

1 The ‘filtering’ metaphor revisited: competition and environment jointly structure
2 invasibility and coexistence

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22 **Keywords:** annual plants; competition; fitness differences; niche differences; precipitation

23

24 **Abstract**

25 ‘Filtering’, or the reduction in species diversity that occurs because not all species can persist in
26 all locations, is thought to unfold hierarchically, at large scales due to the environment and at
27 small scales due to competition. However, the ecological effects of competition and the
28 environment are not independent, and observational approaches preclude investigation into their
29 interplay. We use a demographic approach with 30 plant species to experimentally test (i) the
30 effect of competition on species persistence in two soil moisture environments, and (ii) the effect
31 of environmental conditions on the mechanisms underlying competitive coexistence. We find
32 that competitors cause differential persistence of species across environments even when these
33 effects are lacking in the absence of competition, and that the traits that determine persistence
34 depend on the competitive environment. Changing environmental conditions generated
35 idiosyncratic effects on coexistence outcomes, increasing competitive exclusion of some species
36 while promoting coexistence of others. Our results highlight the importance of considering
37 environmental filtering in light of, rather than in isolation from, competition, and challenge
38 community assembly models and approaches to projecting future species distributions.

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47 **1. Introduction**

48 One of the most fundamental schematics shown in any introductory ecology class depicts the
49 hierarchy of ecological filters thought to give rise to local communities from a regional species
50 pool. The first filter generally depicted is the environment, which excludes any species without a
51 suitably compatible phenotype, whereas the second filter represents competition among
52 environmentally compatible species. This filtering metaphor has been applied to infer ecological
53 process from a wide range of patterns, from the scale-dependence of biodiversity to the
54 distribution of trait/phylogenetic relatedness in communities [1]. However, ‘filtering’, by
55 definition, is the successful or failed persistence of species in a given environment, and is
56 difficult if not impossible to detect without experimentation [2]. For instance, a species might be
57 absent from a locality simply because it has not yet arrived [3] or be present but on an extinction
58 trajectory that has not yet been realized [4]. Additionally, trait/phylogenetic patterns have been
59 shown to lead to incorrect inferences about ecological mechanisms in the presence of
60 competitors, which is the case in most environments [2,5], and studies often consider the
61 environment and competition as alternative explanations for patterns, with little attention paid to
62 their interaction.

63 Experiments are needed to understand how persistence and its demographic drivers are
64 interactively structured by the competition and the environment [2]. In its broadest sense,
65 filtering removes a subset of the potential community, and is quantifiable as population growth
66 rates <1 when at low abundance (λ_{inv} , known as ‘invasion growth rate’ [6]). By contrasting λ_{inv} of
67 a given focal species among different environments, specifically in the presence and absence of
68 competitors in different environments ($\lambda_{inv[C+E]}$ and $\lambda_{inv[E]}$, respectively), we can ask how
69 competition changes predictions about which species can persist in a given environment. Broad-

70 scale tests of the assumption that species are limited by environmental conditions, rather than
71 community responses to those conditions, are rare [7] but needed to be understood to forecast the
72 ecological consequences of environmental change (*e.g.*, species' range limits [8]).

73 A complementary approach to testing persistence is to examine how the environment
74 affects the mechanisms that underlie species coexistence (*i.e.*, the mutual persistence of
75 competing species [6]). Recent years have seen a considerable research effort put towards
76 quantifying niche differences and fitness differences among species, which promote and preclude
77 coexistence, respectively [9]. In doing so, ecologists are now much closer to resolving long-
78 standing questions about how differences among species, such as functional traits [10],
79 provenance [11], and evolutionary history [12], contribute to coexistence and the maintenance of
80 diversity. However, it remains unknown how sensitive niche and fitness differences are to the
81 environment, even in well-studied systems, as most experiments are conducted in single
82 environments (but see [12,13]). Other research examines how environmental heterogeneity and
83 dispersal allow spatial or temporal coexistence, underlain by species-specific environmental
84 responses and dispersal (*e.g.*, storage effects [14], relative non-linearity). As a result, the scale-
85 dependence of coexistence mechanisms are increasingly understood, but we lack empirical
86 evidence of how sensitive local competitive interactions are to environmental context—these
87 data are needed to understand the mechanistic interplay between competition and the
88 environment.

89 To resolve the complex interplay between competition and environmental conditions, we
90 couple a demographic approach [2,15] with trait data and an experimental manipulation of a key
91 resource. We apply this approach to answer four questions: (1) How strong is environmental
92 filtering *sensu stricto*, measured as the exclusion of species based on environmental conditions

93 alone [2]? (2) How do interspecific competitors alter the effect of environmental conditions on
94 persistence? (3) Do species' traits explain differential responses to environmental conditions
95 with and without competition? and (4) How sensitive are niche differences, fitness differences,
96 and coexistence among competing species to the environment? We use annual plant communities
97 from mediterranean-climate regions as a model system, contrasting two soil moisture regimes,
98 'wet' and 'dry', that represent differences between mesic (662 mm/year) and xeric (312
99 mm/year) sites across species' ranges in California [16].

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101 **2. Materials and methods**

102 Our experiment included 30 species grown for seven months in a research greenhouse at
103 the University of Toronto (electronic supplementary material appendix S1). In brief, we grew
104 two types of experimental communities: (1) species grown alone at low densities (7 plants/pot),
105 such that individuals were not experiencing any interspecific competition and minimal
106 intraspecific competition, and (2) species grown in pairs at high densities (70 plants/pot) at a
107 range of relative frequencies to shift the strength of intraspecific and interspecific competition.
108 All experimental communities were replicated under wet and dry conditions, imposed by
109 watering the wet treatment twice as frequently as the dry treatment. All seed was collected from
110 senescing plants, enumerated, and used to estimate per capita seed production, from which we fit
111 separate annual plant competition models (equation S1) for each species pair. Species' traits
112 were measured in separate experiments under identical growing conditions (electronic
113 supplementary material appendix S1).

114 λ_{inv} estimates are species-specific, whereas niche and fitness differences are calculated for
115 each pair of interacting species. $\lambda_{inv[EJ]}$ is the finite rate of increase estimated via model fitting (λ_i

116 in equation S1), whereas $\lambda_{inv|C+Ej}$ is the solution to $\lambda_i/(1+\alpha_{ij}\hat{N}_j)$, where $\alpha_{ij}\hat{N}_j$ is the interspecific
117 effect of species j on i (α_{ij}) when species j is at its single-species equilibrium population size
118 (\hat{N}_j). For each species pair, we used parameter estimates from the fitted competition model to
119 solve for niche and fitness differences according to previous studies of annual plants [10,11].
120 Niche differences are derived from the relative strengths of interspecific and intraspecific
121 competition (equation S2), whereas fitness differences are the product of species' differences in
122 fecundity and sensitivity to competition (equation S3). The joint values of niche and fitness
123 differences can predict whether a species pair can coexist in a given environment (figure 2). We
124 used linear mixed effects models to test differences in λ_{inv} and coexistence mechanisms among
125 soil moisture environments (electronic supplementary materials, appendix S1). Note that our
126 definition of 'environment' is inclusive of non-competitive species interactions, such as among
127 plants and their soil microbes/pollinators.

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129 **3. Results and discussion**

130 We found that filtering caused by the environment alone was dwarfed in comparison to
131 the filtering effect of competition. Specifically, only a single species failed to persist ($\lambda_{inv|Ej}<1$) in
132 the absence of competition compared to 12 per environment in the presence of competitors (pie
133 charts in figures 1a,b). Soil moisture had no mean effect on λ_{inv} across species regardless of the
134 competitor environment (figure 1a,b, table S2; $P>0.70$) despite large effects of soil moisture,
135 competition, or both within species (figures 1a,b and S1)—this discrepancy occurred because
136 equal numbers of species increased and decreased λ_{inv} in response to dry conditions.

137 Our results highlight two ways in which inferences of environmental filtering can be
138 misled by the presence of competitors. First, for some species, the effect of soil moisture on

139 persistence only emerged in the presence of competitors. For example, *Lasthenia californica* had
140 high $\lambda_{inv[E]}$ in both soil moisture environments, but in competition, was predicted to persist in dry
141 conditions only (figure 1a,b). Second, the traits that underlie species persistence ($\lambda_{inv} \geq 1$) differed
142 depending on whether competitors were present or absent (figure 1c and table S3; $P=0.001$). In
143 observational studies, the strength of environmental filtering is typically inferred by tracking
144 occupancy or measuring trait distributions in natural communities, which include competitors
145 [1]. If our results had come from such an observational study, we would erroneously conclude
146 that environmental filtering removes 40% of the species pool, specifically species with low
147 biomass, shallow roots, and small seeds (biplot in figure S3). Previous research in species-poor
148 communities suggests that inferring environmental filtering from trait patterns can mislead
149 conclusions [5]; our experiment is the first to confirm this result using a robust demographic
150 approach.

151 Niche and fitness differences responded strongly to the soil moisture environment for
152 many species pairs (figure 2), shifting coexistence outcomes, despite lacking an average effect
153 across species (table S4). Nine species pairs were predicted to coexist in each environment, but
154 the identities of only six pairs were common to both environments. At first glance, these
155 idiosyncratic responses were surprising—empirical experiments frequently predict that
156 increasing resource supply rates reduces coexistence, specifically by decreasing niche
157 dimensionality [17]. However, as our data suggests, this prediction entirely depends on where
158 resource supply rates fall relative to species' resource requirements and drawdown rates [18].
159 Additionally, theoretical predictions may not hold if phenotypic plasticity causes species'
160 resource requirements and drawdown to differ among environments (*e.g.*, converging root
161 lengths [19]). Indeed, plasticity was high in our experiment for some species pairs (figure S3),

162 but pairs exhibiting large competitive responses despite a lack of plasticity were also observed
163 (*e.g.*, *Lupinus* vs. *Trifolium* in figure S3), thus plasticity alone offers an insufficient explanation
164 for observed environmental responses. In sum, the contrasting soil moisture environments tested
165 here reflect those observed in the field and, although they have important consequences for
166 coexistence, their effects are not generalizable across species.

167 The field of ecology is undergoing rapid conceptual revision, as classical ideas are
168 deconstructed and rebuilt with greater theoretical support and empirical utility [15,18]. Our
169 results speak to the need to critically re-evaluate the conceptual separation of environmental and
170 competitive filters [15] and demonstrate the depth of mechanistic inference that can be drawn by
171 disentangling their effects [2]. Future research opportunities include an examination of (i) a
172 greater range of environmental gradients that species encounter in nature, (ii) multiple axes of
173 resource limitation [17], and (iii) the mechanisms that underlie idiosyncratic environmental
174 effects on coexistence mechanisms (*e.g.*, plasticity [19]). The integration of these approaches,
175 including the results we report here, promise to lead to an understanding of how environmental
176 conditions structure biodiversity and to more accurate forecasts of the impacts of global changes.

177

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181

182 **Author contributions**

183 R.M.G./B.G. designed the experiment, R.M.G. carried out the experiment and performed
184 analyses, R.M.G./M.M.M./B.G. wrote the paper.

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186 **Data accessibility**

187 All data will be deposited on Dryad following manuscript acceptance.

188

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192

193 **Competing interests**

194 The authors declare no competing interests.

195

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236

237 **Figure captions**

238

239 **Figure 1.** Invasion growth rate in the (a) absence ($\lambda_{inv[E]}$) and (b) presence ($\lambda_{inv[C+E]}$) of
240 competitors in dry (yellow) and wet (green) soil moisture conditions, and (c) the underlying
241 traits. (a,b) Points connected by a grey line show the same species in the different moisture
242 treatments. Points ≥ 1 (dashed lines) are predicted to persist; *Lasthenia californica* is highlighted
243 in bold. The subset of species pairs competed twice were not double-counted (table S1). (c)
244 Points are $\lambda_{inv[E]}$ and $\lambda_{inv[C+E]}$ after partialling out variation explained by random effects, with

245 fitted lines and 95% confidence bands. The composite trait is axis 1 from a multivariate analysis
246 (figure S3).

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248

249 **Figure 2.** Joint responses of niche and fitness differences to wet (green) and
250 dry (yellow) soil moisture treatments. Niche differences are maximized at 1, whereas fitness
251 differences are a ratio (equation S3) and equal 10^0 when species have identical fitnesses. The
252 curved dashed lines represent the boundary between coexistence and exclusion. Boxplots in the
253 margins show distributions of niche and fitness differences among environments. Niche
254 differences fell below 0 for four species pairs (figure S4), indicating positive frequency
255 dependence.

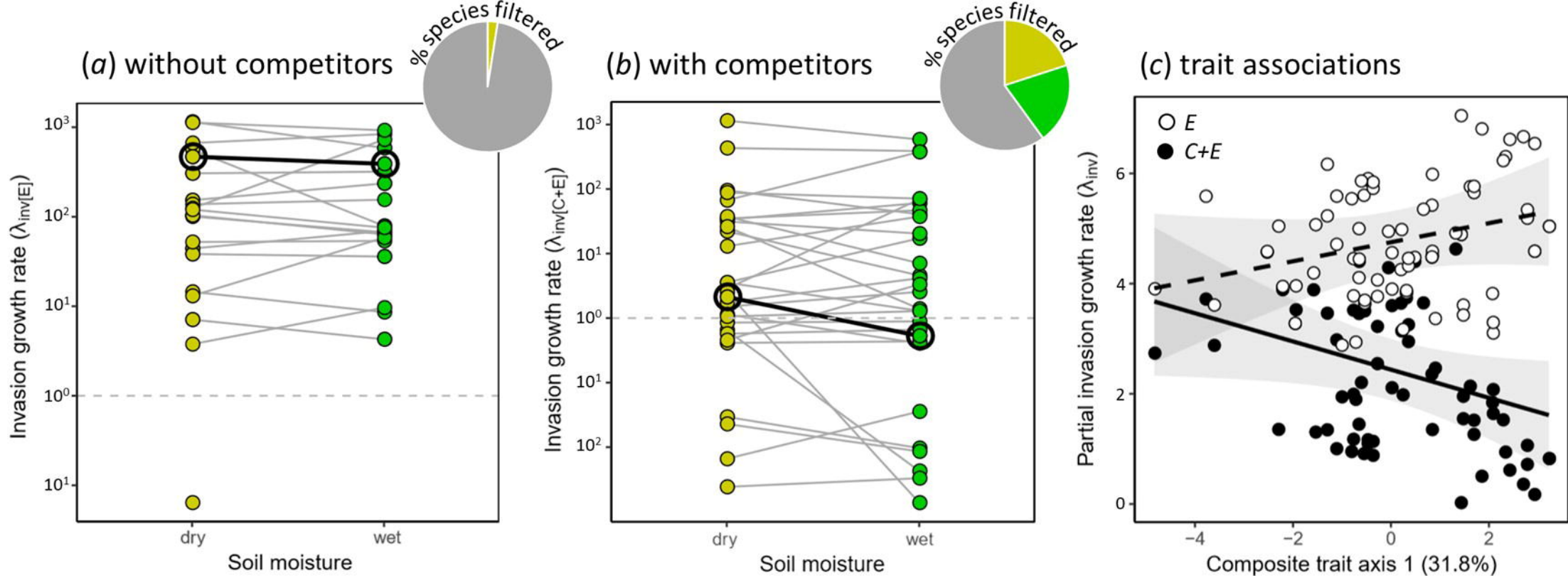


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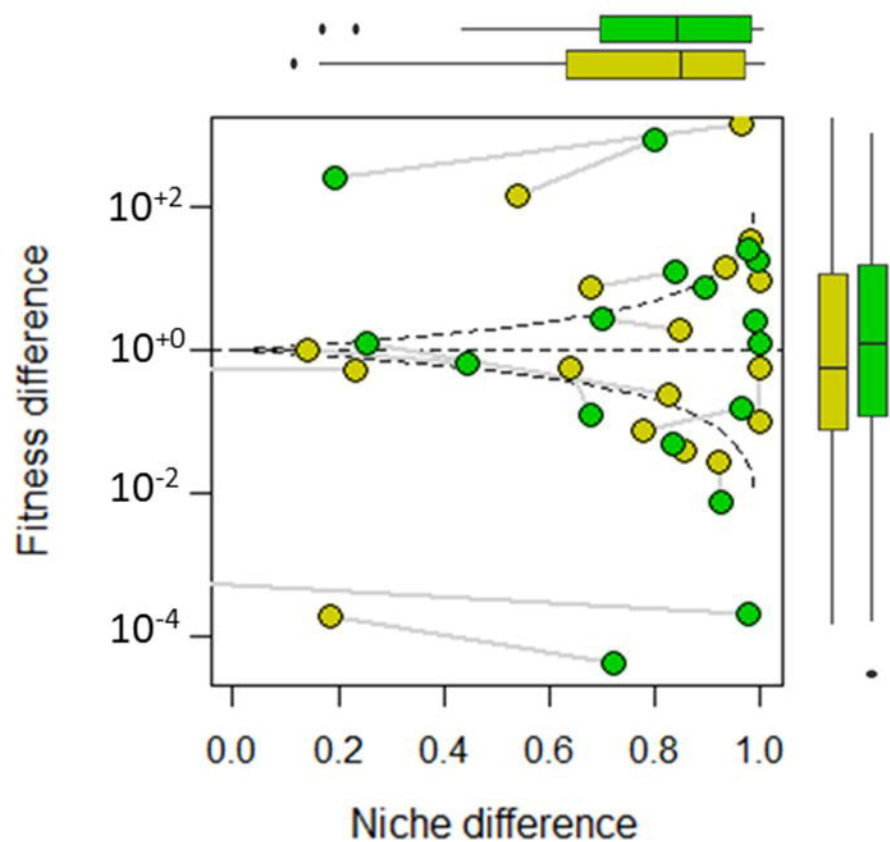


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