processes. If we regard the interspecific interactions a species
301 partakes in as the defining component of its identity, we may recognize these exotic
302 species as components of communities. However, if we regard identity as a function of
303 unique evolutionary trajectories and spatio-temporal boundaries, as outlined in this essay,
304 then exotic species can never be components of communities. This dichotomy has
305 important implications for the debate regarding whether restoration of ecological
306 processes may be more important than the species used to restore them (e.g., Pleistocene
307 re-wilding of North America; Donlan 2005).

308 **Climate Change**

309 We lay out an argument here that a subset of species within an area comprise a
310 unique assemblage, are strongly interacting, and are consistently present within a given
311 community type and not elsewhere. It is these species that help us differentiate among
312 communities. The ECC has immediate implications for how to view changing global
313 dynamics. For example, climate change is expected to elicit species-specific responses
314 (Davis and Shaw 2001) and range shifts among individual species (Parmesan and Yohe
315 2003), which may in turn lead to community disassembly (Thuiller 2004) and eventually
316 the formation of new communities. If one views communities simply as the groups of
317 species residing within a given area, the effects of climate change may be mitigated by
318 complex landscapes, which will likely continue to harbor a diversity of species
319 (Anderson and Ferree 2010). However, if we recognize the importance and unique nature
320 of interspecific interactions, we may be less optimistic regarding how communities will

321 fare in response to anthropogenic-driven climate change, as interacting species may have
322 varying abilities to adapt and persist (e.g., Parmesan 2006). The way we conceptualize
323 communities should not change the adaptation strategies we consider in the context of
324 changing climates (e.g., Stein et al. 2013); however, the ECC offers a baseline against
325 which future management options can be assessed.

326 **Reference Conditions**

327 Many restoration efforts are gauged by comparison to reference communities and
328 environmental trajectories. However, current definitions for communities characterized
329 by dominant species, interactions, or statistical properties are often inconsistent with the
330 goals of restoration ecology. In the United States, for example, restoration ecology is
331 often primarily concerned with returning degraded communities into a condition
332 consistent with the species composition and abundance that may be expected prior to
333 modern agricultural and industrial modification of the landscape, or alternatively, what
334 we would expect to see today in a given area if that past modification had never occurred.
335 It is thought that these target conditions, which will always include some degree of
336 natural variation (White and Walker 1997), likely best represent the ancestral condition.
337 The ECC, which posits that these target communities are natural entities due to their
338 unique species assemblages, evolutionary histories, and interspecific interactions, offers a
339 scientific rationale for this approach.

340 Ethical and aesthetical considerations will remain important in choosing one set
341 of reference conditions over another – for example in determining the point in time used
342 to assess reference communities. However, such deliberations will act as supplements to,
343 rather than replacements for, objective considerations involving the suitability of current

344 climactic conditions and the co-evolved dependencies between different parts of a
345 community. We do not include a particular species as a component of a target condition
346 because it is beautiful or for historical accuracy, but because the rest of the community
347 depends upon it.

348 Disruption of natural disturbance regimes within a given community may
349 encourage the proliferation of a species previously present at low levels. Although these
350 species are not exotic, they may disrupt the continuity of a community. For example, fire-
351 suppression of longleaf pine forests allows oak trees to increase in abundance, resulting
352 in a change in the habitat structure and a reduction in habitat quality for other species
353 (Mitchell et al. 2006). This change may eventually result in a transition to a different
354 community. Therefore, efforts to restore natural disturbance regimes and manage species
355 to levels that best typify a community are warranted, if the goal is to maintain a
356 community that exists due to natural processes.

357 Although a common focus of restoration ecology is restoring lost communities
358 (SER 2004), it is implied by the individuality of Evolutionary Communities that once
359 lost, communities can never be recreated (Katz 2009). Once an organism dies, it is
360 impossible for a new organism to be numerically identical with the lost creature, no
361 matter how similar they may be. This is because the causal-historical connections which
362 bind the parts of an individual together have been severed. Similarly, we once assumed
363 that an extinct species could not be resurrected. Recent technological advancements
364 challenge the idea that extinction is forever (Sherkow and Greely 2013). Similar to
365 species resurrection, we argue that it is possible to conceptualize how Evolutionary
366 Communities can be reborn. For example, constituent species of a community could

367 endure throughout the period in which the Community is missing (such as when habitat
368 quality degrades). If those species are not subject to sufficient evolution such that their
369 response to and interaction with the other members of the Community cannot be re-
370 established, then community rebirth is plausible. In other words, we can consider the
371 relevant ecological interactions to be merely paused, while the Community is
372 disassembled, rather than entirely severed. In these cases, restoration of the abiotic
373 environment and the appropriate assemblage of species can result in the ecological
374 interactions resuming as before (Gibbs et al. 2007).

375 Restoration ecologists often strive to replicate the species composition and
376 abundance derived from a unique evolutionary history and use dominant species,
377 interactions, or statistical properties as secondary metrics to evaluate success. For
378 example, much has been discussed regarding the relative merits of focusing on one
379 species for conservation efforts versus a suite of species (e.g., Lambeck 1997, 2002,
380 Lindenmayer et al. 2002) or even entire communities (Simberloff 2004). However, the
381 ultimate goal is always the same, i.e., to restore, or at least conserve in some form, the
382 group of species in a given area that best represents what was found in the area due to
383 evolutionary processes.

384 **Community Resilience**

385 Resilience refers to the time required for a system to return to its equilibrium
386 following disturbance (Pimm 1984). Our conceptualization allows a community to
387 experience some change, therefore we can incorporate ecological resilience. For example,
388 if we define a longleaf pine community as any forest dominated by *P. palustris*,
389 exhibiting a set of characteristic co-evolved traits, and subject to frequent (<3 yrs) fire,

390 then the forest is no longer a longleaf pine community once some threshold of time has
391 passed without a fire. Although a forest that has been fire-suppressed for a few years will
392 likely appear somewhat different than a forest that was burned more frequently, this is
393 due primarily to fluctuations in the densities of species that were always present. Even
394 after a *P. palustris*-dominated forest is fire-suppressed for decades, restoration of fire
395 alone is sufficient to alter the structural components of the forest (e.g., vegetation, bird
396 and reptile populations) such that they are indistinguishable from forests that have been
397 burned regularly (Outcalt and Brockway 2010; Steen et al. 2013a, b). Over this time
398 period, we argue that it makes most sense to conceive of a longleaf pine community as a
399 single entity that experiences some degree of change over time. However, once the
400 unique species assemblage begins to change through extirpation and colonization, the
401 original community has ceased to exist and can never return to an equilibrium.

402 **Conclusion**

403 We have presented a concept which treats communities as entities that have
404 formed over evolutionary time; this concept allows for a philosophical platform to help
405 us understand what many conservation and restoration efforts are trying to accomplish
406 (Table 1). In doing so, we have built upon the work of Losos (1996), who identified a
407 dichotomy in how communities are conceptualized; specifically, our conceptualization
408 complements work emphasizing the importance of historical influences in current
409 community structure (e.g., Losos 1996, Ricklefs 2008, Cavender-Bares et al. 2009). If the
410 components of a community result from historical forces, it is likely most appropriate to
411 consider these forces when defining a community. Restoration ecology goals and

412 ecological questions should be focused on the unique species assemblage of a given area
413 as well as the associated evolution interactions among species and abiotic factors.

414 **Literature cited**

415 Anderson MG, Ferree CE (2010) Conserving the stage: climate change and the
416 geophysical underpinnings of species diversity. PLoS ONE 5:e11554.

417 Baum DA (1998) Individuality and the existence of species through time. Syst Biol
418 47:641–653

419 Brown JH, Sax DF (2005) Biological invasions and scientific objectivity: reply to Cassey
420 et al. (2005). Austral Ecol 30:481–483

421 Castree N (2004) Nature is dead! Long live nature! Environment and Planning A 36: 191
422 – 194

423 Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of
424 community ecology and phylogenetic biology. Ecol Lett 12:693-715

425 Chase JM, Leibold MA (2003) Ecological Niches. The University of Chicago Press,
426 Chicago, IL

427 Choi YD (2007) Restoration ecology to the future: a call for new paradigm. Restor Ecol
428 15:351-353

429 Clarke KR (1993) Non-parametric multivariate analyses of changes in community
430 structure. Aust J Ecol 18:117-143

431 Clarke E and S Okasha (2013) Species and organisms: what are the problems? In:
432 Bouchard F and P Huneman (eds) From Groups to Individuals: evolution and
433 emerging individuality. The MIT Press, pp 55-76

434 Clements FE (1916) Plant succession. Carnegie Institution of Washington Publishing No.
435 242

436 Coleman KA, Wiley EO (2001) On species individualism: a new defense of the species-
437 as-individuals hypothesis. *Phil Sci* 68:498–517

438 Cracraft J (1983) Species concepts and speciation analysis. *Curr Ornithol* 1:159-187

439 Cracraft J (1987) Species concepts and the ontology of evolution. *Biol Phil* 2:63-80

440 Crother BI, Murray CM (2011) Ontology of areas of endemism. *J Biogeog* 38:1009-1015

441 Davis, MA, Slobodkin LB (2004) The science and values of restoration ecology. *Restor*
442 *Ecol* 12:1-3

443 Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate
444 change. *Science* 292:673-679

445 Donlan, J (2005) Re-wilding North America. *Nature* 436:913-914

446 Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a
447 flexible asymmetrical approach. *Ecol Monogr* 67:345–366

448 Eldredge N (1985) Unfinished synthesis: biological hierarchies and modern evolutionary
449 thought. Oxford University Press, New York, NY

450 Ereshefsky M (1992) Units of evolution: essays on the nature of species. MIT Press,
451 Cambridge, MA

452 Fauth JE, Bernardo J, Camara M, Resetarits WJ Jr, Van Buskirk J, McCollum SA (1996)
453 Simplifying the jargon of community ecology: a conceptual approach. *Am Nat*
454 147:282-286

455 Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies
456 distribution patterns. *Marine Ecology - Progress Series*, 8:37-52

457 Fontaine C, Guimarães PR Jr, Kéfi S, Loeuille N, Memmott J, van der Putten WH et al.
458 (2011) The ecological and evolutionary implications of merging different types of
459 networks. *Ecol Lett* 14: 1170-1181

460 Fritts TH, Rodda GS (1998) The role of introduced species in the degradation of island
461 ecosystems: a case history of Guam. *Ann Rev Ecol Syst* 29:113-140

462 Frost DR, Hillis DM (1990) Species in concept and practice: herpetological applications.
463 *Herpetologica* 46:87-104

464 Ghiselin MT (1987) Species concepts, individuality, and objectivity. *Biol Phil* 2:127-143

465 Gibbs JP, Marquez C, Sterling EJ (2007) The role of endangered species reintroduction
466 in ecosystem restoration: tortoise-cactus interactions on Espanola Island,
467 Galapagos. *Restor Ecol* 16:88-93

468 Gleason HA (1926) The individualistic concept of the plant association. *Bull Torrey Bot*
469 *Club* 53:7-26

470 Gleason HA (1927) Further views on the succession concept. *Ecology* 8:299-326

471 Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 2606-
472 2621

473 Hawkins BA, Diniz-Filho JAF (2002) The mid-domain effect cannot explain the diversity
474 gradient of Nearctic birds. *Global Ecol Biogeog* 11:419-426

475 Helmus MR, Savage K, Diebel MW, Maxted JT and Ives AR (2007) Separating the
476 determinants of phylogenetic community structure. *Ecol Lett* 10:917-925

477 Hennig W (1966) *Phylogenetic Systematics*. University of Illinois Press, Urbana, IL.

478 Higgs ES (1997) What is good ecological restoration? *Cons Biol* 11:338-348

479 Highton R (1989) Biochemical evolution in the slimy salamanders of the Plethodon
480 glutinosus complex in the eastern United States. Part I. Geographic protein
481 variation. Illinois Biol Monogr 57:1-78

482 Holt RD (1977) Predation, apparent competition and the structure of prey communities.
483 Theor Popul Biol, 12:197–229

484 Holsinger KE (1984) The nature of biological species. Phil Sci 51:293-307

485 Huang X, Lei F, Qiao G (2008) Areas of endemism and patterns of diversity for aphids of
486 the Qinghai-Tibetan plateau and the Himalayas. J Biogeog 35:230-240

487 Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography.
488 Princeton University Press. Princeton, NJ

489 Hull DL (1976) Are species really individuals? Syst Zool 25:174–191

490 Hull DL (1994) A matter of individuality. In: Sober E (ed) Conceptual Issues in
491 Evolutionary Biology, 3rd edition. The MIT Press. pp 363-386

492 Hunter ML Jr (1996) Fundamentals of Conservation Biology. Blackwell Science.
493 Cambridge, Massachusetts

494 Jachowski DS, Kesler DC, Steen DA, Walters JR (2015) Redefining baselines in
495 endangered species recovery. J Wild Mgmt 79:3-9

496 Jackson DR, Milstrey EG (1989) The fauna of Gopher Tortoise burrows. In Diemer JE,
497 Jackson DR, Landers JL, Layne JN, Wood DA (ed) Relocation symposium
498 proceedings. Florida Games and Fresh Water Fish Commission, Nongame
499 Wildlife Program Technical Report #5, Tallahassee, FL, pp 86 – 98

500 Jackson LL, Lopoukhine N, Hillyard D (1995) Ecological Restoration: a definition and
501 comments. Rest Ecol 3:71-75

502 Johnson MTJ, Stinchcombe JR (2007) An emerging synthesis between community
503 ecology and evolutionary biology. *Trends Ecol Evol* 22:250-257

504 Katz E (2009) The big lie: human restoration of nature. In: Kaplan DM (ed) *Readings in*
505 *the Philosophy of Technology*, 2nd edition. Rowman & Littlefield Publishers, Inc,
506 pp 443 – 451

507 Kinlaw A, Grasmueck M (2012) Evidence for and geomorphologic consequences of a
508 reptilian ecosystem engineer: the burrow cascade initiated by the gopher tortoise.
509 *Geomorphology* 157-158:108-121

510 Kozak KH, Wiens JJ (2010) Niche conservatism drives elevational diversity patterns in
511 Appalachian salamanders. *Am Nat* 176:40-54

512 Lambeck RJ (1997) Focal species: a multi-species umbrella for nature conservation. *Cons*
513 *Biol* 11:849-856

514 Lambeck RJ (2002) Focal species and restoration ecology: response to Lindenmayer et
515 al. *Cons Biol* 16:549-551

516 Lawton JH (1999) Are there general laws in ecology? *Oikos* 84:177-192

517 Leaper R, Dunstan PK, Foster SD, Barrett NS, Edgar GJ (2014) Do communities exist?
518 Complex patterns of overlapping marine species distributions. *Ecology* 95:2016-
519 2025

520 Lindenmayer DB, Manning AD, Smith PL, Possingham HP, Fischer J, Oliver I et al.
521 (2002) The focal-species approach and landscape restoration: a critique. *Cons*
522 *Biol* 16:338-345

523 Lo Y-S (1999) Natural and artifactual: restored nature as subject. *Environmental Ethics*
524 21:247 – 266

525 Losos JB (1996) Phylogenetic perspectives on community ecology. *Ecology* 77:1344-
526 1354

527 Looijen RC, van Andel J (1999) Ecological communities: conceptual problems and
528 definitions. *Perspectiv Plant Ecol Evol Syst* 2:210–222

529 Mayden RL (2002) On biological species, species concepts, and individuation in the
530 natural world. *Fish and Fisheries* 3:171–196

531 McCain CM (2004) The mid-domain effect applied to elevational gradients: species
532 richness of small mammals in Costa Rica. *J Biogeog* 31:19-31

533 McCoy E, Shrader-Frechette L (1992) Community ecology, scale, and the instability of
534 the stability concept. *PSA: Proc Bienn Meet Phil Sci Assoc.* 1992:184-199

535 McGill BJ (2010) Towards a unification of theories of biodiversity. *Ecol Lett* 13:627-642

536 McLachlan JS, Hellmann JJ, Schwartz MW (2007) A framework for debate of assisted
537 migration in an era of climate change. *Cons Biol* 21:297-302

538 Means DB, Simberloff D (1987) The peninsula effect: habitat-correlated species declines
539 in Florida’s herpetofauna. *J Biogeog* 14:551-568

540 Mikkelson GM (1997) Methods and metaphors in community ecology: the problem of
541 defining stability. *Perspect Sci* 5:481-498

542 Mishler BD, Brandon RN (1987) Individuality, pluralism, and the phylogenetic species
543 concept. *Biol Phil* 2:397–414

544 Mitchell RJ, Hiers JK, O’Brien JJ, Jack SB, Engstrom RT (2006) Silviculture that
545 sustains: the nexus between silviculture, frequent prescribed fire, and
546 conservation of biodiversity in longleaf pine forests of the southeastern United
547 States. *Can J For Res* 36:2723-2736

548 Morrone JJ (1994) On the identification of areas of endemism. *Syst Biol* 43:438-441

549 Mulligan MK, Kirkman LK (2002) Burning influences on wiregrass (*Aristida*
550 *beyrichiana*) restoration plantings: natural seedling recruitment and survival. *Rest*
551 *Ecol* 10:334-339

552 Outcalt KW, Brockway DG (2010) Structure and composition changes following
553 restoration treatments of longleaf pine forests on the Gulf Coastal Plain of
554 Alabama. *For Ecol Manag* 259:1615-1623

555 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Ann*
556 *Rev Ecol Evol Syst* 37:637-669

557 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts
558 across natural systems. *Nature* 421:37-42

559 Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307:321-326

560 Platt WJ, Evans GW, Rathbun, SL (1988) The population dynamics of a long-lived
561 conifer (*Pinus palustris*). *Am Nat* 131:491-525

562 Reydon, TAC (2009) Species and kinds: a critique of Rieppel's "one of a kind" account
563 of species. *Cladistics* 25:660-667

564 Ricciardi A, Simberloff D (2009) Assisted colonization is not a viable conservation
565 strategy. *Trends Ecol Evol* 24:248-253

566 Ricklefs RE (1990) *Ecology*. 3rd edition. W.H. Freeman, New York

567 Ricklefs RE (2008) Disintegration of the ecological community. *Am Nat* 172:741-750

568 Rieppel O (2007) Species: kinds of individuals or individuals of some kind. *Cladistics* 23:
569 373-384

570 Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native
571 species. *Cons Biol* 25:428-437

572 Sherkow JS, Greely HT (2013) What if extinction is not forever? *Science* 340:32-33

573 Simberloff D (2003) Confronting introduced species: a form of xenophobia? *Biological*
574 *Invasions* 5:179-192

575 Simberloff D (2004) Community ecology: is it time to move on? *Am Nat* 163:787-799

576 Sober E (1994) Evolution, population thinking, and essentialism. In: Sober E (ed)
577 *Conceptual Issues in Evolutionary Biology*, 3rd edition. The MIT Press. pp 329-
578 359

579 Society for Ecological Restoration International Science and Policy Working Group
580 (2004) SER international primer on ecological restoration, version 2. Society for
581 Ecological Restoration. [http://www.ser.org/resources/resources-detail-view/ser-](http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration#2)
582 [international-primer-on-ecological-restoration#2](http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration#2). Accessed 12 August 2014

583 Steen DA, Smith LL, Conner LM, Litt AR, Provencher L, Hiers JK et al (2013a) Reptile
584 assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecol*
585 *App* 23:148-158

586 Steen DA, Conner LM, Smith LL, Provencher L, Hiers JK, Pokswinski S et al. (2013b)
587 Bird assemblage response to restoration of fire-suppressed longleaf pine sandhills.
588 *Ecol App* 23:134-147

589 Stein BA, Staudt A, Cross MS, Dubois NS, Enquist C, Griffis R et al. (2013) Preparing
590 for and managing change: climate adaptation for biodiversity and ecosystems.
591 *Front Ecol Environ* 11:502-510

592 Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate
593 change. *Global Change Biol* 10:2020-2027

594 Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian
595 niche through a century of climate change. *Proceed Nat Acad Sci* 106:19637-
596 19643

597 Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of
598 Earth's ecosystems. *Science* 277:494-499.

599 Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community
600 ecology. *Ann Rev Ecol Syst* 33:475-505

601 White PS, Walker JL (1997) Approximating nature's variation: selecting and using
602 reference information in restoration ecology. *Rest Ecol* 5:338-349

603 Wilbur HM (1972) Competition, predation, and the structure of the *Ambystoma-Rana*
604 *sylvatica* community. *Ecology* 53:3-21.

605 Wiley EO (1980) Is the evolutionary species fiction? – A consideration of classes,
606 individuals, and historical entities. *Syst Zool* 29:76–80

607 Wiley EO (1988) Vicariance biogeography. *Ann Rev Ecol Syst* 19:513-542

608 Winterhalder K, Clewell AF, Aronson J (2004) Values and science in ecological
609 restoration-a response to Davis and Slobodkin. *Rest Ecol* 12:4-7

610 Wollenberg KC, DR Vieites, van der Meijden A, Glaw F, Cannatella DC, Vences M
611 (2008) Patterns of endemism and species richness in Malagasy cophyline frogs
612 support a key role of mountainous areas for speciation. *Evolution* 62:1890-1907

613 Yager LY, Heise CD, Epperson DM, Hinderliter MG (2007) Gopher tortoise response to
614 habitat management by prescribed burning. *J Wildl Manag* 71:428-434

615

616 **Fig 1** New communities can arise from a variety of different processes. Transitions
617 (represented here as fuzzy bars in the absence of discrete geologic events) may occur
618 simply because communities change constantly over time and/or space (A). In (B)
619 community X transitions to a new state as a result of either a natural transition (e.g.,
620 succession) or some anthropogenic disturbance. Transitions may also occur as a result of
621 repairing community degradation (fuzzy gray bar in C). It is possible to manage degraded
622 communities such that the structure and function of the original community is replicated
623 (represented by X_1). I In (D) community W transitions into two communities (X and Y)
624 following biogeographic divergence (e.g., the division of a community following a
625 shifting river channel). If a biogeographic convergence event merged communities X and
626 Y, they would form a new community Z. In all of the above scenarios, the scale of
627 relevance to the researcher may allow for a community to experience some degree of
628 change over time while remaining the same entity.

629 **Table 1.** Description of how conceptualizing communities as natural entities changes the way we perceive environmental change and
 630 conduct studies of restoration ecology and community ecology. This table is not mean to be comprehensive; our goal is to be explicit
 631 regarding how the Evolutionary Community Concept (ECC) offers a different perspective. We acknowledge that previous studies
 632 have conceived of communities in manners consistent with one or more of the columns we describe below.

Community

Definition:

Collection of Species

ECC

Focus

Species-based

Ecosystem-based

Species-based

Ecosystem-based

Restoration ecology

Ensure the presence of select species (ecosystem engineers, dominant vegetation types, charismatic species, etc). Goals for restoration may be largely value-driven	Ensure the presence of select species and system functions (ecosystem engineers, dominant vegetation types, and species promoting ecosystem function). Goals for restoration may be largely value-driven or driven by the	Ensure the presence of species selected on the basis of their contribution to community identity (ecosystem engineers, dominant vegetation types, and species with co-evolutionary relationships)	Ensure the presence of species selected on the basis of their contribution to community identity and their associated functions (ecosystem engineers, dominant vegetation types, and species with key co-
--	---	---	---

		need for specific ecosystem services		evolutionary relationships)
Climate change	Focus on individual species responses, adaptation strategies such as assisted migration, and “preserving the stage” (Anderson and Ferree 2010) likely viable options	Focus on system-level response to climate change; adaptation strategies such as assisted migration likely viable – particularly if they result in maintaining ecosystem function/services	Focus on individual species responses; adaptation strategies focused on building resilience, identifying refugia and limiting external stressors promoted over moving species and generating new communities	Focus on system-level response to climate change; adaptation strategies focused on building resilience, identifying refugia and limiting external stressors promoted over moving species and generating new communities

<p>Invasive species</p>	<p>Gauge impact by determining response of other species. So long as all species remain extant, invasive species has no significant impact</p>	<p>Gauge impact by determining total number of present species and presence of interactions of interest, regardless of species identity</p>	<p>Gauge impact by determining response of other species, as measured by alteration of interactions, and relative abundance</p>	<p>Gauge impact by determining response of other species, as measured by alteration of interactions and relative abundance, and by considering whether community identity has become more homogenous to other communities and/or ecosystem function has declined</p>
<p>Studies of Community Ecology</p>	<p>Study of interactions will use species of interest to the researcher</p>	<p>Studies of interactions at the system level will be conducted regardless of the number of communities encompassed by a given interaction</p>	<p>Study of interspecific interactions will include species that share an evolutionary history with a given area and habitat</p>	<p>Study at the system level will consider community boundaries when designating study areas and appropriate spatial extent of interactions. Focal species will include those that share an evolutionary history with a given area and habitat</p>

