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.

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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; Quétier *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

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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.

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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

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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

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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.

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Applications of quantitative trait-based models in restoration ecology

Applying environmental filters to determine future restoration targets

Environmental filters can be applied to restore assemblages of species that are adapted

to a set of environmental conditions (Fattorini & Halle 2004). If high-quality relict sites can

be used as reference conditions for a restoration project, then the trait values present in the

relict community can potentially be used to generate species abundances for the restored

community (Fig. 1). This approach would be similar to the traditional approach of using the

composition of the relict site as the target, but would differ in that the targets are trait values

and that a variety of species abundance distributions could meet a single trait target (Fig. 2).

In theory, functional trait targets should increase the flexibility of restoration projects because

a range of species assemblages can meet a single functional trait target. However,

environmental conditions are being altered by agents of global change, and so a progressive,

forward-thinking restoration goal would seek to restore an indigenous community that is

resilient given the predicted changes in climate in the coming century (Fig. 1) (Suding 2011).

Consider the case of the semi-arid south-western USA, where the effects of climate

change are already inducing landscape-scale changes in tree mortality rates, community

structure and disturbance regimes (Breshears *et al.* 2005; Westerling *et al.* 2006). Currently,

the forests surrounding Flagstaff, Arizona are dominated by *Pinus ponderosa* (ponderosa

pine), but land managers are interested in how these forests will respond to climate change

stressors. A trait-based model was used to determine how traits were filtered by temperature

across this region and showed very predictable relationships between temperature and four

traits in particular: wood density, flowering time, maximum height and bark thickness

(Laughlin *et al.* 2011). As the climate changes, we would expect that the trait values that

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, ecophysiologists,

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 δ^{13}C, and leaf δ^{15}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

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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

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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 vigourous 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 fecue), 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

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*

851

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
Response traits		
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 *et al.* 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 *et al.* 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)
Effect traits		
Mass ratio	Traits of dominant species influence ecosystem processes	Species with resource-conserving leaf traits will slow decomposition and nutrient cycling (Orwin *et al.* 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 *et al.* 2012)

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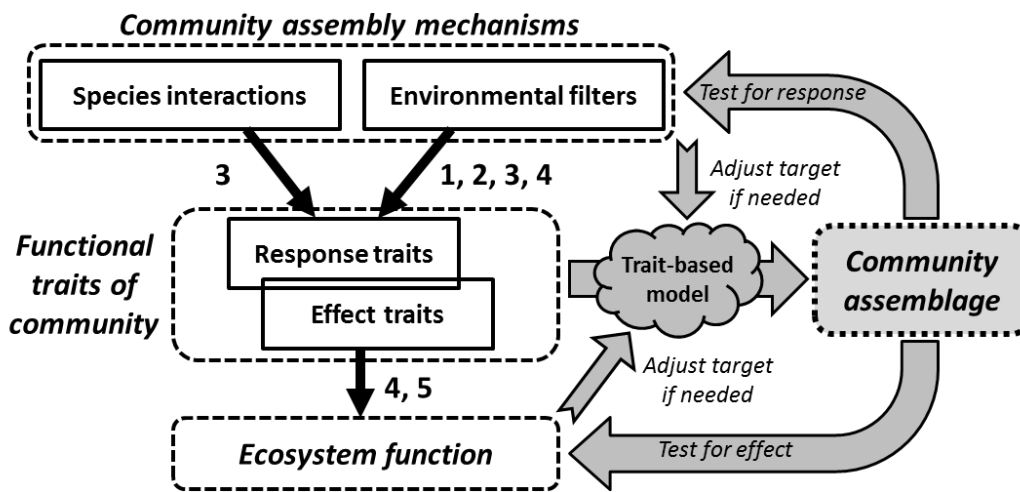
Figure 1. Conceptual diagram of the general framework for generating species assemblages that achieve functional targets for ecological restoration. **a)** Examples of novel stressors that have led to ecosystem degradation, and the restoration goals and functional targets that can be developed to assist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

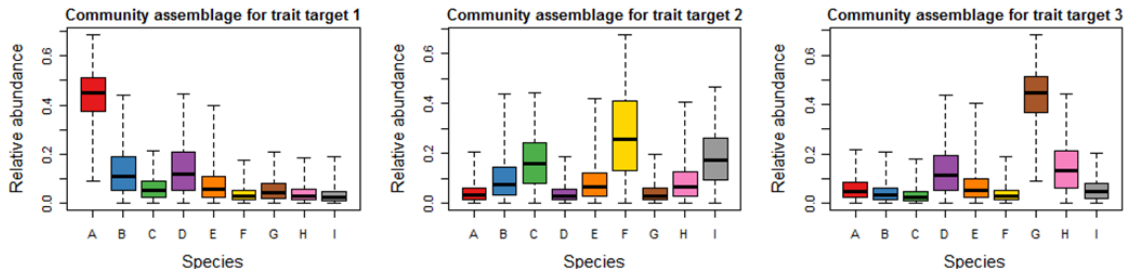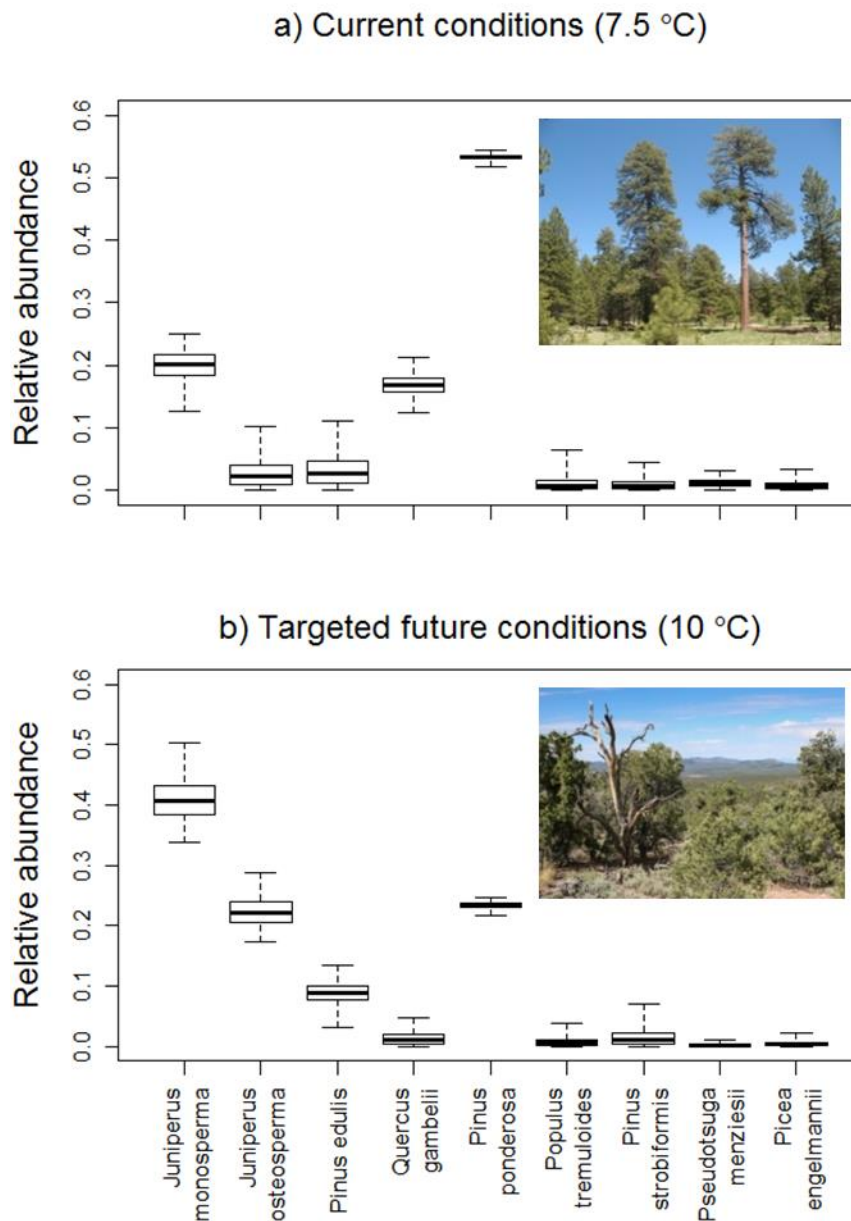**Figure 2.** Operationalising the response-and-effect trait framework for theory-driven

restoration ecology experiments. The hypothetical species abundance distributions were

generated using underdetermined systems of linear equations (Box 1, Appendix S1).

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a) Current conditions (7.5 °C)

b) Targeted future conditions (10 °C)

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Figure 3. Range of variability of tree species relative abundances that meet the trait targets in
a) current climatic conditions and **b)** projected future climatic conditions in the Southwest
USA (e.g., Flagstaff, Arizona; Lat: 35.14, Long: -111.67) (Laughlin *et al.* 2011). Values
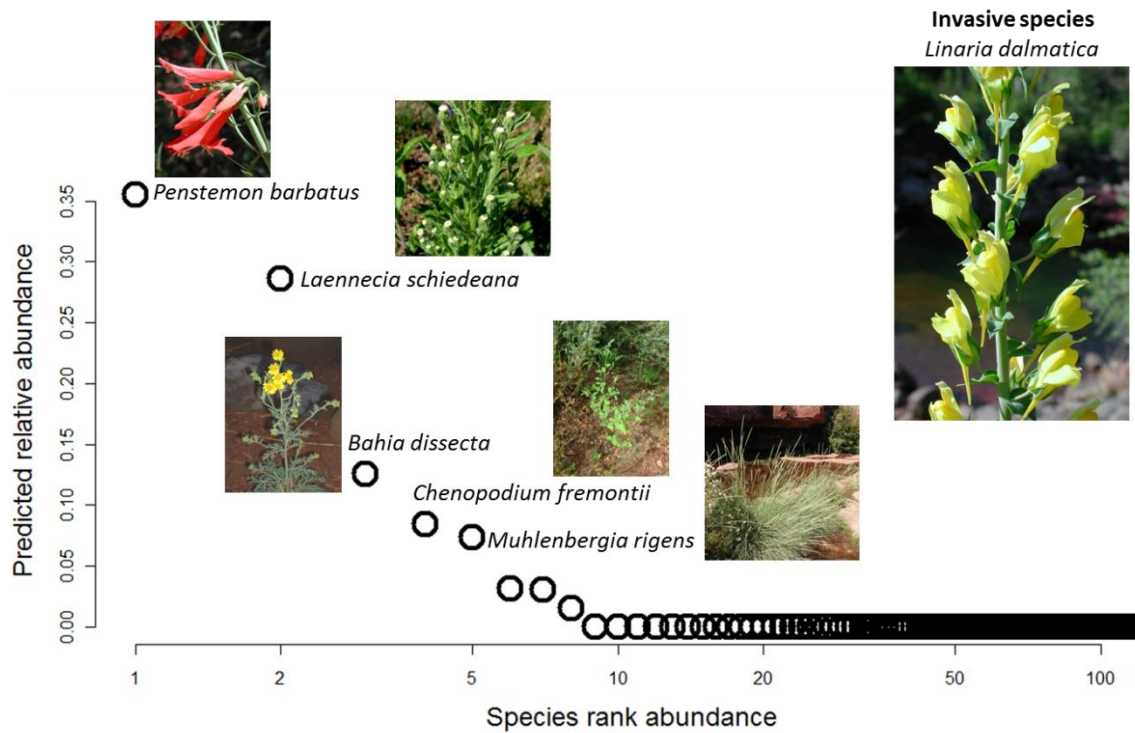represent a uniform sample of the solutions to the systems of linear equations (Box 1). Photo
credits: upper photo by Daniel Laughlin, lower photo by Guy Starbuck
(http://www.starbuck.org/exploring/) with permission.

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

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

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

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

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

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

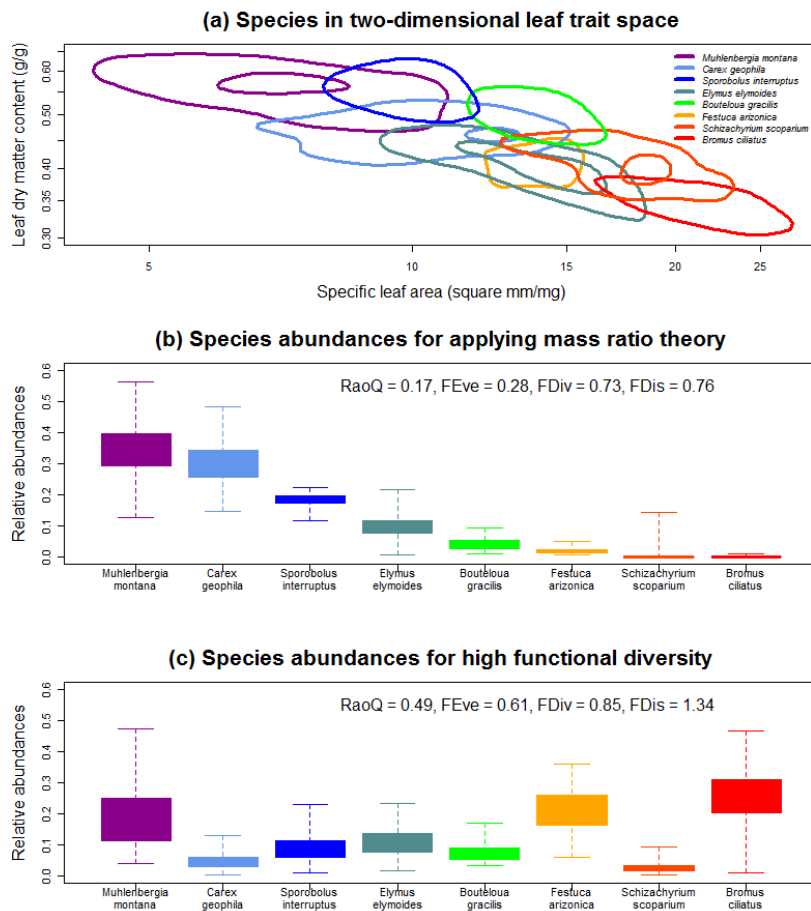growing in a ponderosa pine forest near Flagstaff, Arizona (Laughlin *et al.* 2010). All photos

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

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(a) Species in two-dimensional leaf trait space

(b) Species abundances for applying mass ratio theory

RaoQ = 0.17, FEve = 0.28, FDiv = 0.73, FDis = 0.76

(c) Species abundances for high functional diversity

RaoQ = 0.49, FEve = 0.61, FDiv = 0.85, FDis = 1.34

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

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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       $\sum_{i=1}^{S} t_{ik} p_i = \overline{T_k}$ (Eqn 1),

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

923       $p_i > 0$ (Eqn 3).

924 Equation 1 states that the linear combination of the kth trait from the ith 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 kth

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 $$\sum_{i=1}^{S} t_{ik}p_i = \overline{Invader_k} \qquad \text{(Eqn 4)},$$

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).

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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 ith 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 $P(S_i|E)_j \cong \frac{1}{N}\sum_{k=1}^{N} P(S_i|T_k,E)P(T_k|E),$ (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.