

1 ***IDEAS AND PERSPECTIVES***

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3 **Applying trait-based models to achieve functional targets for theory-driven ecological**
4 **restoration**

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Abstract

Manipulating community assemblages to achieve functional targets is a key component of restoring degraded ecosystems. The response-and-effect trait framework provides a conceptual foundation for translating restoration goals into functional trait targets, but a quantitative framework has been lacking for translating trait targets into assemblages of species that practitioners can actually manipulate. This paper describes new trait-based models that can be used to generate ranges of species abundances to test theories about which traits, which trait values, and which species assemblages are most effective for achieving functional outcomes. These models are generalizable, flexible tools that can be widely applied across many terrestrial ecosystems. Examples illustrate how the framework generates assemblages of indigenous species to (1) achieve desired community responses by applying the theories of environmental filtering, limiting similarity and competitive hierarchies, or (2) achieve desired effects on ecosystem functions by applying the theories of mass ratios and niche complementarity. Experimental applications of this framework will advance our understanding of how to set functional trait targets to achieve the desired restoration goals. A trait-based framework provides restoration ecology with a robust scaffold on which to apply fundamental ecological theory to maintain resilient and functioning ecosystems in a rapidly changing world.

51

52 **Restoration goals and functional targets**

53 The restoration of degraded ecosystems is one of the greatest environmental
54 challenges of the 21st Century (Dobson *et al.* 1997; Hobbs & Harris 2001). Changing land-
55 uses, novel disturbances, invasive species, over-harvesting, and climate change have led to
56 increasing rates of species extinction and habitat degradation, thereby reducing the capacity
57 of ecosystems to produce goods and maintain critical services (Chapin *et al.* 2000; Cardinale
58 *et al.* 2012). Society will inevitably place increasing pressure on ecologists to restore
59 functioning ecosystems and the services they provide (Suding 2011); however, there are still
60 many uncertainties about how to restore dynamic communities and ecosystems in an era of
61 rapid environmental change (Hobbs & Cramer 2008). This paper introduces quantitative trait-
62 based models that can be used to generate ranges of species abundances to test hypotheses
63 about which trait values and species assemblages will be most effective for achieving
64 functional restoration targets.

65 Ecological restoration, broadly defined, is the practice of assisting the recovery of
66 degraded ecosystems and therefore includes a wide variety of goals (Fig. 1). In cases of
67 extreme degradation, such as open-pit mines or channelized streams, the remediation and
68 rehabilitation of abiotic physical site characteristics is required before the biotic community
69 can be re-established (Hobbs & Cramer 2008). If the abiotic conditions of a site are relatively
70 intact, then restoration activities focus on manipulating the biotic community. Such
71 manipulations are done to achieve a broad variety of restoration objectives (Fig. 1). For
72 example, many government agency-based and community-based restoration projects target
73 the establishment of native plant cover to achieve conservation-oriented goals, such as
74 increasing wildlife habitat or replacing lost communities due to land-use change.

75 The first step in restoring degraded ecosystems is quantifying the differences between
76 current conditions, desired future conditions, and the range of natural variability in ecosystem
77 structure, function, and composition (White & Walker 1997; Landres *et al.* 1999). The
78 concept of the ‘range of natural variability’ of community composition acknowledges that
79 native communities are dynamic across space and time and encompass a range of species
80 abundance distributions (Landres *et al.* 1999). Many ecologists have demonstrated that the
81 historical range of natural variability under pre-industrial human influence is an appropriate
82 target because it reflects the evolutionary environment that has shaped the adaptations of the
83 local species pool (Moore *et al.* 1999; Swetnam *et al.* 1999).

84 Using history as a frame of reference has been challenged because it is difficult to
85 justify the choice of a specific time period in history when many landscapes have experienced
86 centuries of human modification (Thorpe & Stanley 2011). Moreover, climate change and
87 other significant global change processes (e.g., nitrogen deposition) are making historical
88 ecosystem conditions less relevant (Harris *et al.* 2006; Millar *et al.* 2007; Choi *et al.* 2008;
89 Hobbs *et al.* 2009). Changing biotic and abiotic conditions are forcing ecosystems across
90 thresholds into alternative stable, novel states that have not been witnessed in human history
91 (Suding *et al.* 2004; Quétiér *et al.* 2007; Hobbs *et al.* 2009). There are circumstances when
92 historical ecosystems are still useful references because they may be resilient to predicted
93 future changes (Fulé 2008), but, in general, these new challenges have raised the stakes and
94 heightened the importance of deciding how we set targets in restoration projects. The
95 objectives of ecological restoration are evolving into more complicated, forward-looking
96 goals of maintaining resilient assemblages and ecosystem functions in environments that may
97 have no historical analog (Suding 2011).

98 Restoration practitioners require rigorous, theory-based approaches to restore
99 degraded ecosystems under novel conditions. Increasing emphasis is therefore being placed

100 on defining functional targets for maintaining vital ecosystem processes and for responding to
101 changing abiotic conditions, rather than on restoring historical assemblages that may not
102 survive in a rapidly changing world (Hobbs & Cramer 2008; Seastedt *et al.* 2008; Jackson &
103 Hobbs 2009). Functional traits and functional diversity metrics can be used to evaluate
104 functional responses to restoration projects (van Bodegom *et al.* 2006; Sandel *et al.* 2011;
105 D'Astous *et al.* 2013; Hedberg *et al.* 2013). Translating restoration goals into functional trait
106 targets can be accomplished by viewing ecosystem restoration as a process of reassembly
107 (Funk *et al.* 2008) that, in turn, has important consequences for ecosystem functioning
108 (Lavorel *et al.* 2013).

109 The 'response-and-effect trait framework' (Suding *et al.* 2008) provides a conceptual
110 foundation on which to ground a trait-based restoration ecology because it unifies the
111 processes of community assembly and biodiversity effects on ecosystem function (Fig. 1).
112 Response traits are functional properties that determine the response of organisms to
113 environmental conditions, such as resource availability and disturbance. Response traits
114 influence how communities are assembled via environmental filtering and species
115 interactions (Fig. 1, Table 1). Environmental filters determine which species from the
116 regional species pool can survive in the given environmental conditions (Keddy 1992;
117 Fattorini & Halle 2004; White & Jentsch 2004). Environmental filters select for functional
118 traits that promote fitness and select against traits that yield poor performance, so restoration
119 projects can target trait values that will optimise fitness. Under this framework, assemblages
120 of species with strategically-chosen functional traits may establish more successfully and be
121 more able to adapt to changing environmental conditions than historical assemblages.
122 Applying the theory of environmental filtering has enabled practitioners to select the most
123 appropriate species in order to enhance germination, establishment, growth and reproduction
124 (Pywell *et al.* 2003; Jentsch 2007; Brudvig & Mabry 2008; Roberts *et al.* 2010), and will

125 improve our understanding of the long-term dynamics of restored communities (White &
126 Jentsch 2004). Manipulation of environmental filters can also be used to eliminate non-native
127 species (Funk & McDaniel 2010). Abiotic conditions are rapidly changing around the planet,
128 which means that historical filters will no longer be operating in the same manner (Harris *et*
129 *al.* 2006). Climate-change induced tree mortality and shifts in functional composition are
130 already occurring at a global scale (Allen *et al.* 2010), so restoration ecology needs to
131 determine how the filters are changing, in order to maintain functioning ecosystems of
132 indigenous species into the future.

133 Response traits also influence the outcome of biotic interactions (*e.g.*, competition)
134 that impose additional filters within communities (Fig. 1, Table 1). Two theories in particular
135 use traits to make predictions about the outcome of competitive interactions: limiting
136 similarity and competitive hierarchies. The theory of limiting similarity originally sought to
137 explain how multiple species can coexist by partitioning resources via niche differentiation
138 and is guided by the principle of competitive exclusion (MacArthur & Levins 1967). Under
139 this theory, species that are functionally similar cannot stably coexist. Limiting similarity has
140 been proposed as a theory to apply when restoring ecosystems that have been invaded by
141 non-native species (Table 1) (Funk *et al.* 2008). Numerous theories seek to explain why some
142 species can be so invasive outside their native range, including enemy release, altered
143 disturbance regimes, resource availability, and the functional traits of the invader, to name a
144 few (Keane & Crawley 2002). If a non-native species is invading a native habitat of high
145 conservation value, one potential management strategy is to increase the abundance of native
146 species that are functionally similar to the non-native species (D'Antonio & Chambers 2006;
147 Funk *et al.* 2008). Assuming that functional traits are reliable proxies for comparing resource
148 acquisition and utilization, managers may be able to seed or plant native species with trait
149 values that are optimally similar to the invader to competitively exclude the invader. On the

150 other hand, competitive hierarchies may also drive species interactions (Table 1) (Keddy &
151 Shipley 1989). Rather than trait similarity, it may be that certain trait values are always more
152 competitive than others. For example, taller species may consistently outcompete shorter
153 neighbours for light (Keddy & Shipley 1989), or species with high wood density and high
154 specific leaf area (SLA) may have stronger competitive effects on neighbours with lower
155 wood density and SLA (Kunstler *et al.* 2012). In these instances, native species with these
156 more competitive trait values can be selected to exclude non-native species.

157 Effect traits are functional properties that determine the effect of organisms on
158 ecosystem functions, such as biogeochemical cycling (Fig. 1, Table 1). Awareness of plant
159 species effects on ecosystem processes is rapidly increasing, and the role of plant traits is
160 central to this understanding (Kardol & Wardle 2010). Plant traits have been shown to
161 influence primary production, litter decomposition, soil respiration, nutrient cycling, and soil
162 moisture retention (Eviner & Chapin 2003), and their potential for altering ecosystem
163 processes in desirable ways has not yet been fully exploited in ecological restoration projects.
164 Effect traits are not always mutually exclusive from response traits (Lavorel & Garnier 2002;
165 Funk *et al.* 2008), but their conceptual distinction is useful when setting restoration targets.
166 Two hypotheses have been proposed to explain how communities drive ecosystem processes.
167 Mass ratio theory proposes that plant species effects on ecosystem processes are in proportion
168 to their relative input to primary production and are therefore driven by the traits of dominant
169 species (Grime 1998). Diversity theory proposes that the range of functional traits in a
170 community positively affects ecosystem functioning through complementary use of resources
171 (Cardinale *et al.* 2012) (Fig. 1, Table 1). Tests of the relative importance of each mechanism
172 indicate that both are important, depending on the function and the ecosystem (Díaz *et al.*
173 2007; Laughlin 2011). Mass ratio effects and functional diversity effects may also be
174 complementary mechanisms. For example, average leaf nitrogen concentration and

175 complementarity of rooting depth may enhance productivity simultaneously. A framework
176 for translating trait diversity, and not just trait means, into species abundance distributions is
177 clearly needed.

178

179 **Operationalising the response-and-effect trait framework**

180 Applying the response-and-effect trait framework to achieve quantitative functional
181 targets in ecological restoration is currently hindered by a straightforward mechanism of
182 translating functional trait targets into species assemblages that can be manipulated by
183 practitioners. Ecological restoration projects have historically selected species based on
184 categorical tables of habitat requirements (*e.g.*, mesic vs. xeric, shade vs. sun), uses (*e.g.*,
185 wildlife uses, conservation value, horticultural value, livestock grazing), and ecosystem
186 functions (*e.g.*, adds nitrogen, retains nitrogen) (*e.g.*, Packard and Mutel (1997)). Restoration
187 practitioners have a wealth of practical experience for choosing species in restoration projects
188 based on years of trial and error (Rosenthal 2003; Padilla *et al.* 2009) and they already use
189 traits implicitly when they choose species with physiological adaptations to match particular
190 environmental conditions (Ehleringer & Sandquist 2006). Deriving lists of species in this way
191 has proven useful in practice over the years for establishing native plant cover and achieving
192 conservation-oriented goals. However, this classic approach does not allow for a rigorous
193 quantification of specific functional trait targets and the derivation of species abundance
194 distributions that will achieve such targets, and it does not inform restoration under novel
195 conditions because it is less predictive in nature.

196 Land managers do not explicitly manage functional traits because these are properties
197 of the organisms that they are managing. As such, managers also do not directly manage
198 functional diversity metrics (*e.g.*, FDiv or RaoQ) or community-weighted mean traits (*i.e.*,
199 community-level mean trait values weighted by the relative abundance of species), but they

200 are experts at managing species abundances. Therefore, in order to operationalise the
201 response-and-effect trait framework for ecological restoration, a quantitative mapping from
202 functional trait targets onto species assemblages is required to enable restoration practitioners
203 to make specific manipulations of species abundances to achieve a functional outcome.

204 Quantitative frameworks can move ecological restoration forward from a practice that
205 relies on simple lists of candidate species to one that can target specific species abundance
206 distributions based on functional traits. Different relative abundance distributions derived
207 from a common list of species can produce communities with strongly contrasting
208 community-level mean traits, so paying careful attention to abundance distributions is critical.
209 Generalizable trait-based models are necessary because they can generate abundance
210 distributions for any number of species using any number of traits. Suppose that a restoration
211 project has decided that the restored community should have low specific leaf area (SLA)
212 values to maximise survival in an increasingly stressful environment. It is relatively straight-
213 forward to rank species from a regional pool based on their SLA values and then select
214 species from the list that have low SLA. But suppose the practitioners wish to select species
215 according to multiple traits simultaneously (e.g., low SLA, high wood density, and early
216 flowering times) that may be independent from each other (Eviner & Chapin 2003). This
217 selection is not always straightforward, especially when the species pool is large. Quantitative
218 frameworks operationalise this process to determine which species meet these multiple
219 criteria.

220 Recently proposed trait-based models of community assembly have potential to be
221 very useful in restoration ecology for translating trait-based targets into ranges of species
222 abundances (Laughlin & Laughlin 2013). As they are currently formulated, these models
223 produce discrete relative abundance distributions, *i.e.*, proportional abundances for every
224 species in a regional species pool in a given environment (Shipley *et al.* 2006; Laughlin *et al.*

225 2012). However, ecological communities are not static (White & Jentsch 2004) and rigid
226 restoration targets, such as discrete relative abundance distributions, are unachievable and
227 unrealistic considering the range of variability that exists in nature (White & Walker 1997).
228 Trait-based models in their current form need to be modified to be more appropriate for
229 restoration and management.

230 Two mathematical models can be applied to derive ranges of species abundances that
231 meet functional trait targets. The first model uses mean trait values and uniformly samples
232 solutions from underdetermined systems of linear equations to obtain a range of species
233 abundance distributions. The mathematical formulation of this model is described in Box 1
234 and is a modification of the CATS model (Shipley *et al.* 2006). The trait targets serve as the
235 constraints on the right-hand sides of the linear equations (Box 1). The second model uses
236 full trait distributions (*i.e.*, mean and variance-covariance) and applies Bayes Theorem and
237 Monte Carlo integration to obtain a range of species abundance distributions. The
238 mathematical formulation is a modification of the TraitSpace model (Laughlin *et al.* 2012)
239 and is described in Box 2. The trait targets are distributions of trait values, which
240 acknowledges that there is a range of variability in appropriate functional trait values and
241 takes intraspecific trait variability into account.

242 To apply these models, restoration goals need to first be translated into functional trait
243 targets (Fig 1, Fig. 2, Table 1). Setting realistic goals with clear targets is fundamental for any
244 restoration and management project. Targets are quantifiable values that can be monitored to
245 evaluate whether the goals of the restoration project have been achieved (Hobbs & Norton
246 1996). In this framework, the targets are trait values (either mean trait values or full trait
247 distributions) for a community that are chosen to either optimise the response of the
248 community to an environmental condition or to optimise the effect of the community on an
249 ecosystem process. For example, if the goal of the restoration project is to apply the theory of

250 environmental filtering to restore a community that is resilient to climate change, then the
251 trait targets are values of the traits that will maximize fitness and performance under
252 projected future climate scenarios (Table 1, Fig. 2). Achieving a trait target by successfully
253 manipulating a community to have the desired traits implies that a functional objective is
254 being met; however, whether the particular functional objective is actually being achieved
255 requires experimental testing. We are still learning which specific trait values achieve such
256 goals.

257 The quantitative framework can be used to generate testable hypotheses about which
258 traits, which trait values, and therefore which species abundances will be most effective at
259 achieving the functional targets of a restoration project by generating different communities
260 that meet different trait targets. Applying these models under experimental conditions will
261 enhance our ability to set appropriate trait targets to meet specific restoration objectives.
262 Consider a hypothetical scenario where a species pool is comprised of nine species that are
263 evenly distributed throughout a two-dimensional trait space (Fig. 2). Suppose that not enough
264 is known about the ecosystem and process under consideration to choose specific trait values
265 as targets. Perhaps we wish to determine which traits will yield optimum fitness under future
266 climate change scenarios. In these cases, the experimenter can select multiple trait targets to
267 test their effectiveness, and for each of the selected trait targets we can derive distinct
268 community assemblages (Fig. 2). The effectiveness of these targeted trait values for
269 achieving a functional outcome can then be monitored over time in a variety of experimental
270 conditions (*e.g.*, ambient vs drought conditions) (Fig. 2). Experiments such as these will
271 advance theory-driven restoration ecology to enhance our capacity to restore dynamic
272 ecosystems in an era of rapid environmental change. The use of this framework will now be
273 described using four real-world examples where ecological theories can be applied to achieve
274 functional targets.

275

276 **Applications of quantitative trait-based models in restoration ecology**

277 *Applying environmental filters to determine future restoration targets*

278 Environmental filters can be applied to restore assemblages of species that are adapted
279 to a set of environmental conditions (Fattorini & Halle 2004). If high-quality relict sites can
280 be used as reference conditions for a restoration project, then the trait values present in the
281 relict community can potentially be used to generate species abundances for the restored
282 community (Fig. 1). This approach would be similar to the traditional approach of using the
283 composition of the relict site as the target, but would differ in that the targets are trait values
284 and that a variety of species abundance distributions could meet a single trait target (Fig. 2).
285 In theory, functional trait targets should increase the flexibility of restoration projects because
286 a range of species assemblages can meet a single functional trait target. However,
287 environmental conditions are being altered by agents of global change, and so a progressive,
288 forward-thinking restoration goal would seek to restore an indigenous community that is
289 resilient given the predicted changes in climate in the coming century (Fig. 1) (Suding 2011).

290 Consider the case of the semi-arid south-western USA, where the effects of climate
291 change are already inducing landscape-scale changes in tree mortality rates, community
292 structure and disturbance regimes (Breshears *et al.* 2005; Westerling *et al.* 2006). Currently,
293 the forests surrounding Flagstaff, Arizona are dominated by *Pinus ponderosa* (ponderosa
294 pine), but land managers are interested in how these forests will respond to climate change
295 stressors. A trait-based model was used to determine how traits were filtered by temperature
296 across this region and showed very predictable relationships between temperature and four
297 traits in particular: wood density, flowering time, maximum height and bark thickness
298 (Laughlin *et al.* 2011). As the climate changes, we would expect that the trait values that
299 optimise fitness will also change, thereby altering population dynamics and community

300 structure. By anticipating which traits will optimise establishment, growth, survival, and
301 reproduction under projected future conditions, we can predict which species will be best
302 adapted to persist in the changing environment. By promoting the establishment of such
303 species we can minimise the extent of forest crown die-off events and maintain woodland
304 cover on the landscape. As mean annual temperature is expected to rise around Flagstaff from
305 the current 7.5 °C to a future scenario of 10 °C, we can predict how the optimum trait value
306 will change. We can predict that optimum bark thickness in the future will remain thick
307 because fires will still be very likely to occur and perhaps increase in frequency (Laughlin *et*
308 *al.* 2011). Flowering date is expected to become earlier given the longer growing seasons and
309 maximum height is expected to decline because water availability will be reduced. Wood
310 density is expected to become slightly greater given the increased frequency of drought
311 (Hacke *et al.* 2001). These expected trait values can be used as the constraints on the right
312 hand side of Equation 1 to generate communities that may be more resilient to climate change
313 (Box 1; see Appendix S1 in Supporting Information for R scripts to run this analysis).

314 Solving these systems of linear equations yields an infinite set of possible solutions
315 because there are far fewer traits than species in the system (*i.e.*, it is underdetermined). Since
316 there are nine species, four trait constraints (Eqn 1), and one normalization constraint (Eqn 2),
317 the solution is a four-dimensional (*i.e.*, $9 - 4 - 1 = 4$) hyperplane embedded within a nine-
318 dimensional space. The MCMC samples of the solutions (*i.e.*, the species abundances)
319 obtained from the *limSolve* package are plotted as boxplots for each species in Fig. 3. By
320 plotting the MCMC samples of the solution space we are able to determine a range of species
321 abundances that reflects the mapping from functional traits to community composition using
322 a system of linear equations.

323 The current conditions indicate that the trait values are optimum for a ponderosa pine-
324 dominated forest (Fig. 3a), which validates the proposition that the range of variability of

325 community composition predicted by the model matches the reality of current forest
326 conditions. Many sites in the southwestern USA have been severely degraded following
327 stand-replacing fires and could convert to grasslands without active management (Savage &
328 Mast 2005). If managers want to plan ahead for these sites and promote tree species that will
329 be resilient to a warmer climate and that will maintain the structural element of a forest for
330 maximising carbon storage, then, in addition to ponderosa pine, the species that reflect
331 optimum trait values in the warmer climate include *Juniperus monosperma* (one-seed
332 juniper), *Juniperus osteosperma* (Utah juniper), and *Pinus edulis* (pinyon pine) (Fig. 3b).
333 Note that *Pinus ponderosa* is still predicted to be a dominant species, which suggests that a
334 gradual transition is a reasonable objective for managing this ecosystem with the future in
335 mind. Moreover, in overstocked ponderosa pine forests slated for restoration thinning and
336 burning (Moore *et al.* 1999), land managers may want to passively allow or, in some
337 transitional areas, actively promote the advancement of pinyon-juniper woodland species into
338 thinned forests to enable the community to be resilient and able to respond to predicted future
339 conditions (Millar *et al.* 2007).

340 The framework, as described in Box 1, uses a model where community-weighted
341 mean traits are regressed on environmental conditions in order to obtain optimum trait values
342 from a single forecasted value of an environmental variable (e.g., mean annual temperature).
343 Rather than finding solutions for a single mean environmental condition, one can also 1)
344 include additional environmental variables, such as soil properties or vapour-pressure deficit,
345 or 2) expand the range of environmental conditions. In the case of the latter, rather than
346 determining the range of species abundances that satisfies trait constraints that optimise
347 fitness at 10 °C exclusively, one can explore the solutions that span a range of temperatures
348 from 9 to 11 °C by solving and sampling the solution sets at 0.1 °C intervals. This approach
349 acknowledges that future environmental conditions themselves are uncertain, which will

350 influence the range of traits that promote high performance, which will influence the
351 abundances of species that will satisfy those trait constraints.

352 Setting functional targets that are relevant for future conditions requires a
353 fundamental understanding of how traits are filtered by the environment, and how those traits
354 might interact in novel conditions. Determining functional trait targets that will be optimal for
355 a future environment can be estimated by applying existing models of current trait-
356 environment relationships, as done in this example here. These approaches differ from simply
357 looking at the composition of communities from warmer climates because projections under
358 climate change do not look like simple up-slope shifts in species response curves (Laughlin *et*
359 *al.* 2011). This is because some environmental conditions are changing (*e.g.*, temperature),
360 while other conditions will remain the same (*e.g.*, soil texture), and the interaction of all these
361 conditions will influence the predicted optimal trait value in a changing climate. In some
362 places of the world there may be no analogs that can be used as direct community
363 comparisons because of novel abiotic conditions and species pools (Hobbs *et al.* 2009), hence
364 the critical need for theory-driven approaches and experimental tests of which traits achieve
365 desired responses and effects. Applications of this restoration approach will likely be most
366 successful if multidisciplinary teams of restoration practitioners, ecologists, ecophysiologicals,
367 and climatologists work together to develop, test, and validate these future functional targets.
368 Restoration goals under climate change will also include objectives such as maximising
369 carbon storage or maintaining key structural features of an ecosystem. Determining optimum
370 functional targets for the future may be one of the most important empirical challenges facing
371 restoration ecologists.

372

373 *Applying competition theories to exclude non-native invaders*

374 The theory of limiting similarity has recently been enlisted in the battle against non-
375 native species invasion (Fig. 1, Table 1). One potential restoration activity to reduce non-
376 native invasion is to strategically increase the abundance of native species that are
377 functionally similar to the non-native species (D'Antonio & Chambers 2006; Funk *et al.*
378 2008). Selecting native species based on a single trait, such as growth rate or plant height, is
379 straightforward. However, using a system of linear equations is more efficient when using
380 multiple functional traits simultaneously, and they have the additional advantage of
381 producing species abundance distributions (Box 1).

382 Consider the case of *Linaria dalmatica* (Dalmatian toadflax), a non-native forb that is
383 invading understories of forests in the Southwestern United States (Dodge *et al.* 2008). The
384 theory of limiting similarity is linked to resource use, so the most appropriate traits for
385 consideration are response traits (Funk *et al.* 2008). One hundred and fifteen native
386 herbaceous species in this ecosystem were systematically screened by measuring the
387 following functional response traits: maximum height, leaf area, leaf dry matter content,
388 specific leaf area, specific root length, seed mass, flowering time, flowering duration, leaf
389 carbon (C) concentration, leaf nitrogen (N) concentration, leaf phosphorus concentration, root
390 C concentration, root N concentration, leaf $\delta^{13}\text{C}$, and leaf $\delta^{15}\text{N}$ (Laughlin *et al.* 2010). In this
391 example, all response traits are used, but this framework can be used to test hypotheses about
392 which traits are most effective when applying competition theory in this context.

393 By applying the framework described in Box 1 (see Appendix S1 for R code), it was
394 determined that a combination of two dominant species, *Penstemon barbartus* (red
395 penstemon) and *Laennecia schiedeana* (pineland marshtail), in addition to other less
396 abundant species (*e.g.*, *Bahia dissecta*, *Chenopodium fremontii*, *Muhlenbergia rigens*) would
397 combine to create a native community with optimally similar trait values as *Linaria*
398 *dalmatica* (Fig. 4). These species are intuitively appealing because they are known as

399 competitive, fast-growing, fecund native species (Laughlin *et al.* 2010) that can match the
400 competitive nature of *Linaria dalmatica*. Restoration practitioners could seed these five
401 species into invaded communities in combination with control measures as a mechanism to
402 competitively exclude toadflax.

403 Understanding how traits of invasive species influences their success is an active area
404 of research (Pyšek & Richardson 2007; Van Kleunen *et al.* 2010). This application of
405 ecological theory has not been rigorously tested in an experimental context, and some have
406 recently questioned the use of functional traits for understanding invasion success (Thompson
407 & Davis 2011). Moreover, others have questioned the use of trait similarity for predicting
408 competitive interactions in a restoration context (Abella *et al.* 2012), and others have shown
409 that trait hierarchies are better predictors of competition (Keddy & Shipley 1989; Kunstler *et*
410 *al.* 2012). The framework can be used to test these theories by generating communities based
411 on different trait targets, where trait targets for limiting similarity are the traits of the non-
412 native invader, whereas trait targets for competitive hierarchies would be different from the
413 invader and values would need to be based on previous empirical work. For example, if the
414 invader was short-statured with low SLA values, then a taller native species with higher SLA
415 could potentially be a stronger competitor. Identifying native species that can out-compete
416 non-native species based on their functional trait values would enhance our capacity to
417 manage degraded ecosystems.

418 Another challenge with the application of competition theories is how to approach
419 systems that are invaded by multiple species that differ functionally. One option would be to
420 apply the framework on each species separately to derive two sets of species for use in
421 stemming the invasion. For example, the top five species chosen to competitively exclude
422 another problematic invasive weed, *Centaurea diffusa* (diffuse knapweed), includes two of
423 the five species (*Laennecia schiedeana* and *Penstemon barbatus*) that were chosen to exclude

424 *Linaria dalmatica*. But such overlap will not always be the case, making species selection
425 potentially problematic in cases of multiple invasions. Additionally, dominant natives may
426 have negative effects on other native species. Moreover, selecting vigorous native species to
427 exclude invasives may lead to a functionally redundant community dominated by just a few
428 species, which may conflict with other targets of maintaining functionally diverse
429 communities. These challenges reflect a common problem of conflicting objectives within
430 ecosystem management (Mendoza & Martins 2006). Ecologists should carefully evaluate the
431 trade-offs when applying these theories to meet specific management objectives, and to
432 acknowledge that not all targets can be achieved everywhere simultaneously.

433

434 *Applying mass ratio theory to influence ecosystem processes*

435 Effect traits govern how species influence ecosystem processes and the linkages
436 between aboveground and belowground components is an important aspect of ecosystem-
437 based ecological restoration (Kardol & Wardle 2010). Soil properties impose important
438 constraints on ecosystem restoration (Dobson *et al.* 1997; Suding *et al.* 2004), and in some
439 cases these properties can be altered through strategic manipulation of the plant community
440 (Fig. 1). Effect traits can influence the soil microclimate, pH, organic matter content, rates of
441 nutrient cycling, microbial biomass, water infiltration, water-holding capacity, and soil
442 cohesion (Eviner & Chapin 2003). The mass ratio theory proposes that plant community
443 effects on ecosystem processes and properties are driven by the traits of the dominant species
444 (Grime 1998). For example, plant communities dominated by species with acquisitive leaf
445 economics traits (e.g., high leaf N concentration and short leaf life span) are associated with
446 soils that have higher N transformation rates (Orwin *et al.* 2010). Mass ratio theory assumes a
447 linear impact of abundance-weighted traits on ecosystem processes, but non-additive and
448 threshold responses are also common, and sometimes low biomass species have

449 disproportionate effects on function (Díaz *et al.* 2007; Peltzer *et al.* 2009). This framework
450 can be used to empirically test where these thresholds lie along gradients of community-level
451 trait values or community composition. It is not clear how to operationalise non-additive
452 effects into the general framework proposed here. This is certainly an important challenge for
453 theoretical ecology.

454 Consider an example where the objective of the restoration project is to slow rates of
455 internal nutrient cycling. This objective could be useful for slowing invasions of resource-
456 demanding non-native species or for returning soil properties to a lower nutrient state
457 following excessive N deposition. Native species in northern Arizona with low SLA and high
458 leaf dry matter content (LDMC) have slower rates of litter decomposition (Laughlin *et al.*
459 2010) and are associated with soils with low nitrification potential (Laughlin 2011). Eight
460 native graminoids demonstrate this broad range of leaf trait variation among and within
461 species (Fig. 5a). Unlike the system of linear equations, a modified version of the hierarchical
462 Bayesian TraitSpace model can utilize intraspecific trait variability to translate functional trait
463 targets into ranges of variability of species abundances (Box 2).

464 To slow nutrient transformation rates, the restoration practitioner would target a range
465 of low SLA and high LDMC trait values because these trait values are associated with low
466 leaf nutrient concentrations. This simple example is limited to two strongly correlated traits,
467 but the framework can handle as many independent traits as are required to achieve
468 ecosystem multifunctionality (Fig. 2) (Eviner & Chapin 2003). Model results (see Appendix
469 S1 for R scripts) indicate that seeding or planting swards dominated by *Muhlenbergia*
470 *montana* (mountain muhly), *Carex geophila* (ground-loving sedge), and *Sporobolus*
471 *interruptus* (black dropseed) would maximise success of achieving slower decomposition and
472 nutrient transformation rates based on these species intra- and interspecific variation of SLA
473 and LDMC (Fig. 5b). Successful application of this theory was demonstrated experimentally

474 in a different ecosystem where manipulations of species assemblages according to variation
475 in leaf functional traits had significant influence on rates of nutrient cycling (Orwin *et al.*
476 2010).

477 Using effect traits to influence ecosystem processes requires that species with the
478 desired effect traits must also possess response traits that allow them to persist and compete
479 in the environmental conditions of the site (Lavorel *et al.* 2013). Resources will be wasted if
480 plants with the desired effect traits are seeded or planted only to be eliminated by the
481 environmental filters. The above example where mass ratio theory was applied may prove
482 difficult given that high SLA species may invade and become dominant in the high nutrient
483 soils, so control measures may be needed to successfully establish the low SLA species.
484 Careful selection of species with desired effect traits and appropriate response traits will be
485 required (Funk *et al.* 2008; Lavorel *et al.* 2013). These trait-based models can be used to
486 determine which species may possess such a combination of traits, *i.e.*, one can derive species
487 abundances based on any combination of response and effect trait values.

488

489 *Applying diversity theory to influence ecosystem processes*

490 Experimental evidence suggests that, in some ecosystems, high functional diversity
491 can increase average rates of some processes, such as primary productivity (Cardinale *et al.*
492 2012). Increasing primary productivity to provide forage for higher trophic levels can be an
493 important restoration goal. The mathematical formulations of the trait-based models
494 emphasise environmental filtering over niche complementarity and so naturally yield species
495 abundances that reflect trait convergence over divergence (Laughlin & Laughlin 2013).
496 Simple modifications to the Bayesian framework can translate functional trait diversity
497 targets into species assemblages (Box 2). Functionally diverse communities are often
498 characterised by dominant species having contrasting trait values (Mason *et al.* 2005).

499 Therefore, to generate functionally divergent communities it is necessary to constrain the
500 species abundances by trait values located at multiple locations along the trait axes, rather
501 than constraining by a single optimal trait value. Systems of linear equations cannot elegantly
502 accommodate multiple trait value constraints for the same trait, whereas the Bayesian
503 framework can develop probability density functions for any desired multi-modal trait
504 distribution (Box 2). Importantly, in the circumstances where mass ratio effects and niche
505 complementarity act in concert, this framework can simultaneously accommodate single
506 mean values for traits predicted to act through mass ratio effects, and multiple values for
507 traits predicted to act through niche complementarity.

508 To derive a functionally diverse community from the pool of eight Arizona grass
509 species, trait values were simulated from a bimodal trait distribution where the modes were
510 located toward the ends of the leaf trait spectrum (Fig. 5a). The model results indicate that
511 seeding or planting swards dominated by *Muhlenbergia montana* (mountain muhly), *Festuca*
512 *arizonica* (Arizona fescue), and *Bromus ciliatus* (fringed brome) will establish a functionally
513 diverse community (Fig. 5c). For confirmation that this community is more functionally
514 diverse, note that the functional diversity indices of the community in Fig. 5c are larger than
515 the functional diversity indices of the community in Fig. 5b. Monitoring the effectiveness of
516 functionally diverse communities on ecosystem processes is important. When restoring
517 naturally low diversity ecosystems, such as salt marshes, the short-term positive effects of
518 diversity on ecosystem function may disappear in the long-term when productive species rise
519 to dominance (Doherty *et al.* 2011). This framework can be used to test when niche
520 complementarity can be useful in restoration contexts (Srivastava & Vellend 2005).

521

522 **Concluding remarks**

523 Both of these mathematical models (Boxes 1 and 2) could be used to determine ranges
524 of species abundances that meet functional trait constraints in the application of the theories
525 of environmental filtering, limiting similarity, competitive hierarchies, and mass ratio theory
526 (Table 1). However, only the Bayesian framework can be applied to generate species
527 abundances to increase functional diversity because it can accommodate multimodal trait
528 distributions (Mason *et al.* 2005). The system of linear equations may be more pragmatic in
529 cases where only mean trait values are available for each species. If intraspecific trait
530 variation is thought to be particularly important, then the Bayesian framework would be more
531 useful. Trait data is becoming more available at both inter- and intraspecific levels, which
532 may enable restoration ecologists and practitioners to apply these approaches without needing
533 to measure primary trait data themselves (Kattge *et al.* 2011). Given the increasing
534 availability of trait data, it would be useful to re-analyse published results to ask whether the
535 traits of restored communities could have predicted their response to environmental
536 conditions imposed by restoration treatments or their effect on ecosystem functions.

537 Several years ago it was noted that there was considerable disconnect between the
538 ecological theories proposed by academic scientists and the practice of restoration ecology by
539 practitioners (Young *et al.* 2005). A trait-based perspective has been gaining traction within
540 the community of restoration ecologists (Temperton *et al.* 2004; Funk *et al.* 2008), but a
541 mechanism for translating functional trait targets into species abundance distributions that
542 can be used by restoration practitioners remained elusive. Recently developed trait-based
543 models are not only useful for testing community assembly theory, they have here been
544 extended to provide tools for translating functional trait targets into ranges of variability of
545 species abundances for achieving functional outcomes in ecological restoration. These
546 modified trait-based models are generalizable, flexible tools that can be widely applied in any
547 ecosystem on the planet, given adequate knowledge and information. The examples

548 demonstrate how this new framework can be applied to confront some of the most pressing
549 ecological challenges of our time and advance our understanding of the processes of
550 community assembly and ecosystem functioning, but there is still much to be learned about
551 which specific trait target values will achieve our functional objectives. The application of
552 these models within experimental contexts will accelerate our learning and will bring us
553 closer to achieving our goals. A trait-based framework provides restoration ecology with a
554 robust scaffold on which to apply fundamental theory to achieve functional targets in this era
555 of global change.

556

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562

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846 **SUPPORTING INFORMATION**

847 Additional Supporting Information may be downloaded via the online version of this article
848 at Wiley Online Library (www.ecologyletters.com).

849 **Appendix S1** *User's guide and R code for applying trait-based models in ecological*
850 *restoration*

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852

853

854 **Table 1.** Trait-based applications of ecological theory to achieve functional targets in

855 ecological restoration

| Trait-based theories for restoration ecology | Functional trait targets | Examples |
|---|--|---|
| <i>Response traits</i> | | |
| Environmental filtering | Traits that optimize fitness and performance in a given set of environmental conditions | Species with resource-conserving traits (i.e., higher wood density) will be adapted to drier conditions (Hacke <i>et al.</i> 2001) |
| Limiting similarity | Traits of non-native invader are the constraints for selecting native species with the most similar traits | Functionally similar native species may compete more strongly for resources with non-native invaders (Funk <i>et al.</i> 2008) |
| Competitive hierarchies | Different trait values of non-native invader are the constraints for selecting native species | Taller native species may outcompete a non-native invader for light (Keddy & Shipley 1989) |
| <i>Effect traits</i> | | |
| Mass ratio | Traits of dominant species influence ecosystem processes | Species with resource-conserving leaf traits will slow decomposition and nutrient cycling (Orwin <i>et al.</i> 2010) |
| Niche complementarity | Diversity of trait values maintains ecosystem processes | Divergent leaf strategies within a community may enhance temporal stability and rate of primary production (Cardinale <i>et al.</i> 2012) |

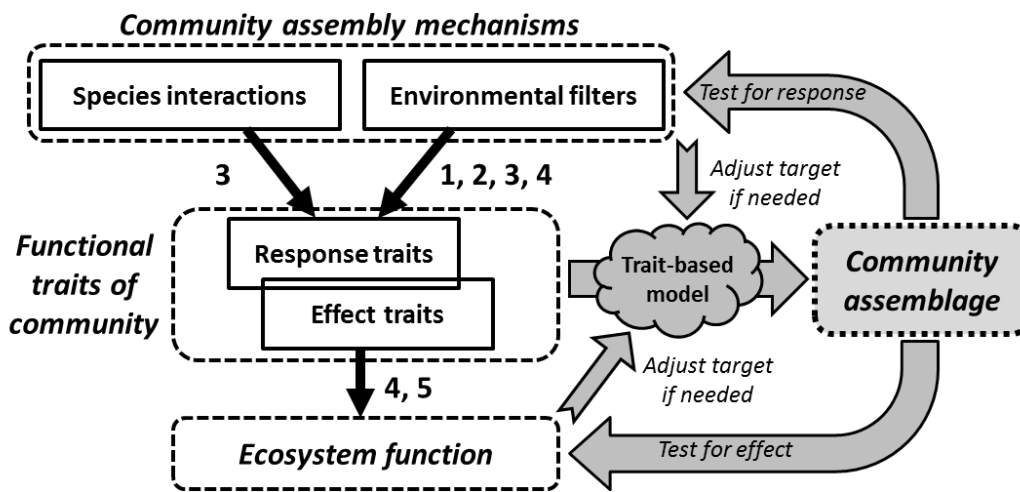
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857

(a) Examples of stressors and the functional trait targets that can be established to restore degraded ecosystems

| Ecosystem stressors | Restoration goals | Possible trait targets |
|------------------------|---------------------------------|------------------------------------|
| 1) Land-use change | Restore lost community | Traits of reference sites |
| 2) Climate change | Restore resilient community | Traits resilient to future climate |
| 3) Invasive species | Control and exclude non-natives | Traits of invasive species |
| 4) Abiotic degradation | Rehabilitate site conditions | Trait dominance (mass ratio) |
| 5) Species loss | Maintain primary productivity | Trait diversity (complementarity) |

(b) Translating response-and-effect traits into species assemblages that can be manipulated by practitioners and tested in the field



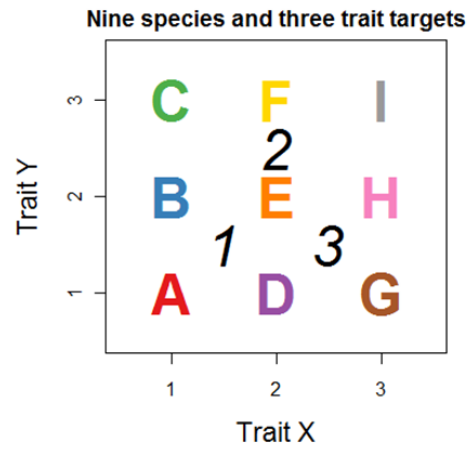
858

859 **Figure 1.** Conceptual diagram of the general framework for generating species assemblages
 860 that achieve functional targets for ecological restoration. **a)** Examples of novel stressors that
 861 have led to ecosystem degradation, and the restoration goals and functional targets that can be
 862 developed to assist the recovery of the ecosystem. **b)** Operationalising the response-and-
 863 effect trait framework (Suding *et al.* 2008) by translating functional trait targets into
 864 experimental species assemblages that can be manipulated by restoration practitioners to
 865 achieve the functional targets. The grey arrows illustrate that the response of the assemblages
 866 to environmental conditions and the effects on ecosystem function can be tested, and the
 867 functional trait targets can be adjusted as we learn which traits and trait values achieve the
 868 restoration goals. The functional targets (numbers 1-5) depend on the specific restoration goal
 869 and relate to each of the processes (illustrated as black arrows) within the response-and-effect
 870 trait framework as shown.

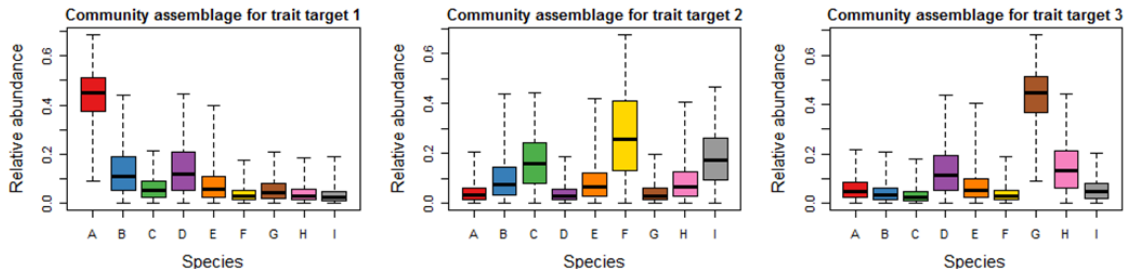
Operationalising the response-and-effect trait framework for theory-driven restoration ecology

Step 1. Set targets by selecting relevant traits and trait values to optimise the response or effect of interest. For experimentation, select multiple trait values as trait targets to test their effectiveness.

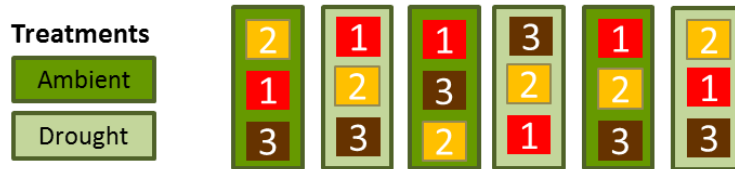
Step 2. Define the species pool, and determine the mean (and possibly variance-covariance) of the traits of each species.



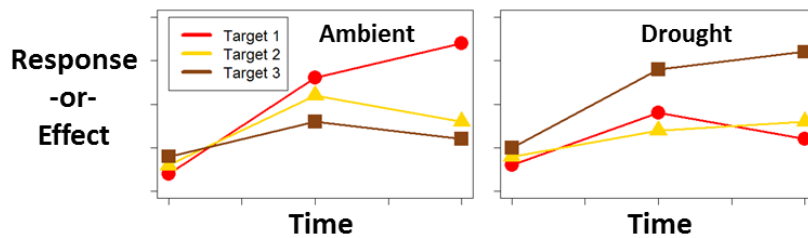
Step 3. Apply quantitative trait-based models to derive species abundance distributions.



Step 4. Establish experimental communities, and maintain species abundances within the range of variability set by the models to keep trait targets at desired level.

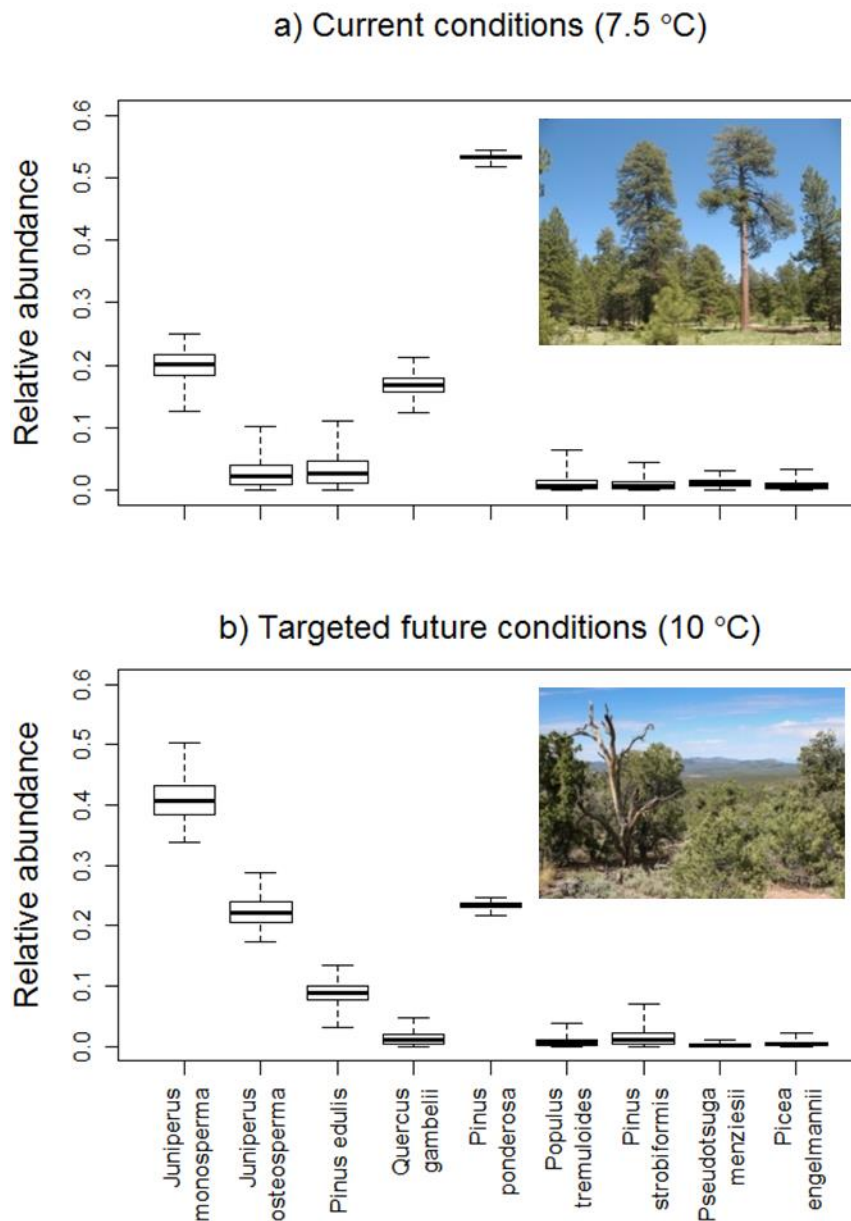


Step 5. Monitor community response or ecosystem effect by trait target and treatment to test effectiveness of trait targets and community assemblages.



871

872 **Figure 2.** Operationalising the response-and-effect trait framework for theory-driven
 873 restoration ecology experiments. The hypothetical species abundance distributions were
 874 generated using underdetermined systems of linear equations (Box 1, Appendix S1).



876

877

878 **Figure 3.** Range of variability of tree species relative abundances that meet the trait targets in

879 **a)** current climatic conditions and **b)** projected future climatic conditions in the Southwest

880 USA (e.g., Flagstaff, Arizona; Lat: 35.14, Long: -111.67) (Laughlin *et al.* 2011). Values

881 represent a uniform sample of the solutions to the systems of linear equations (Box 1). Photo

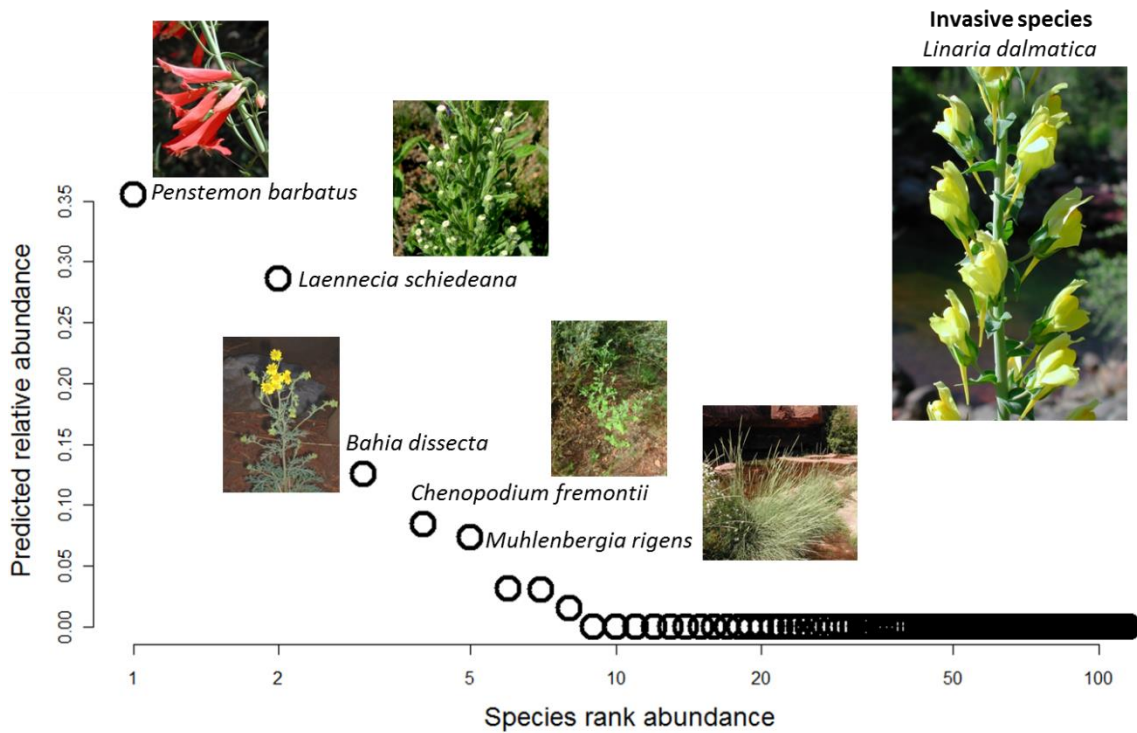
882 credits: upper photo by Daniel Laughlin, lower photo by Guy Starbuck

883 (<http://www.starbuck.org/exploring/>) with permission.

884

885

886



887

888 **Figure 4.** The top five native species that were selected from the native species pool of 115

889 herbaceous plants are illustrated here based on their similarity of 15 functional response traits

890 with the non-native invasive species *Linaria dalmatica* (Dalmatian toadflax). To test the

891 usefulness of applying limiting similarity to competitively exclude non-native invaders, these

892 five species are the best candidates for seeding or planting into invaded habitats because they

893 have the most similar response traits. The data were obtained on understory plant species

894 growing in a ponderosa pine forest near Flagstaff, Arizona (Laughlin *et al.* 2010). All photos

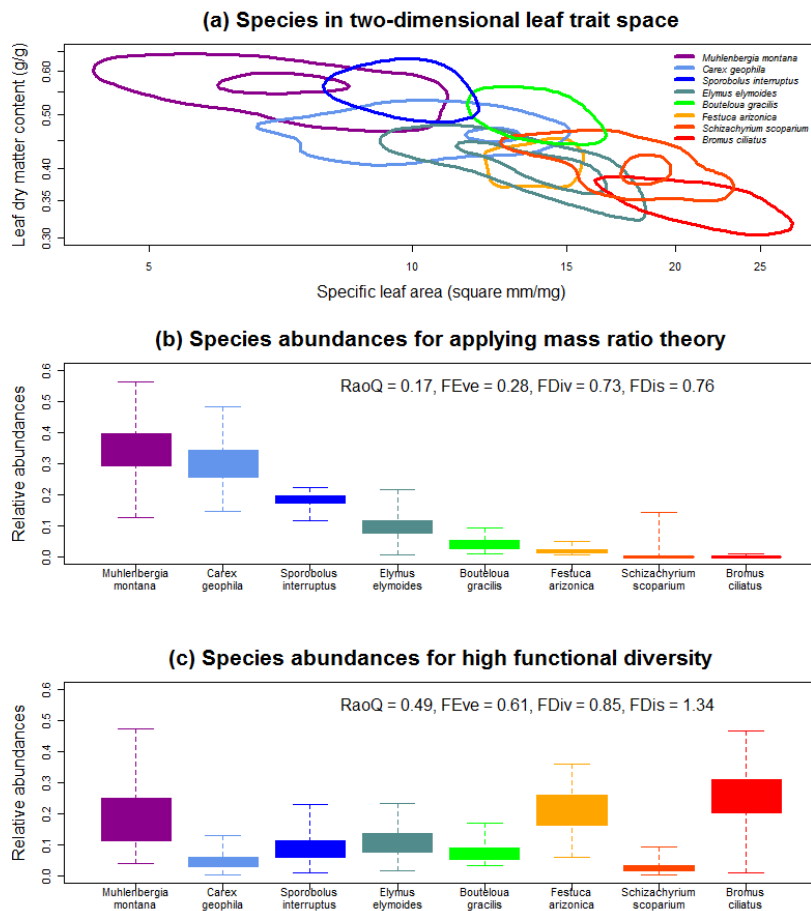
895 courtesy of Max Licher and the Southwest Environmental Information Network (SEINet).

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901

902 **Figure 5. (a)** Bivariate contour density plots illustrating the location and intraspecific
 903 variability of eight native graminoid species in trait space defined by specific leaf area and
 904 leaf dry matter content (log-scale). **(b)** Traitspace model output (Box 2) illustrating the range
 905 of variability of species that would be appropriate to use in restoration projects if the desired
 906 effect was to slow down litter decomposition and nitrogen transformations by applying mass
 907 ratio theory. **(c)** Traitspace model output (Box 2) illustrating the range of variability of
 908 species that would be appropriate to use in restoration projects if the desired goal was to
 909 maximize functional diversity. Average functional diversity indices (Villéger *et al.* 2008;
 910 Laliberté & Legendre 2010) are listed for each set of generated communities in panels b and c.
 911 The trait data were obtained on understory plant species growing in a ponderosa pine forest
 912 near Flagstaff, Arizona (Laughlin *et al.* 2010).

913 **Text Boxes**

914 **Box 1. Underdetermined systems of linear equations**

915 Systems of linear equations are useful for estimating species probabilities given a set
916 of constraints and have many potential applications in ecology. For example, systems of
917 linear equations have been used to estimate the probability that a species of prey was
918 consumed by a predator based on the isotopic ratios of both the predator and prey (Phillips &
919 Gregg 2003). A vector of unknown species relative abundances (p_i) can be estimated by
920 developing a system of linear equality and inequality constraints:

921
$$\sum_{i=1}^S t_{ik} p_i = \overline{T}_k \quad (\text{Eqn 1}),$$

922
$$\sum_{i=1}^S p_i = 1 \quad (\text{Eqn 2}),$$

923
$$p_i > 0 \quad (\text{Eqn 3}).$$

924 Equation 1 states that the linear combination of the k th trait from the i th species (t_{ik}) and
925 unknown species relative abundances (p_i) is equal to the constraint \overline{T}_k , where \overline{T}_k is the k th
926 trait value of an average unit of biomass or individual in a community. There are K (the
927 number of traits) of these constraint equations, and S is the size of the species pool. Equation
928 2 constrains the abundances to sum to one to reflect relative abundances or probabilities.
929 Equation 3 constrains the abundances to be non-negative (there are S of these equations). In
930 practice, there are typically far fewer traits than unknown species abundances, which results
931 in an underdetermined system of equations with many possible solutions. The CATS model
932 uses this framework, but chooses the distribution that maximises the entropy function to
933 obtain a single discrete relative abundance distribution (Shipley *et al.* 2006). However, the
934 range of potential species abundances provides us with valuable information about the
935 potential range of variability that also satisfies the trait constraints. How do we quantify this
936 range of variability?

937 The most straightforward approach to quantify the range of potential solutions to any
938 underdetermined system of linear equations is to obtain a sample from the solution set. Van
939 den Meersch *et al.* (2009) developed the R package `limSolve` for solving constrained linear
940 equations. The ‘`xsample`’ function uses a Markov chain Monte Carlo (MCMC) algorithm to
941 uniformly sample the solution set of any constrained linear problem. We can apply this
942 application of linear algebra to the problem at hand by rewriting Equations 1 and 2 in matrix
943 form $\mathbf{Ax} = \mathbf{b}$, where \mathbf{A} is a matrix of coefficients (i.e., species mean traits), \mathbf{x} is a matrix of
944 unknown relative abundances, and \mathbf{b} is a vector of constants (i.e., trait constraints)
945 representing the right-hand side of the equations. As long as the constraints are consistent
946 (i.e., either one or an infinite number of solutions exists), one can obtain a uniform sample
947 from \mathbf{x} , which will represent the range of species abundances that meet the functional trait
948 constraints. It is important to select reasonable trait targets that fall within the range of trait
949 values present in the species pool.

950 Multiple solutions exist for underdetermined systems of linear equations, but there
951 may not be a solution where all species abundances are non-negative, which would violate
952 the inequality constraint of Equation 3. It is therefore important to determine whether a
953 solution exists. It is possible to allow for the solutions to only approximately match the
954 constraints. The `limSolve` package can sample the solutions by selecting likely values given
955 approximate equations, where the constraints follow a Gaussian probability distribution with
956 a given standard deviation (Van den Meersche *et al.* 2009). In these situations, it is
957 recommended that Equation 1 be defined as an approximate equality, and Equation 2 be
958 defined as an exact equality. This procedure will greatly increase the flexibility of
959 determining species abundances for selected trait targets.

960 In order to determine an assemblage of native species that optimises trait similarity
961 with a non-native species, the following modification to Equation 1 can be made:

962
$$\sum_{i=1}^S t_{ik} p_i = \overline{Invader}_k \quad (\text{Eqn 4}),$$

963 where $\overline{Invader}_k$ is a vector of K mean trait values of the non-native invasive species. In this
964 case, a discrete probability distribution may be more useful than a range of species
965 abundances, so one can apply the maximum entropy formalism to obtain species relative
966 abundances (Shipley *et al.* 2006). Note that this differs from the standard application of the
967 model where the constants on the right-hand side of the equations are community-weighted
968 mean trait values. This approach allows us to determine the abundances of species that would
969 maximize functional trait similarity with the non-native species. Using the maxent function in
970 the FD library of R (Laliberté & Shipley 2010), one can quantify the probability of each
971 species given the non-native trait constraints (Appendix S1).

972

973 **Box 2: Trait-based models that apply Bayes Theorem**

974 Systems of linear equations do not permit an elegant incorporation of intraspecific
975 variation and covariation, nor do they permit the derivation of functionally diverse
976 communities because they emphasize trait convergence. An alternative Bayesian framework
977 was recently proposed for predicting species relative abundances using inter- and intra-
978 specific trait variation and covariation (Laughlin *et al.* 2012). Quantifying intraspecific trait
979 variation and covariation is required for understanding the functional trait space of a species.
980 The objective of the model is to estimate the relative abundance of the i^{th} species for a given
981 environment $P(S_i/E)$, by incorporating information about individual-level functional traits.
982 Details of the proposed method can be found elsewhere (Laughlin *et al.* 2012) and so are not
983 repeated here (see Appendix S1 for complete R code to fit the model). The major differences
984 with previous applications are within Step 1a and Step 2d.

985 In Step 1a, the trait targets are defined by determining the probability density function
986 of the trait target range. To apply mass ratio theory, one simply needs to define a unimodal

987 trait distribution centered on the trait targets. However, applying niche complementarity
988 requires a different approach. In contrast to the theories of environmental filtering and mass
989 ratio, which both imply convergence of traits within a community, the theory of niche
990 complementarity implies functional trait divergence. Functionally diverse communities are
991 often characterised by dominant species having contrasting trait values (Mason *et al.* 2005).
992 Therefore, to generate functionally divergent communities it is necessary to establish trait
993 targets that include multiple modes along the trait axes, rather than constraining by a single
994 optimal trait value. The ‘mclust’ library of R can be used to develop probability density
995 functions for any desired multi-modal trait distribution.

996 In Step 2d, the original formulation requires modification if it is to be used to quantify
997 a range of variation in species abundances rather than simply compute a static relative
998 abundance distribution. It is possible to explore the range of possible solutions by repeating
999 the final step of the method J times. This step integrates the traits out using Monte Carlo
1000 integration to obtain the relative abundances of species given the environmental conditions,
1001 and is approximated as

$$1002 \quad P(S_i|E)_j \cong \frac{1}{N} \sum_{k=1}^N P(S_i|T_k, E)P(T_k|E), \quad (\text{Eqn 5})$$

1003 where $P(S_i|E)_j$ represents the j th repetition of this step, $N =$ a relatively small (*e.g.*, 10 to 100)
1004 number of Monte Carlo samples for each repetition, $P(S_i|T_k, E)$ represents the probability of
1005 the species given the traits and environment obtained by applying Bayes theorem, and
1006 $P(T_k|E)$ is the probability of the trait given the environmental conditions or the trait target
1007 range. Repeat the inference stage a large number of times (*e.g.*, $J = 100$) to obtain J estimates
1008 of the relative abundances. The range of $P(S_i|E)_j$ represents the range of potential relative
1009 abundances of species that could occur within a particular environmental filter, or it can
1010 represent the range of potential relative abundances of species for influencing an ecosystem
1011 process.