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[Jesus N. Pinto Ledezma](#), [Fabricio Villalobos](#), [Peter B. Reich](#), [Peter B. Reich](#) ...+3 more authors

Institutions: [University of Minnesota](#), [University of Sydney](#), [King's College London](#)

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1 **TESTING DARWIN'S NATURALIZATION CONUNDRUM BASED ON TAXONOMIC,**
2 **PHYLOGENETIC AND FUNCTIONAL DIMENSIONS OF VASCULAR PLANTS**

3
4 **Jesús N. Pinto-Ledezma^{1*}, Fabricio Villalobos², Peter B. Reich^{3,4}, Daniel J. Larkin⁵,**
5 **Jeannine Cavender-Bares¹**

6
7 ¹Department of Ecology, Evolution and Behavior, University of Minnesota, 1479 Gortner Ave,
8 Saint Paul, MN 55108, USA

9 ²Instituto de Ecología, A.C., Red de Biología Evolutiva, Carretera antigua a Coatepec 351, El
10 Haya, 91070 Xalapa, Veracruz, México

11 ³Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave, Saint Paul, MN
12 55108, USA

13 ⁴Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South
14 Wales 2753, Australia;

15 ⁵Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 135
16 Skok Hall, 2003 Upper Buford Circle, Saint Paul, MN 55108, USA

17

18 ***Corresponding Author:** jpintole@umn.edu, jesuspintoledezma@gmail.com

19 **Running Header:** Dissecting Darwin's naturalization conundrum

20 **Keywords:** Cedar Creek, community phylogenetics, co-occurrence patterns, invasion dynamics,
21 fire frequency, focal-species, functional traits, limiting similarity, long-term oak savanna
22 experiment, species sorting

23 **Abstract**

24 Charles Darwin posited two alternative hypotheses to explain the success of nonnative species
25 based on their relatedness to incumbent natives: coexistence between them should be (i) more
26 likely with greater relatedness (due to trait similarity that correlates with better matching to the
27 environment), or (ii) less likely (due to biotic interference, such as competition). The paradox
28 raised by the opposing predictions of these two hypotheses has been termed ‘Darwin’s
29 naturalization conundrum’ (DNC). Using plant communities measured repeatedly over a 31-year
30 time span across an experimental fire gradient in an oak savanna (Minnesota, USA) we evaluated
31 the DNC by explicitly incorporating taxonomic, functional and phylogenetic information. Our
32 approach was based on ‘focal-species’ such that the taxonomic, functional and phylogenetic
33 structure of species co-occurring with a given nonnative species in local communities was
34 quantified. We found three main results: first, nonnatives colonizers tended to co-occur most
35 with closely related incumbent natives in recipient communities, except in the extreme ends of
36 the fire gradient (i.e., communities with no fire and those subjected to high fire frequencies);
37 second, with increasing fire frequency, nonnative species were functionally more similar to
38 native species in recipient communities; third, functional similarity of co-occurring nonnatives
39 and natives in recipient communities showed a consistent pattern over time, but the phylogenetic
40 similarity shifted over time, suggesting that external forces (e.g., climate variability) are also
41 relevant in driving the phylogenetic relatedness of nonnatives to natives in invaded communities.
42 Our results provide insights for understanding the invasion dynamics across environmental
43 gradients and highlight the importance of evaluating different dimensions of biodiversity in order
44 to produce more powerful evaluations of species co-occurrence at different spatial and temporal
45 scales.

46 **Introduction**

47 The assembly and maintenance of ecological communities is a dynamic process operating over
48 multiple spatial and temporal scales, that incorporates local niche-based interactions and sorting
49 to stochastic and historical processes that may operate over large spatial scales (Tilman 2004,
50 Cavender-Bares et al. 2009, 2018a, Pinto-Ledezma et al. 2019). Over the past millennium,
51 human activities have greatly influenced these natural processes, through habitat degradation and
52 biological invasions by moving species out of their native ranges, with negative consequences
53 for biodiversity, ecosystem functioning, and human well-being (Sax et al., 2007, Thuiller et al.
54 2010, Vilà et al. 2011, Simberloff et al. 2013, Capinha et al. 2015).

55 Given the importance of biological invasions in determining current community structure
56 (Pearson et al. 2018), understanding the causes of invasion success have become a major goal in
57 ecology, evolution and conservation (Dawson et al. 2017). While there are many competing
58 hypotheses for the success and failure of colonizing species (Blumenthal 2005, Jeschke et al.
59 2012, Jeschke 2014, Prins and Gordon 2014), two major hypotheses have been proposed as
60 explanations for species invasion success that incorporate evolutionary relatedness as a primary
61 consideration (Gallien and Carboni 2017, Ma et al. 2016, Cadotte et al. 2018). First, Darwin's
62 naturalization hypothesis (DNH; Box 1: Fig. 1A) suggests that nonnative species closely related
63 to resident natives are less likely to invade native assemblages because the niches they could
64 invade are already occupied by ecologically similar relatives (Daehler 2001). In contrast, the pre-
65 adaptation hypothesis (PAH; Box 1: Fig. 1B) postulates that nonnative species closely related to
66 resident natives should be favored precisely because of their niche similarity with native species,
67 sharing traits that make them well-suited to the novel range (Ricciardi and Mottiar, 2006).
68 Accordingly, the extent to which nonnative species are closely or distantly related to resident

69 species may teach us whether competitive interactions or environmental filters, respectively, are
70 dominant factors determining invasion success (Gallien and Carboni 2017, Cadotte et al. 2018).
71 These opposing hypotheses both trace back to Darwin (1859) and together comprise ‘Darwin’s
72 naturalization conundrum’ (DNC, Diez et al. 2008, Thuiller et al. 2010, Cadotte et al. 2018).

73 Deciphering the connection between ecological and evolutionary processes in driving
74 species distributions and the assembly of communities is crucial to understand the invasion
75 success of nonnative species in recipient communities (Gallien and Carboni 2017, Cadotte et al.
76 2018, Pearson et al. 2018). Although the DNC represents an integrative explanation that links
77 both ecological and evolutionary processes (reviewed in Cadotte et al. 2018), invasion is a
78 dynamic process, i.e., nonnative species are continually expanding or retracting their
79 geographical ranges across the regions they have recently colonized (Sax et al. 2007, Blackburn
80 et al. 2015, Pannell 2015). Thus, the presence of nonnative species in a community does not
81 necessarily indicate that they are optimally-adapted to the new environmental or niche
82 conditions. One potential explanation for the spread of invasive species is the ‘ecological fitting
83 hypothesis’ (EFH, Janzen 1985), which suggests that widespread species can occupy new places
84 or environmental conditions without being perfectly adapted to them (Janzen 1985, Cavender-
85 Bares et al. 2018b, but see Odour et al. 2016). In addition, functional traits underlie composition,
86 community assembly and ecosystem processes (Cavender-Bares et al. 2009, Cavender-Bares et
87 al. 2016, Lavorel et al. 2011, Reich 2014, Catford et al. 2019); thus, different functional traits or
88 trait combinations can modulate the degree to which nonnative species are able to colonize and
89 further adapt to the ecological conditions found in recipient communities (Blumenthal 2005, van
90 Kleunen et al. 2010, Carboni et al. 2018; Catford et al 2019). Recent evidence suggests that
91 successful invasive species tend to have higher values for traits associated with resource

92 acquisition, dispersal, and establishment and competitive ability than local native species (van
93 Kleunen et al. 2010, Carboni et al. 2018, Catford et al. 2019), indicating that they have similar or
94 higher performance in the novel range than native species (Sax et al. 2007, Odour et al. 2016, but
95 see González-Muñoz et al. 2014).

96 Several studies have evaluated the DNC across different spatial scales and systems (for a
97 review see Cadotte et al. 2018, Gallien and Carboni 2017, Ma et al. 2016). However, few studies
98 have explored the dynamics of species composition and relatedness within communities during
99 the invasion process (Blackburn et al. 2015, Li et al. 2015) or the role of functional traits in
100 modulating colonization and establishment by nonnative species (Marx et al. 2015, Carboni et al.
101 2018; but see Catford et al 2019). Although these studies have generally found similar results—
102 from a phylogenetic perspective, nonnative species tend to coexist more with their close relatives
103 (e.g., Li et al. 2015, Marx et al. 2015, Kusumoto et al. 2019)—the incorporation of functional
104 information into analyses provides new insights regarding functional differentiation between
105 coexisting species (Cavender-Bares et al. 2009, Cadotte et al. 2018); and consequently a way
106 forward to understand how species' ecological differences regulate the colonization,
107 establishment and persistence of nonnative species within local native communities across
108 spatial and temporal scales.

109 Here, using plant communities sampled over decades across an experimental fire gradient
110 at Cedar Creek Ecosystem Science Reserve (hereafter Cedar Creek) in Minnesota, USA, we
111 evaluate the DNC while explicitly incorporating taxonomic, functional, and phylogenetic
112 information into our analyses. To do so, we apply a novel approach based upon the framework of
113 Villalobos et al. (2013, 2017), extending the concept of species' *functional/phylogenetic fields*—
114 the overall functional/phylogenetic structure within a given species' geographical range—to

115 describe the functional and phylogenetic structure of species co-occurring with a focal species;
116 for simplicity, we call this approach ‘focal-species’ (Box 1). In this approach, each species
117 within a community is in turn selected as a focal species; and its phylogenetic/functional distance
118 to each of the other species within the community is calculated, and the resulting values per focal
119 species are averaged (mean pairwise distance per focal species, MPD_{focal} ; Box 1: Fig. 1). This
120 simple extension enables quantification of the degree to which a given species co-occurs with
121 other species, by measuring whether a nonnative species occurs more frequently with
122 phylogenetically close/functionally similar or phylogenetically distant/functionally dissimilar
123 species (Box 1: Fig. 1). The idea of focal-species is not novel *per se* and is conceptually similar
124 to the α niche concept (Pickett and Bazzaz 1978), which can be interpreted as differences in
125 functional traits between a given species and those of co-occurring species (Ackerly and
126 Cornwell 2007). The focal-species approach as extended here is advantageous for incorporating
127 different dimensions of biodiversity (i.e., taxonomic, functional, phylogenetic) and can be
128 adapted at different spatial and temporal scales (e.g., Villalobos et al. 2013, 2016, Herrera-Alsina
129 and Villegas-Patracá 2014, Miller et al. 2017a).

130 Considering previous studies that evaluated Darwin’s naturalization conundrum (e.g.,
131 Diez et al. 2008, Davies et al. 2011, Carboni et al. 2013, Bezeng et al. 2015, Marx et al. 2016),
132 we expect (1) based on Darwin’s naturalization hypothesis, that nonnative species will tend to
133 co-occur with distantly related species (overdispersion), or (2) based on the pre-adaptation
134 hypothesis, that nonnative species will tend to co-occur more with closely related species
135 (clustering) (Box1: Fig. 1C). The same logic extends to the influence of functional traits on
136 species co-occurrence (Box 1: Fig. 1C): if co-occurring nonnative and native species are
137 functionally similar, this would support the hypothesis that environmental fit mediates species

138 co-occurrence within invaded communities; conversely, if co-occurring species are functionally
139 distinct, this would support the premise that competition governs co-occurrence between native
140 and nonnative species (Gallien et al. 2014, Carboni et al. 2018, Cadotte et al. 2018).

141 The fifty-year experimental fire frequency gradient at Cedar Creek (Peterson and Reich
142 2001, Reich et al. 2001, Willis et al. 2010, Cavender-Bares and Reich 2012), provides a unique
143 opportunity to explore the changes in focal-species relatedness—in both phylogenetic and
144 functional dimensions (Box 1: Fig. 1), given that nonnative species distribution and abundances
145 are dynamic in time and space (Fig. S1) and the degree of interaction within invaded
146 communities depends on species' adaptability (Janzen 1985, Blackburn et al. 2015). The
147 experiment thus provides a means to understand how stressful gradients influence focal-species
148 phylogenetic relatedness/functional similarity, ergo Darwin's naturalization conundrum. More
149 specifically, as local conditions become more and/or differentially stressful (e.g., repeated fires
150 versus deep shade at the two ends of the fire frequency gradient), species populations are
151 expected to change, thereby increasing the role of species sorting (Nowacki and Abrams 2008,
152 Cavender-Bares et al. 2009, Mayfield and Levine 2010, Willis et al. 2010, HilleRisLambers et al.
153 2012). Consequently, only species that have evolved to tolerate fire exposure and dry, high light
154 conditions on the frequently burned end gradient, or to compete successfully for light at the
155 unburned end of the gradient, are able to recruit and persist over time. Relevant functional
156 traits—such as specific leaf area ($\text{cm}^2 \text{g}^{-1}$) [SLA], plant height (m), seed mass (mg) and rooting
157 depth (m) that are related with dispersal facilitation, establishment, persistence, resource
158 acquisition and recovery after disturbance (Moles et al. 2005, Peterson and Reich 2008, Willis et
159 al. 2010, Cavender-Bares and Reich 2012, Díaz et al. 2015, Pinto-Ledezma et al. 2018)—are
160 likely to change based on species niche requirements and resistance to disturbances.

161 Across fire gradients within the Cedar Creek system, plant height and tree cover are
162 generally negatively associated with fire frequency, with taller and short plants distributed in low
163 and high fire regimes, respectively; in turn, overstory tree cover decreases and light availability
164 to the understory increases (Reich et al. 2001, Peterson and Reich 2008, Willis et al. 2010). SLA
165 is predicted to decrease with increasing light availability in the oak savanna. In the understory of
166 unburned dense forest canopies, high SLA maximizes light interception. In contrast, in
167 frequently burned open areas prone to high solar radiation and desiccation, low SLA, which is
168 associated with high leaf hydraulic resistance, limits plant desiccation (Givnish and Vermeij
169 1976, Ackerly 2004). Similarly, seed mass tends to decline with increasing fire frequency.
170 Larger seeds are able to establish and survive as seedlings in competitive communities with low
171 light availability, whereas small seeds are able to disperse farther and to reproduce in large
172 numbers, allowing small-seed species to colonize patches that are not reached by large-seeded
173 species ('colonization-competition trade-off' Tilman et al 1994; Leishman et al. 1995, Moles et
174 al. 2005). Conversely, rooting depth tends to increase with increasing fire frequency, given that
175 deeper roots enhance access to groundwater resources and increase plant recovery after fire
176 disturbance (Peterson and Reich 2008, Willis et al. 2010, Pierret et al. 2016).

177 Considering species' evolutionary as well as ecological differences and given that traits
178 and phylogeny are linked due to underlying trait evolution (Box1: Fig. 1C), we test multiple
179 predictions for explaining the variation in focal nonnative species phylogenetic
180 relatedness/functional similarity across environmental gradients (Fig. 1). We posit that frequent
181 fire—which is accompanied by nutrient depletion in this system—represents a higher degree of
182 environmental stress than deep shade and heavy competition for light. Moreover, we hypothesize
183 that there is antagonism between environmental stress and competitive interactions between the

184 invader and its closely related native species—such that the likelihood of competitive exclusion
185 weakens as environmental stress becomes greater. An alternative hypothesis would be that deep
186 shade and strong light competition are equally stressful, but in other ways, than frequent fire.
187 Testing our hypotheses, as articulated below, will illuminate these scenarios and how they relate
188 to invasion and the DNC.

189 On the one hand, if species' functional traits are conserved over evolutionary time (Box
190 1: Fig. 1C), we predict the relatedness of focal nonnative species to their native incumbents to
191 shift from a pattern of phylogenetic overdispersion (low phylogenetic relatedness) to
192 phylogenetic clustering (high phylogenetic relatedness) with increasing fire frequency (Fig. 1A).
193 That is, we might expect that closely related and functionally similar plants—those with low
194 SLA, deep roots and short height—will co-occur more in communities subjected to high fire
195 frequency. We might further expect these same plants to be excluded from low frequency fire
196 regimes that, instead, are dominated by functionally distinct and distantly related taller species
197 that can persist under conditions of low understory light and soil fertility (e.g., shade-tolerant
198 woody and herbaceous species; Cavender-Bares et al. 2004, Peterson and Reich 2008, Willis et
199 al. 2010). On the other hand, if functional traits are convergent throughout species evolutionary
200 history (Box 1: Fig. 1C), shifts from phylogenetic clustering to phylogenetic overdispersion are
201 predicted with increasing fire frequency (Fig. 1B). That is, we might expect nonnatives to co-
202 occurring more with distantly related but functionally similar natives with increasing fire
203 frequency (Box 1: Fig. 1C). Notice that these predictions are based on the phylogenetic distance
204 between nonnative species and their co-occurring species within the recipient communities (Box
205 1). Under this prediction, the steeper the environmental gradient—i.e., a gradient from unburned
206 to high fire frequency (Fig. 1B)—the more nonnative species are able to avoid competition with

207 ecologically similar native species (C_4 grasses versus forbs; Leach and Givnish 1999) and as a
208 consequence are not excluded from native communities subjected to high fire frequency where
209 environmental filtering and sorting processes dominate due to the sunny, hot, dry, and nutrient-
210 poor conditions where these communities are distributed (White 1983, Leach and Givnish 1999,
211 MacArthur and Levins 1967, Peterson and Reich 2008, Cavender-Bares et al. 2009).

212 Real world possibilities may be complex. If biotic and abiotic filtering and sorting
213 processes are acting simultaneously (Ackerly 2003, 2004, Swenson and Enquist 2009, Germain
214 et al. 2018) and functional traits show phylogenetic signal—traits of the focal nonnative species
215 could be either similar to (clustered) or distinct from (overdispersed) the native species in the
216 community (Box 1: Fig. 1C); this would result in a complex nonlinear trend (polynomial) of
217 changes in the focal nonnative species relatedness across the fire frequency gradient. For
218 instance, as environmental conditions shift from communities with no fire to communities
219 frequently subjected to fire (Fig. 1C), nonnative species would tend to co-occur mostly with
220 closely related species, given that disturbances—such as fire regimes—filter or eliminate
221 disturbance-sensitive species (Huston 1979). Thus, different fire regimes can select for fire-
222 resistant (e.g., graminoids and forbs) species over shade-tolerant and fire-sensitive (e.g., woody
223 plants) species (Peterson and Reich 2001, 2008). Once functionally similar species capable of
224 tolerating conditions of frequent fire co-occur (e.g., grass-like plants and forbs), biotic forces
225 may become more important such that nonnative species may co-occur with distantly related but
226 ecologically similar (e.g., light-demanding and fire-resistant) species (Box 1: Fig. 1C).

227

228 **Methods**

229 *Study site*

230 A detailed description of the study site, burn units and sampling protocols can be found in
231 Peterson and Reich (2001), Reich et al. (2001) and Cavender-Bares and Reich (2012) but is
232 provided elsewhere.

233 The Cedar Creek Ecosystem Science Reserve is a 2300-ha reserve and National Science
234 Foundation (NSF) Long Term Ecological Research since 1982 and is located on the Anoka Sand
235 Plain in eastern Minnesota, USA. The climate is continental with cold and long winters and
236 short, warm and humid summers. Mean annual temperature and mean annual precipitation are
237 6°C (ranging from ~-12° in January and ~22° in July) and ~800 mm, respectively. The terrain is
238 relatively flat, and soils varies according the elevation, with infertile, sandy and well drained in
239 uplands areas and relatively fertile and poorly drained soils in lowland areas. Vegetation is
240 variable from abandoned croplands to well preserved vegetation types, like dry oak savannas.
241 The major vegetation types comprises deciduous forests, coniferous forests, deciduous
242 woodlands and savannas, upland prairies and hardwood and coniferous swamps.

243 In order to characterize the responses of plant communities and to restore oak savanna
244 vegetation a prescribed fire experiment started in 1964 (Peterson and Reich 2001, Cavender-
245 Bares and Reich 2012). Within this fire experiment, an area of nearly 300 ha was divided into 19
246 management units ranging from 2.4 to 30 ha and each one was assigned a fire frequency
247 treatment (five levels) that range from complete fire exclusion (unburned treatment) to yearly
248 fire frequency (high fire frequency treatment). Following Cavender-Bares and Reich (2012) we
249 categorized the fire frequency treatments into five levels: unburned (no fire), low frequency or
250 Fire 1 (once per decade), medium frequency or Fire 2 (2-3× per decade), mid-high frequency or
251 Fire 3 (4-5× per decade), and high frequency or Fire 4 (7-8× per decade). In addition, within each
252 fire treatment, permanent sample plots of 0.375 ha (50 × 75 m) were established to collect plant

253 species occurrence and abundance (Peterson and Reich 2008, Willis et al. 2010, Cavender-Bares
254 and Reich 2012).

255

256 *General approach*

257 Our aim was to evaluate both sides of Darwin’s naturalization conundrum (i.e., the DNH and
258 PAH) by taking advantage of a long-term, frequently resampled (five-year intervals from 1984 to
259 2015) fire-frequency experiment that has established a gradient from unburned, dense woodland
260 to frequently burned, open savanna. We evaluated DNH and PAH using taxonomic, functional,
261 and phylogenetic information at local and landscape scales. At the local scale, species-level
262 diversity metrics (see below) were estimated within each permanent plot of 0.375 ha (50 × 75 m)
263 across fire experiments ($N = 5$) and for each five-year time interval ($N = 7$). For analysis at the
264 landscape scale, species abundances and incidences were averaged across all plots representing
265 each fire treatment by time interval combination.

266

267 *Functional and phylogenetic data*

268 Data for four functional traits (specific leaf area [SLA], seed mass, plant height, and rooting
269 depth)—selected based on the current understanding of key traits related to dispersal,
270 establishment, resource acquisition, and persistence of plants across environmental gradients
271 (Reich 2014, Moles 2017)—were obtained from previous studies (i.e., Willis et al. 2010,
272 Cavender-Bares and Reich 2012). This trait dataset was not complete, with SLA available for
273 108 (44,44%) species, plant height for 86 (35,39%) species, and rooting depth for 85 (34,97%)
274 species, respectively. We filled these gaps by supplementing the original trait dataset using the

275 TRY (Kattge et al. 2011) and BIEN (Enquist et al. 2016) databases. In cases where missing traits
276 were not available from these sources, we used genus-level averaged trait values.

277 The phylogenetic hypothesis was obtained from the recently published Spermatophyta
278 mega-phylogeny (hereafter SB-tree; Smith and Brown 2018). The SB-tree was reconstructed
279 under a hierarchical framework where individual major clades were first constructed and then
280 placed into two different backbones (i.e., OTB [Open Tree of Life backbone] and MB [Magallón
281 backbone]) and missing taxa were imputed—i.e., the insertion of missing species to an observed
282 phylogeny—according to relationships in Open Tree of Life (see Smith and Brown 2018 for
283 details). The final SB-tree contains a total of 353,185 and 356,305 species for the OTB and MB
284 backbones, respectively, and to date is the most comprehensive phylogeny for seed plants (Smith
285 and Brown 2018). In this study, we used the SB-tree constructed under the OTB backbone as this
286 phylogenetic hypothesis provides more resolution towards the tips (Smith and Brown 2018).
287 After checking species names in our community dataset and the pruned SB-tree OTB backbone,
288 we found that 41 species were not sampled in the phylogenetic tree, but these 41 species all had
289 congeners represented in the SB-tree. Thus, to build a complete phylogenetic hypothesis, we
290 added missing species into the pruned SB-tree using taxonomic constraints (i.e., adding terminal
291 branches at the midpoint of their sister lineages) and estimated branching times under a birth-
292 death model of diversification using the addTaxa package (Mast et al. 2015) in R version 3.4 (R
293 Development Core Team 2018). We repeated the process 1000 times to account for phylogenetic
294 uncertainty in the topology and the final phylogenetic hypothesis used in this study comprises a
295 sample of 1000 fully dichotomous trees. Due to computational demand, we randomly selected a
296 sample of 100 trees and all subsequent analyses were performed using these 100 trees.

297

298 *Nonnative species classification*

299 We defined nonnative species as those that were introduced to the region by humans since early
300 European-American activities in the region (~1850s). Among the 243 vascular plants recorded in
301 all permanent plots at the Cedar Creek Ecosystem Science Reserve, 26 species were identified as
302 nonnative based on these criteria. Note that both nonnative and native plant species abundances
303 are not stationary over time or across fire regimes, and certain plant species were not recorded in
304 a particular time interval or fire experiment (Fig. S1).

305

306 *Calculation of diversity metrics*

307 Taxonomic diversity was calculated by recording the number, abundance, and identity of species
308 co-occurring with a nonnative focal-species in each permanent plot. We also estimated the
309 pairwise species co-occurrence patterns by estimating the normalized checkerboard score (C-
310 Score; Stone and Roberts 1990) between focal nonnative species and the co-occurring species
311 within each plot ($N = 5$) in each fire treatment ($N = 5$) at each time interval ($N = 7$), i.e., 35
312 matrices per fire treatment for a total 175. This metric is commonly used to quantify species'
313 associations (Gotelli 2000, Bar-Massada 2015). We constructed null models that maintain
314 species' frequency and species richness within communities (i.e., permanent plots) (the trial-
315 swap algorithm; Miklos and Podani 2004) to standardize C-Scores. This was done by calculating
316 standardized effect sizes (SES), comparing an observed value (empirical C-Score) to the mean
317 expected value under a null model, while accounting for variance (their standard deviation). For
318 standardized C-Scores, positive and negative values denote segregated (negative species
319 associations or competition) and aggregated (positive species associations or facilitation)

320 patterns, respectively, while values close to zero, are consistent with random patterns (Callaway
321 and Walker 1997, Tirado and Pugnaire 2005, Bar-Massada 2015).

322 Using functional and phylogenetic distance matrices as input data, we calculated different
323 metrics accounting for abundance and/or presence-absence of co-occurring species with focal-
324 species within each permanent plot. Prior to calculating functional metrics, a functional distance
325 matrix was calculated using Euclidean distances given that our functional traits are continuous
326 data. Metrics included mean pairwise phylogenetic and functional distances (MPD and MFD,
327 respectively) and mean phylogenetic and functional nearest taxon distance (MPNTD and
328 MFNTD, respectively). To facilitate comparisons and interpretation of the results, we also
329 standardized phylogenetic and functional metrics using standardized effect sizes, with SES
330 values >0 indicating phylogenetic or functional overdispersion and values <0 indicating
331 clustering (Webb et al. 2002). The null model applied was the same used to standardize the C-
332 Scores and the statistical significance of each metric was tested using thresholds ($|SES| > 1.96$)
333 (Pinto-Ledezma et al. 2019). All calculations were conducted using customized scripts and
334 functions modified from the picante (Kembell et al. 2010), metricTester (Miller et al. 2017b) and
335 ecospat (Di Cola et al. 2017) packages in R.

336 Presence-absence and abundance-weighted metrics were highly correlated with one
337 another (Fig. S2). Therefore, we only report results for the metrics abundance-weighted (aw)
338 MPD/MFD and MPNTD/MFNTD because they are more sensitive for detecting sharp shifts in
339 phylogenetic and functional structure (Miller et al. 2017b) and are more suitable for exploration
340 of long-term data, such as ours.

341

342 *Phylogenetic signal in functional traits*

343 We tested for phylogenetic signal in functional traits using Pagel's λ (Pagel 1999) under a
344 Bayesian approach. Pagel's λ assumes a Brownian motion (BM) evolutionary model and its
345 values range from 0 to 1, with values close to 0 and 1 indicating that traits evolved independently
346 of the phylogeny (phylogenetic independence or no phylogenetic signal) and that traits evolved
347 according to BM model (equivalent levels of phylogenetic covariance as expected under a BM
348 model or phylogenetic signal), respectively (Münkemüller et al. 2012, Harmon 2018). We
349 estimated Pagel's λ for the same sample of 100 trees used in previous analyses and ran MCMC
350 chains for 10 million generations, discarding the first million as burnins and sampling every
351 1000 generations in BayesTraits, version 3 (available from <http://www.evolution.rdg.ac.uk/>).
352 Before this analysis, traits were log-transformed to meet the assumption of normality (Harmon
353 2018). We additionally estimated Pagel's λ under a maximum likelihood approach and
354 calculated values for Blomberg's K (Blomberg et al. 2003). Both of these analyses produced
355 results similar to those observed the Bayesian analysis of Pagel's λ ; we present only the latter for
356 simplicity.

357

358 *Statistical analyses*

359 To evaluate the probability of changes in the relatedness/similarity of focal-nonnative species to
360 species in their surrounding communities through time (1984-2015) and across fire regimes
361 (unburned to high-frequency), we modeled focal-species (for the three dimensions of diversity)
362 as a function of fire regime (5 levels) and time interval (7 levels) under a Bayesian Multilevel
363 Modeling (MLMs) framework (Gelman and Hill 2007, Finch et al. 2014). Using MLM models,
364 metrics for each of the three dimensions of diversity were used to predict changes in focal-
365 species relatedness by fire experiments and time periods—i.e., focal-species metrics values were

366 nested within higher level units (fire experiments and time periods) (Finch et al. 2014). We used
367 a bivariate tensor spline (Wood et al. 2013) to model the interaction effect of the predictors,
368 which are of unknown, potentially non-linear form on focal-species relatedness (Bürkner 2017).
369 MLMs were performed for all nonnative species together and for major taxonomic groups (i.e.,
370 dicots and monocots). In total, we constructed six models (3 levels x 2 metrics) related to
371 changes in within-focal-species abundance and richness, 12 (3 levels x 4 metrics) related to
372 changes in phylogenetic relatedness, and 12 (3 levels x 4 metrics) related to changes in
373 functional similarity. In addition, given that environmental stressors like fire (or its absence) can
374 influence species coexistence, we built several models in which species relatedness within fire
375 experiments were a function of time intervals. This allowed us to explore how focal-species
376 responded to environmental conditions over time. All MLMs were run using 4 NUTS sampling
377 chains for 5000 generations, discarding 20% of each run as burnins, using the R package brms
378 (Bürkner 2017), which implements Bayesian MLM in R using the probabilistic programming
379 language Stan (Carpenter et al. 2017).

380 We also used permutational multivariate analysis of variance (PERMANOVA, Anderson
381 2001) to evaluate the uncertainty—the lack of complete knowledge about a parameter—
382 associated with the imputation of missing species in the phylogenies. To do so, we modelled
383 MPD/MPNTD as a function of fire regimes (5 levels) and time intervals (7 levels), using focal-
384 species identities as random variables ($N = 26$) and phylogenetic trees ($N = 100$) as replicates.
385 Under this modeling framework, the variance not explained by individual factors and their
386 interactions can be attributed to differences resulting from phylogenetic uncertainty caused by
387 species imputation (Rangel et al. 2015).

388

389 **Results**

390 Native and nonnative species exhibited similar trait values to each other (Fig. S3). Statistical
391 comparison—using Bayes factors (BF; Kass and Raftery 1995)—showed negligible evidence for
392 differences in trait values between these two species categories (SLA [BF = 0.2725], plant height
393 [BF = 0.2725], rooting depth [BF = 0.6065], and seed mass [BF = 0.2231]) (Fig. S4). Despite the
394 similarity among natives and nonnatives, overall trait values varied considerably among all
395 species at Cedar Creek (Fig. S4). In addition, while imputation of missing species in
396 phylogenetic trees has been considered an important source of phylogenetic uncertainty in
397 comparative studies, our results show that species imputation contributed little of the total
398 variation in phylogenetic structure of focal-nonnative species (awMPD = 4.95%, wMPNTD =
399 10.10%). Most of the variation instead was attributable to evolutionary and ecological patterns of
400 interest, i.e., phylogenetic and functional correlations among co-occurring species.

401

402 *Patterns of taxonomic, phylogenetic, and functional structure of focal-nonnatives*

403 Species co-occurrence of focal nonnatives—measured as the tendency of focal species to occur
404 in species-rich or species-poor communities—varied considerably among the 26 focal species
405 (Fig. S5A-D). We found evidence for differences in species co-occurrence (abundance and
406 richness) of focal nonnatives for dicots (Fig. S5 A and C; BF = 323.7592 and BF = 3498.187 for
407 abundance and richness, respectively) but not for monocots (Fig. S5 B and D; BF = 0.3396 and
408 BF = 0.4819 for abundance and richness, respectively). Co-occurrence patterns based on C-
409 Scores also indicated high variability among focal species, although no statistical evidence was
410 found for differences in species-pairs associations between dicots and monocots (Fig. S5E-F; BF
411 = 0.2441 for dicots and BF = 0.1827 for monocots). Despite the lack of evidence for differences

412 between species pairs, positive and negative interactions were observed between nonnatives and
413 native species in recipient communities (Fig. S5E-F). For example, *Poa pratensis* (Kentucky
414 bluegrass) that occurs in species rich and abundant communities (Fig. S5B-D), also tended to co-
415 occur with species that interact positively with it (i.e., negative SES C-Score; Fig. S5-F).

416 In general, co-occurrence patterns for focal nonnative species varied strongly across both
417 phylogenetic and functional dimensions (Fig. 2). All possible patterns were observed, e.g.,
418 greater co-occurrence with closely related but functionally distinct species (e.g., *Pyrus malus*
419 [Fig. 2A and 2E] with *Digitaria sanguinalis* [Fig. 2B and 2F]), distantly related but functionally
420 similar species (e.g., *Glechoma hederacea* [Fig. 2A and 2E] with *Setaria viridis* [Fig. 2B and
421 2F]), closely related and functionally similar species (e.g., *Linaria vulgaris* [Fig. 2A and 2E]
422 with *Phleum pratense* [Fig. 2B and 2F]), and distantly related and functionally distinct species
423 (e.g., *Plantago major* [Fig. 2A and 2E]). Despite this high degree of variation, there was no
424 evidence for differences in co-occurrence patterns among dicots and among monocots (Fig. 2),
425 whether for phylogenetic (BFs = 1.073 for dicots and 2.034 for monocots) or functional metrics
426 (BFs = 0.270 for dicots and 2.034 for monocots).

427 At the landscape scale, phylogenetic and functional metrics did not significantly differ
428 from expectations under null models (Fig. 2), suggesting stochastic patterns of co-occurrence of
429 nonnative species in recipient communities. However, at local scales we did detect significant
430 deviations from null expectations (Fig. S6 and S7). For instance, the most common monocot and
431 dicot species (*Poa pratensis* [Kentucky bluegrass] and *Polygonum convolvulus* [Black
432 bindweed]) showed significant deviations from null expectations for phylogenetic clustering in
433 31% and 17% of all plots, respectively; and no significant deviations were found for
434 phylogenetic overdispersion (Fig. S6). Additionally, in these same recipient communities, both

435 Kentucky bluegrass and Black bindweed tended to co-occur more with functionally distinct
436 species (overdispersion of traits, Fig. S7). Local-scale patterns showed shifts from overdispersion
437 to clustering, and vice versa, across fire gradients and time periods for both phylogenetic and
438 functional measures, indicating that co-occurrence patterns were dynamic over space and time
439 across multiple axes of diversity (Fig. S6 and S7).

440

441 *Effects of fire regimes and time on co-occurrence patterns of focal nonnatives*

442 For all three dimensions of diversity, the individual and combined effects of fire frequency and
443 time were non-linear (Figs. 3 and 4). Focal nonnatives tended to co-occur more in species
444 abundant (left panels in Fig. 3) and rich communities (middle panels in Fig. 3) with increasing
445 fire frequency, although co-occurrence peaked at intermediate fire frequencies for some, e.g.,
446 abundance response for nonnative dicots (Fig. 3D). Co-occurrence under species-pairs
447 associations (C-Score) showed complex, nonlinear patterns across fire experiments (right panels
448 in Fig. 3), with positive associations found in the unburned and frequently burned treatments,
449 and negative associations under intermediate fire frequencies. Notably, both dicot and monocot
450 nonnatives responded similarly to fire gradients (Fig. 3, panels D to I).

451 Bayesian MLMs revealed a complex nonlinear response of focal nonnatives' co-
452 occurrence patterns to fire frequency (Fig. 4). These results were consistent regardless of
453 phylogenetic scale—all species vs. dicots and monocots analyzed separately—and metric
454 (awMPD/MFD, awMPNTD/MFNTD). Overall, there were changes from overdispersion to
455 clustering in functional traits, with nonnative species tending to co-occur more with functionally
456 similar species under increasing fire frequency (right-hand panels in Fig. 4). Furthermore, for the
457 phylogenetic dimension, Bayesian MLM provided evidence for nonlinear changes in the

458 phylogenetic structure of focal nonnatives in native communities with increasing fire frequency
459 (left-hand panels in Fig. 4). Phylogenetic clustering was highest in communities subjected to low
460 fire frequency, and phylogenetic overdispersion was greatest under intermediate and high-fire
461 regimes, albeit with a return to phylogenetic clustering at medium-high fire regimes. Note that
462 based on MPNTD, phylogenetic overdispersion was greatest under intermediate and high fire
463 regimes (Fig. 4B).

464 Increased clustering of traits with increasing fire frequency was robust through time (Fig.
465 5 bottom panels). The phylogenetic dimension also revealed a complex temporal pattern (Fig 5.
466 top panels). Although focal nonnatives tended to co-occur more with closely related species in
467 unburned plots and with distantly related species in frequently burned plots, there were
468 interannual changes in phylogenetic structure of nonnative species (Fig. 5). For example, there
469 was a change from clustering to overdispersion in unburned plots in 2000 (Fig. 5 top-left panel),
470 which may indicate that external factors (e.g., interannual climate variability) influenced co-
471 occurrence patterns of focal nonnative species.

472

473 *Phylogenetic signal in functional traits*

474 Phylogenetic signal exhibited intermediate to high λ values (Fig. 6; though λ was weak for
475 SLA), suggesting that trait values of co-occurring species in permanent plots at Cedar Creek
476 resemble each other, although not at similar levels of phylogenetic covariance as would expected
477 under a Brownian motion model of evolution ($\lambda = 1$; Fig. 6). These results were consistent across
478 all 100 phylogenetic trees, i.e., regardless of phylogenetic uncertainty introduced by missing
479 terminal branches.

480

481 **Discussion**

482 The temporal dynamics of co-occurrence patterns of nonnative species in recipient oak savanna
483 communities across a long-term experimental fire gradient revealed that neither of Darwin's
484 competing hypotheses fully explain species invasiveness in plant community assembly. We
485 found that co-occurrence of the 26 nonnative species within invaded communities (Fig. S1) did
486 not follow a general tendency of clustering (which would support the pre-adaptation hypothesis)
487 or overdispersion (which would support Darwin's naturalization hypothesis) (Fig. 2). Instead, we
488 found that community assembly was influenced by species differences in evolutionary history
489 (i.e., shared ancestry) and by ecological differences associated with functional traits that
490 ultimately regulate the colonization and persistence of nonnatives within invaded communities
491 (Box 1: Fig. 1C).

492 Applying our focal-species approach to three different dimensions of vascular plants
493 diversity (i.e., taxonomic, phylogenetic and functional) in communities sampled over decades
494 across an experimental fire gradient, we found that nonnatives tend to be phylogenetically
495 distantly related to the recipient communities in the unburned treatment and in the high fire
496 frequency treatment. In other words, nonnatives are closely related to native species in recipient
497 communities—except in the extreme ends of the fire gradient, where they are more distantly
498 related than expected—which might suggest a filtering process at intermediate fire frequencies
499 favoring the co-occurrence of phylogenetically close relatives. This pattern is consistent between
500 monocots and dicots and contrast with functional similarity. Indeed, nonnatives are functionally
501 dissimilar in the unburned treatment, consistent with biotic interactions that limit ecologically
502 similar species from co-occurring. As fire frequency increases, nonnative species become
503 increasingly similar in function to the recipient native species, indicating that similar functions

504 are required for the persistence of nonnative species in recipient communities subjected to strong
505 environmental filtering caused by the fire regimes. Importantly, these patterns are similar within
506 both monocots and dicots; hence not simply function of tree versus grass dynamics. Moreover,
507 when co-occurrence of nonnatives to recipient natives was evaluated through time, new insights
508 regarding the assembly processes emerge. We found a consistent pattern through time for the
509 functional dimension, with nonnatives co-occurring with functionally dissimilar and similar
510 natives in the unburned and the highest fire regimen treatments, respectively. The phylogenetic
511 dimension, on the other hand, showed shifts in nonnative co-occurrence patterns that suggest
512 additional external forces influencing the phylogenetic relatedness of nonnatives with their
513 recipient native species. Altogether, our findings provide insights for understanding the invasion
514 dynamics of native communities across environmental gradients and at multiple temporal and
515 spatial scales in a highly diverse region of North America.

516 The degree to which (and the mechanisms at work by which) nonnative species
517 successfully invade new communities has remained controversial (Prins and Gordon 2014),
518 particularly because a variety of assembly processes are involved in the effective establishment
519 of introduced species outside their native ranges (Gallien and Carboni 2017, Cadotte et al. 2018,
520 Redding et al. 2019). This has generated growing interest in the role of evolutionary and
521 ecological differences among taxa in predicting nonnative species invasiveness (Carboni et al.
522 2013, Gallien and Carboni 2017, Cadotte et al. 2018). Studies have reported contrasting results in
523 terms of phylogenetic relatedness of nonnative species to recipient assemblages (Carboni et al.
524 2013, Li et al. 2015, Marx et al. 2016), with mixed support for both hypotheses comprising
525 Darwin's naturalization conundrum, i.e., Darwin's naturalization hypothesis and pre-adaptation
526 hypothesis (Kusumoto et al. 2019). Our results showed differential patterns of relatedness of

527 focal nonnative species to recipient native communities, with some nonnatives co-occurring
528 more with closely related natives, and others with distantly related natives (Fig. 2 upper panel).
529 These results suggest that different assembly processes—e.g., biotic interactions, environmental
530 filtering—have simultaneous effects on focal nonnative co-occurrence patterns (Boulangeat et al.
531 2012, Gallien and Carboni 2017, Kusumoto et al. 2019; see also Box 1: Fig. 1C). Integrating
532 multiple dimensions of diversity (i.e., taxonomic, phylogenetic, and functional) in the study of
533 invasions can offer new insights about assembly processes driving nonnative species co-
534 occurrence patterns (Gallien and Carboni 2017, Cadotte et al. 2018).

535 Evaluating the taxonomic dimension, we found that both positive and negative
536 interactions appear to be important in the co-occurrence of nonnative species with native species
537 in invaded communities (Fig. S5E-F). Functional patterns differed from those observed for the
538 phylogenetic dimension (Fig. 2 lower panel). This may indicate that functional traits are
539 modulating co-occurrence patterns between nonnative and native species (Marx et al. 2016,
540 Carboni et al. 2018), by controlling or regulating the species response to different assembly
541 processes (Cavender-Bares et al. 2004, Swenson and Enquist 2009, Pinto-Ledezma et al. 2018).
542 For example, similarity in ecologically relevant traits of closely related species should result in
543 patterns of phylogenetic clustering under similar environmental conditions, while similarity in
544 distantly related species would be associated with a pattern of phylogenetic overdispersion
545 (Cavender-Bares et al. 2004, 2009). In other words, evolutionary conservatism and convergence
546 of functional traits help to explain why nonnative species tend to co-occur with closely related
547 natives (as suggested in PAH) and distantly related natives (as indicated by DNH), respectively
548 (Box 1: Fig. 1C) because functional traits in co-occurring species at Cedar Creek resemble each
549 other. In other words, nonnative species have similar trait values to those of native species (Fig.

550 6) a pattern that is expected to emerge over time due to environmental sorting and not by random
551 introductions of species in the study region.

552 Species composition and structure within communities is dynamic in space and time,
553 varying from short timeframes at small scales (e.g., Fig. S1) to millions of years across
554 biogeographical regions (Chesson 2000, Williams et al. 2004, Cavender-Bares and Reich 2012,
555 Pinto-Ledezma et al. 2018). Thus, a better understanding of invasion dynamics and their
556 relationship to DNC requires evaluation across multiple temporal scales. Indeed, recent evidence
557 indicates that a single snapshot in time could mislead interpretations on both sides of Darwin’s
558 conundrum (Li et al. 2015, Cadotte et al. 2018) or prevent observation of the full range of
559 impacts of nonnative species on invaded communities (Gilbert and Levine 2013). Our results
560 support these time-scale dependent findings, as we found shifts over time in the phylogenetic and
561 functional co-occurrence structure of focal nonnatives across the fire frequency gradient (Fig. S6
562 and S7). For example, considering a single time period, *Poa pratensis* (Kentucky bluegrass)—
563 the most common and abundant nonnative species in our study region (Fig. S1)—tended to co-
564 occur more with closely related species, supporting the PAH (Fig. 2B); however, in plots
565 protected from fire, phylogenetic clustering from 1984 to 2005 gave way to phylogenetic
566 overdispersion in 2010 and 2015 (Fig. S6). Thus, depending on the time periods considered, the
567 co-occurrence patterns of *Poa pratensis* could support PAH or DNH. These findings highlight
568 the importance of multi-temporal evaluations in the study of biological invasions, given that co-
569 occurrence patterns are an emergent characteristic of dynamic population changes across many
570 species (Chesson 2000, Cavender-Bares and Reich 2012, Li et al. 2015). Indeed, an observed
571 species may be only fleetingly present in a community, because it recently colonized it (Gilbert
572 and Levine 2013, Germain et al. 2018).

573 Environmental conditions and disturbances constrain patterns of species diversity within
574 communities by acting as filters that alter species co-occurrence patterns (Connell 1978, Peterson
575 and Reich 2008, Pinto-Ledezma et al. 2018). Disturbances such as fire can generate stressful
576 environmental conditions in which only a subset of tolerant species will recruit and persist,
577 thereby diminishing the strength of density-dependency interactions (Peterson and Reich 2008,
578 HilleRisLambers et al. 2012, Coyle et al. 2014). These factors also influence the degree to which
579 nonnative species co-occur with natives in invaded communities (Thuiller et al. 2010, Cadotte et
580 al. 2018). Our results show that fire frequency generated idiosyncratic effects on co-occurrence
581 patterns in invaded communities (Fig. 4), indicating the simultaneous and interacting effect of
582 assembly processes across environmental gradients—i.e., as environmental conditions change,
583 density-dependent interactions promote the coexistence of some species while excluding others
584 (Germain et al. 2018). In fact, we found that functional similarity of focal nonnatives to natives
585 increased with increasing fire frequency, which might suggest a strong influence of
586 environmental filtering (right panels in Fig. 4). However, phylogenetic distance exhibited a
587 complex nonlinear trend (left panels in Fig. 4), matching our third prediction (Fig. 1C).
588 Specifically, phylogenetic clustering of nonnatives to natives was maximized under low fire
589 frequency. Shifts to phylogenetic overdispersion appeared under medium-high fire frequency,
590 possibly as a consequence of competitive interactions (Fig. 4). In other words, both
591 environmental filtering and biotic interactions are acting in concert in shaping co-occurrence
592 patterns of nonnative species across environmental gradients. This is consistent with prior
593 experimental studies (e.g., Germain et al. 2018) highlighting the importance of simultaneous
594 effects of environmental filtering and competitive interactions on community assembly (Chesson
595 2000, Ackerly 2003, Germain et al. 2018).

596

597 *Perspectives*

598 Extending the diversity fields' framework to focal-species under combined phylogenetic and
599 functional perspective (Box 1) offers an innovative way to evaluate patterns of species-level co-
600 occurrence at local scales, enhancing our understanding of the mechanisms driving the assembly
601 of natural communities. For example, by combining different dimensions of vascular plant
602 diversity under the focal-species framework, we were able to detect shifts in the phylogenetic
603 relatedness and functional similarity of focal nonnatives with respect to recipient communities
604 across environmental gradients and time periods. This is particularly important given that
605 individual species—including nonnative species—respond differently to changes in the
606 environmental conditions of local communities (Tilman 2004, Ackerly and Cornwell 2007, Li et
607 al. 2015, Redding et al. 2019). Further analyses addressing different taxa, biogeographical
608 regions, or environmental conditions could reveal more insights about the mechanisms driving
609 co-occurrence of nonnative species in recipient communities, or elucidate the role of other axes
610 of variation shaping species co-occurrence patterns. Finally, the integration of multiple
611 dimensions of biodiversity within the “focal species” framework can enhance our ability to
612 produce reliable information of species co-occurrence at different spatial and temporal scales,
613 facilitating our ability to monitor changes in both individual species and whole communities, and
614 thus helping to guide conservation efforts.

615

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622

623 **Statement of authorship**

624 JC-B, JNP-L and DJL conceived the ideas presented and tested herein. JNP-L managed the
625 project. JNP-L performed the analyses, and wrote the first draft. FV and PBR contributed to the
626 ideas and interpretation of data, and all authors contributed throughout the whole writing
627 process. PBR has co-led the implementation and management of the long-term fire frequency
628 experiment and associated community censusing and data curation.

629

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923

924 **BOX 1**

925 Species co-occurrence patterns in local communities are a consequence of ecological processes
926 (species interactions with other organisms and the environment) and historical processes
927 (biogeographic history, long-term dispersal, past diversification) that operate over short and long
928 time scales, respectively (Cavender-Bares et al. 2016, 2018, Pinto-Ledezma et al. 2019).
929 Different metrics have been used to measure the degree of relatedness/similarity (see Miller et al.
930 2017, Scheiner et al. 2017) of species co-occurring within local communities to infer assembly
931 processes from community phylogenetic/functional structure (Cavender-bares et al. 2006,
932 Mayfield and Levine 2010). These metrics are calculated using a community data matrix
933 (CDM)—in which rows are communities and columns are species—in combination with a
934 distance matrix, either phylogenetic or functional. Generally, CDMs are analyzed by rows (*Q*-
935 mode in Arita et al. 2008, see also Villalobos and Arita 2010), summarizing information at the
936 community level; however, CDMs can also be analyzed by columns (*R*-mode in Arita et al.
937 2008, Villalobos and Arita 2010), summarizing information at the species level. In addition, by
938 intersecting rows and columns (*Qr*-mode and *Rq*-mode in Arita et al. 2008), it is possible to
939 obtain new information, e.g., the ‘diversity field’ of a given species (Arita et al. 2008), which
940 represents the species richness of communities within the distribution of a species. This can be
941 interpreted as the tendency of a given species to occur in species-rich or species-poor
942 communities, i.e., to coexist with many or with few species (Villalobos and Arita 2010).

943 Building on this framework, Villalobos et al. (2013, 2017) extended the concept of
944 diversity fields—the set of diversity values of sites within the geographical range of a given
945 species (Arita et al. 2008)—to ‘phylogenetic fields’ (Villalobos et al. 2013) and ‘functional
946 fields’ (Villalobos et al. 2017, see also Miller et al. 2017) that describe the overall

947 phylogenetic/functional structure of species co-occurring with a given species geographical
948 range. These fields are interpreted as the tendency of a focal species to co-occur either with
949 closely related/functionally similar or distantly related/functionally dissimilar species (Villalobos
950 et al. 2013, 2017). Similarly, phylogenetic/functional fields can be used as metrics of species-
951 level coexistence. All three of these approaches—diversity, phylogenetic, and functional fields—
952 are usually applied at macroecological scales (Arita et al. 2008, 2010, Villalobos and Arita 2010,
953 Villalobos et al. 2013, 2016, 2017) with some local-scale exceptions (e.g., Elliot et al. 2016,
954 Miller et al. 2017a, Kusumoto et al. 2019). Given that the observational units in our study are
955 species within local communities, we downscale the concept of fields applied at large
956 geographical scales to co-occurring species within local communities (Box1: Fig. 1A-B). This
957 extension enables evaluation of co-occurrence patterns and inferences regarding assembly
958 processes to be applied at the level of individual species rather than entire communities. In doing
959 so, we obtain separate estimates for each species occurring in a local community rather than a
960 single mean across all species co-occurring in a community (Box 1: Fig. 1A-B).

961

962

963

964 **FIGURES**

965 **Box 1: Fig. 1.** Conceptual framework for the estimation phylogenetic/functional structure of
966 focal-species contrasted with the traditional estimation of phylogenetic/functional structure at the
967 community level. Here we show the difference between estimates for standard mean pairwise
968 phylogenetic distance (MPD) between species occurring within a community (a single,
969 community-level value) and MPD_{focal} (multiple, species-level values). Again, while traditional
970 MPD is calculated based on the mean distance among all possible pairs of species within a
971 community, MPD_{focal} is based on the mean distance of a focal species relative to the co-occurring
972 species in a local community (e.g., nonnative species in A and B). Under this simple framework,
973 it is possible to evaluate both the phylogenetic relatedness and functional similarity of nonnative
974 species in native communities and consequently conduct a more comprehensive analysis of both
975 sides of Darwin's naturalization conundrum (C). (A) Darwin's naturalization hypothesis
976 (DNH)—that nonnative species closely related to native species are less likely to successfully
977 invade native communities because they share similar and already occupied niches (continuous
978 boxes in panel C). (B) Pre-adaptation hypothesis (PAH)—that nonnative species closely related
979 to native species should be favored because they share similar traits with native species, making
980 them well-suited (“preadapted”) to the novel range, and permitting them to colonize and further
981 adapt (dashed boxes in panel C). Panel C adapted from Cavender-Bares et al. (2004)

982

983 **Fig. 1.** Hypotheses and predictions for co-occurrence patterns of focal-nonnative species with
984 plants in their surrounding communities across environmental gradients at Cedar Creek. The
985 curves depict theoretical expectations of changes in phylogenetic/functional structure across fire
986 and light-availability gradients, explained in the main text.

987

988 **Fig. 2.** Patterns of phylogenetic relatedness and functional similarity of focal species relative to
989 the plants in their surrounding communities for 26 nonnative species within the oak savanna
990 understory permanent plots at the Cedar Creek Ecosystem Science Reserve, USA. Values
991 correspond to abundance-weighted metrics averaged across all permanent plots (landscape scale)
992 for both phylogenetic (top panel) and functional dimensions (bottom panel).

993

994 **Fig. 3.** Marginal effect plots of changes in the taxonomic dimension across the fire gradient.
995 Continuous blue lines represent the fitted slopes (with 95% confidence intervals in gray) that
996 smooth over the fire frequency gradient from the Bayesian MLMs. Left-hand and middle
997 columns show the variation of species co-occurrence of focal nonnatives for abundance and
998 richness metrics, respectively and estimated as the tendency of focal nonnatives to occur in
999 species-rich or species-poor communities. Right-hand column show the variation of focal species
1000 co-occurrence using the C-Score metric. Note that at the both extreme ends (i.e., unburned and
1001 fire 4 treatments) of the fire frequency gradient, nonnatives tend to co-occur with native species
1002 under positive interactions. Also, Bayesian MLMs show similar patterns for dicots and
1003 monocots, confirming that nonnative plant species respond in a similar way to fire regimes and
1004 not as a simple function of trees versus grass species.

1005

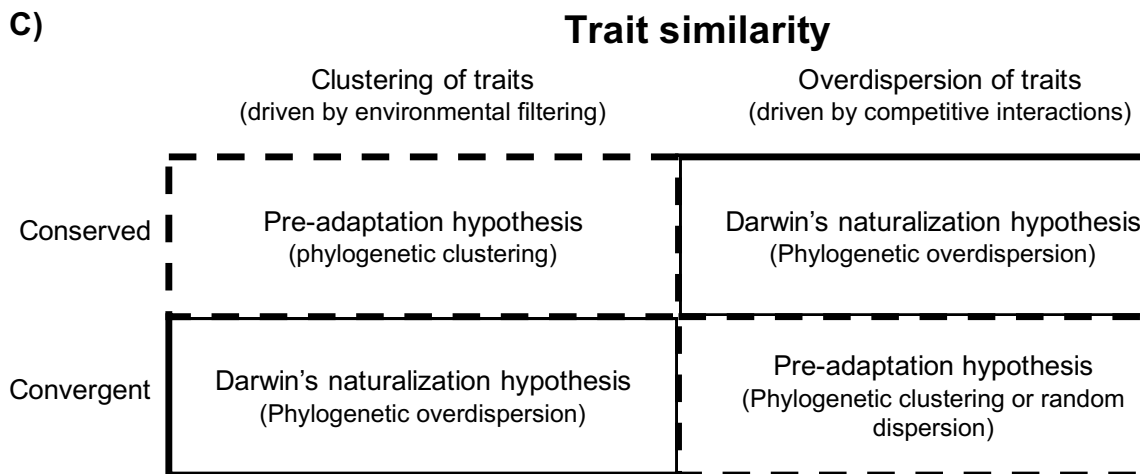
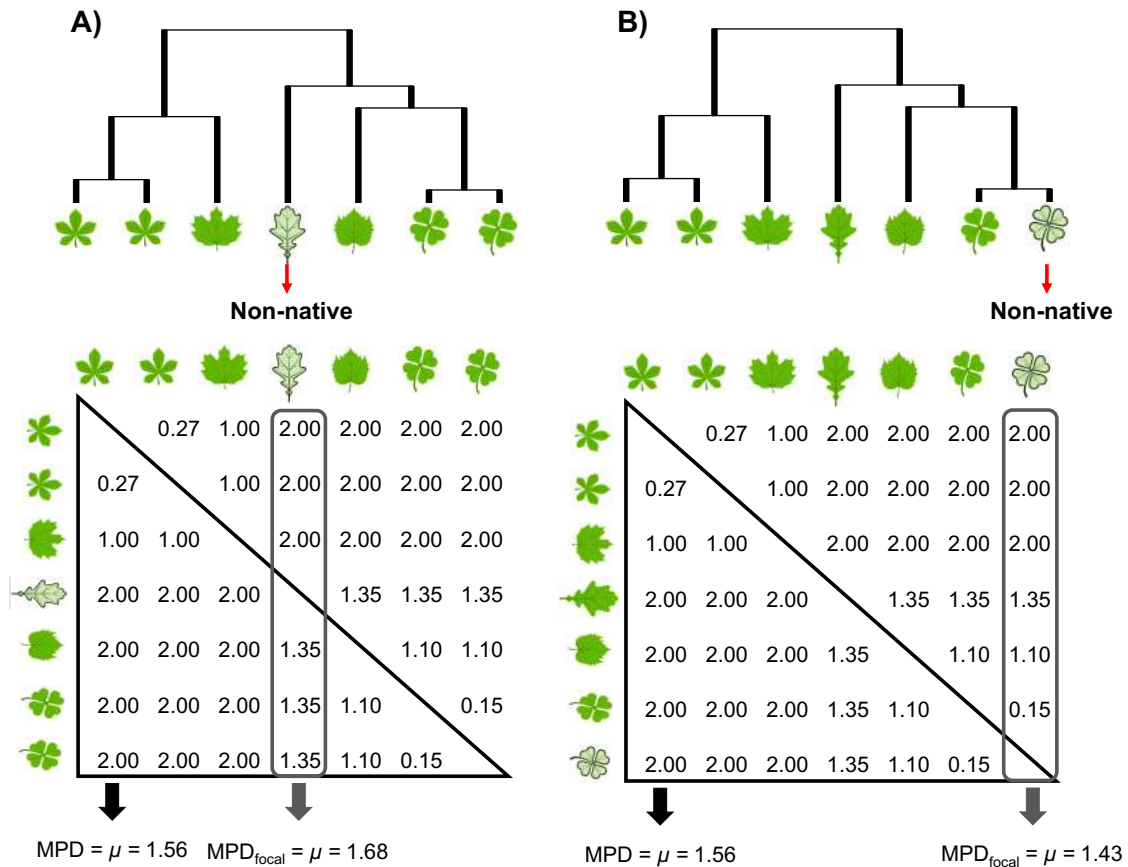
1006 **Fig. 4.** Marginal effect plots of changes in phylogenetic structure and functional structure of
1007 focal nonnative species in recipient communities across the fire frequency gradient. Continuous
1008 blue lines represent the fitted slopes (with 95% confidence intervals in gray) that smooth over the
1009 fire frequency gradient from the Bayesian MLMs. Left-hand columns (A, B, E, F, I and J) show

1010 the variation in focal nonnative species co-occurrence in recipient communities for the
1011 phylogenetic dimension and the right-hand columns (C, D, G, H, K and L) for the functional
1012 dimension. Y-axis for all panels represent fitted abundance-weighted metrics values (MPD/MFD
1013 and MPNTD/MFNTD) across the fire frequency gradient. See calculation diversity metrics in the
1014 method section for details of metric calculations.

1015
1016 **Fig. 5.** Fitted metric values from Bayesian multi-level models over time for the two extreme ends
1017 of the fire frequency gradient, i.e., unburned and fire 4 treatments. Upper and lower panels
1018 correspond to phylogenetic and functional dimensions, respectively.

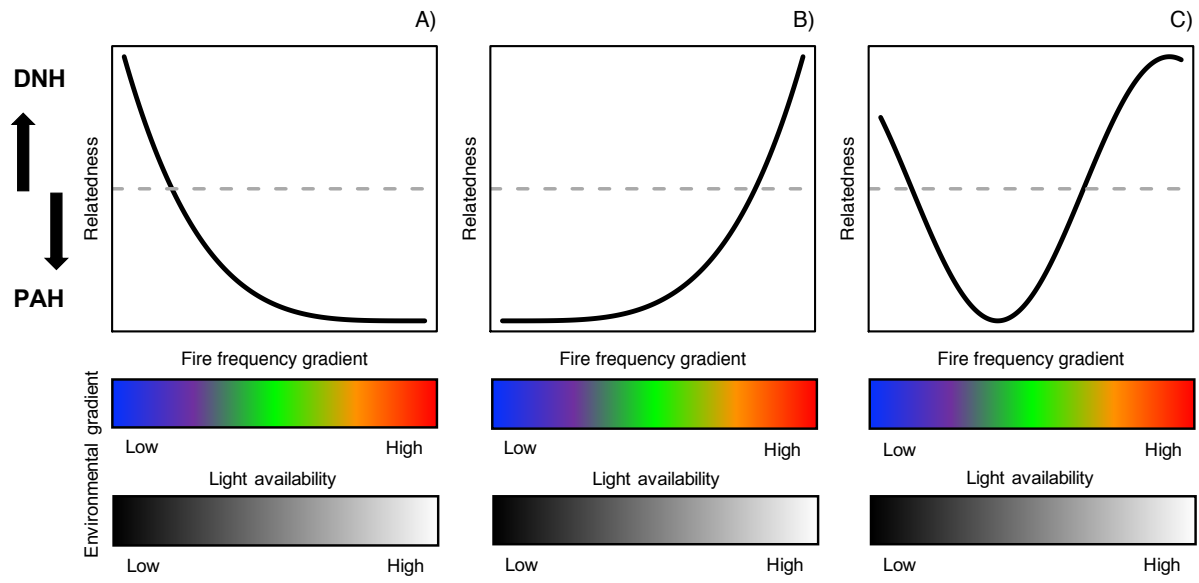
1019
1020 **Fig. 6.** Bayesian phylogenetic signal estimated using Pagel's λ and a sample of 100 phylogenetic
1021 trees. Posterior probability distributions of (A) specific leaf area, (B) plant height, (C) rooting
1022 depth, and (D) seed mass. Posterior distribution (and 95% confidence interval, vertical gray
1023 dotted lines) show λ values from 10 million generations sampled every 1000 generations.
1024 Vertical dashed gray line represent the mean λ value estimated under a maximum likelihood
1025 approach over a sample of 100 trees.

1026
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1033

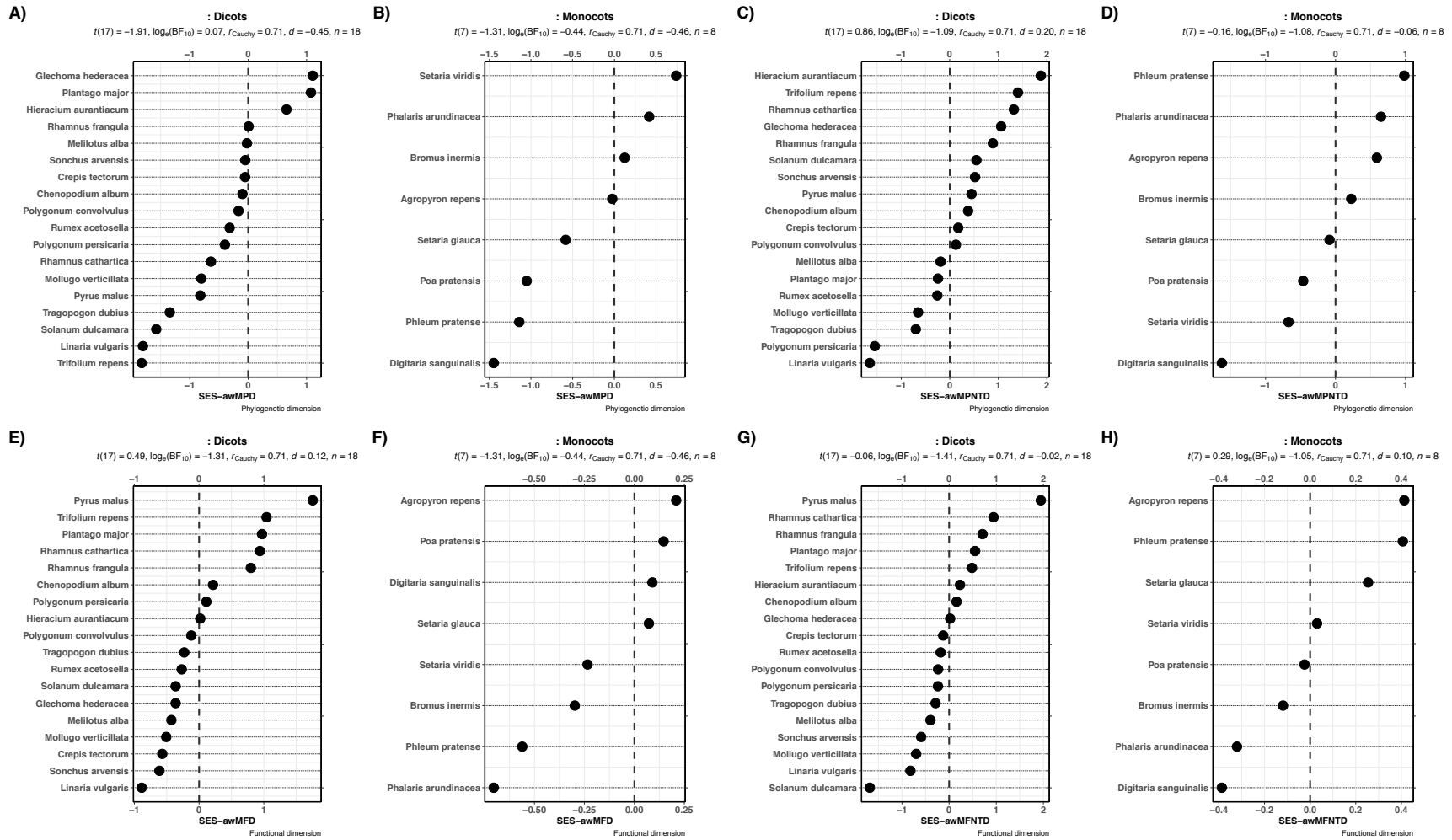
1034 **Fig. 1**



1035

1036

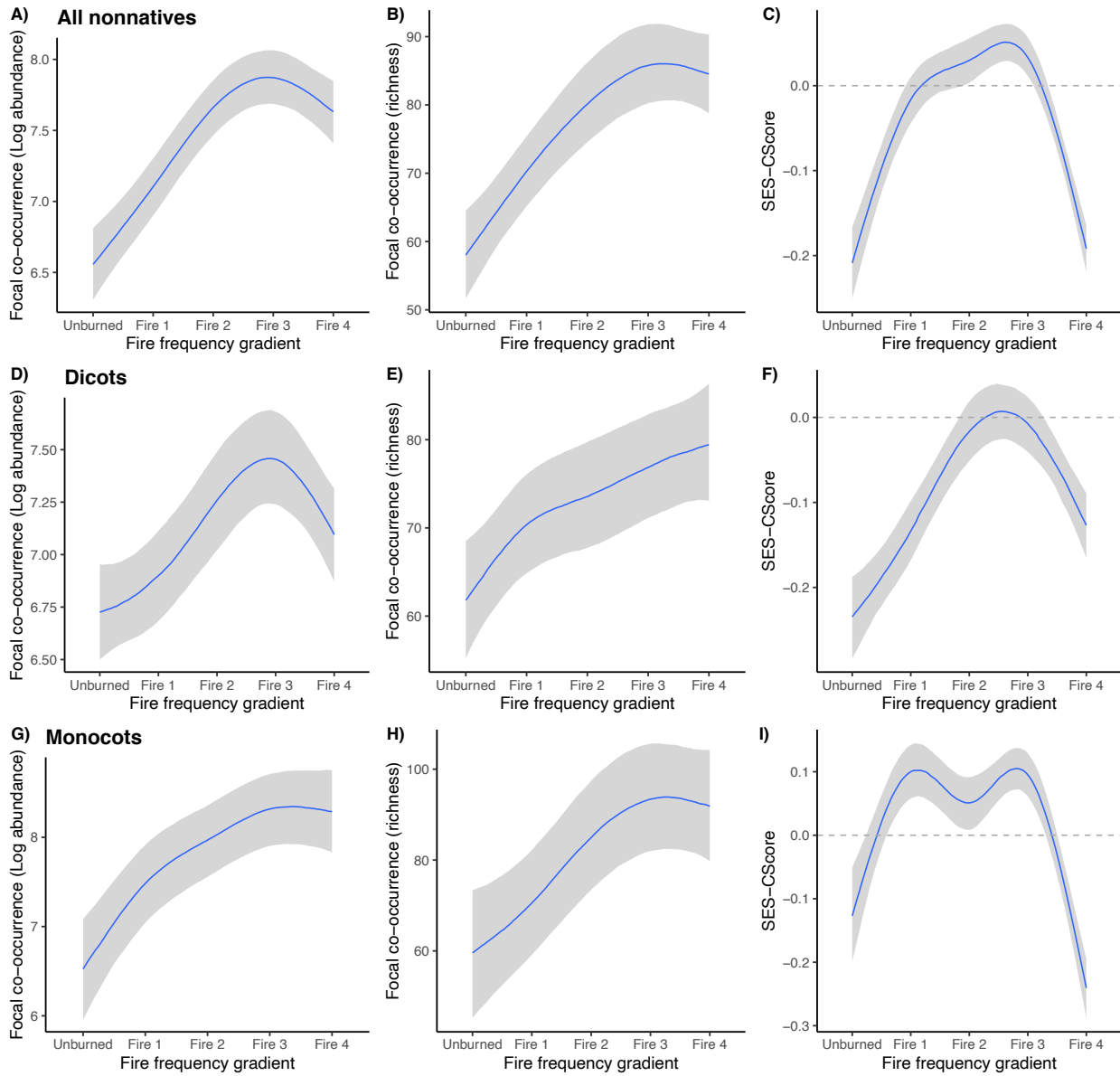
1037



1041

1042 **Fig. 3**

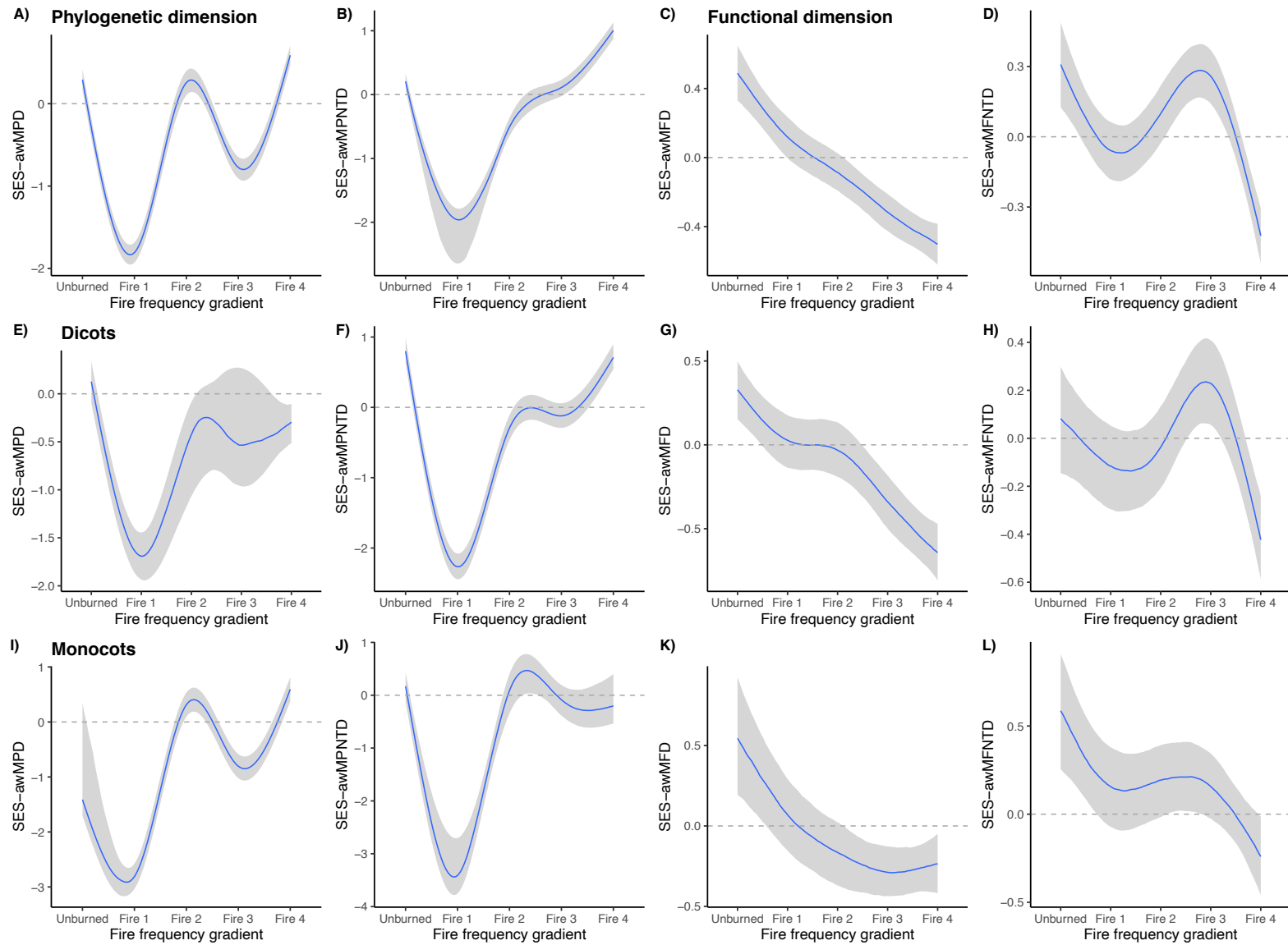
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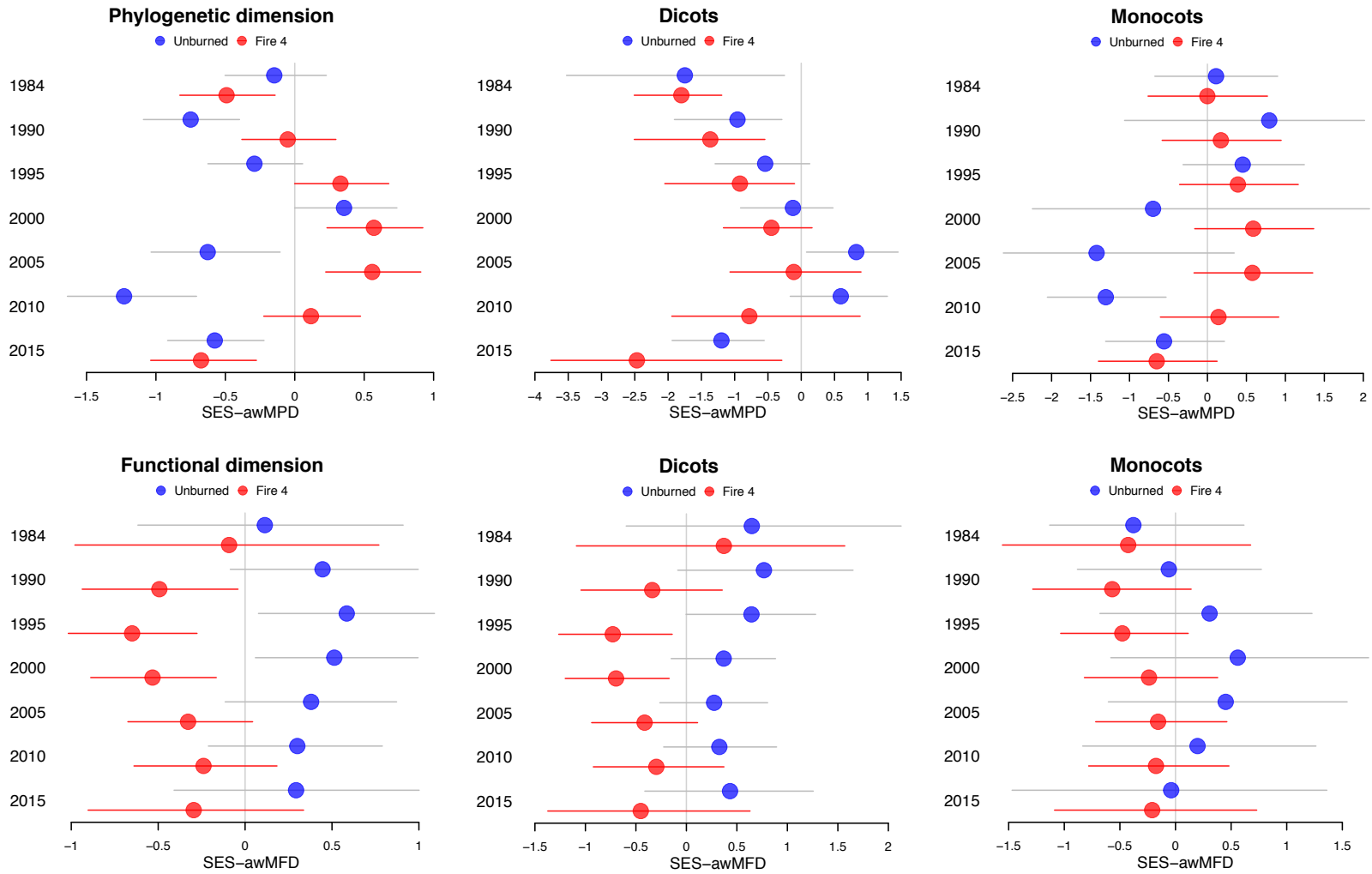
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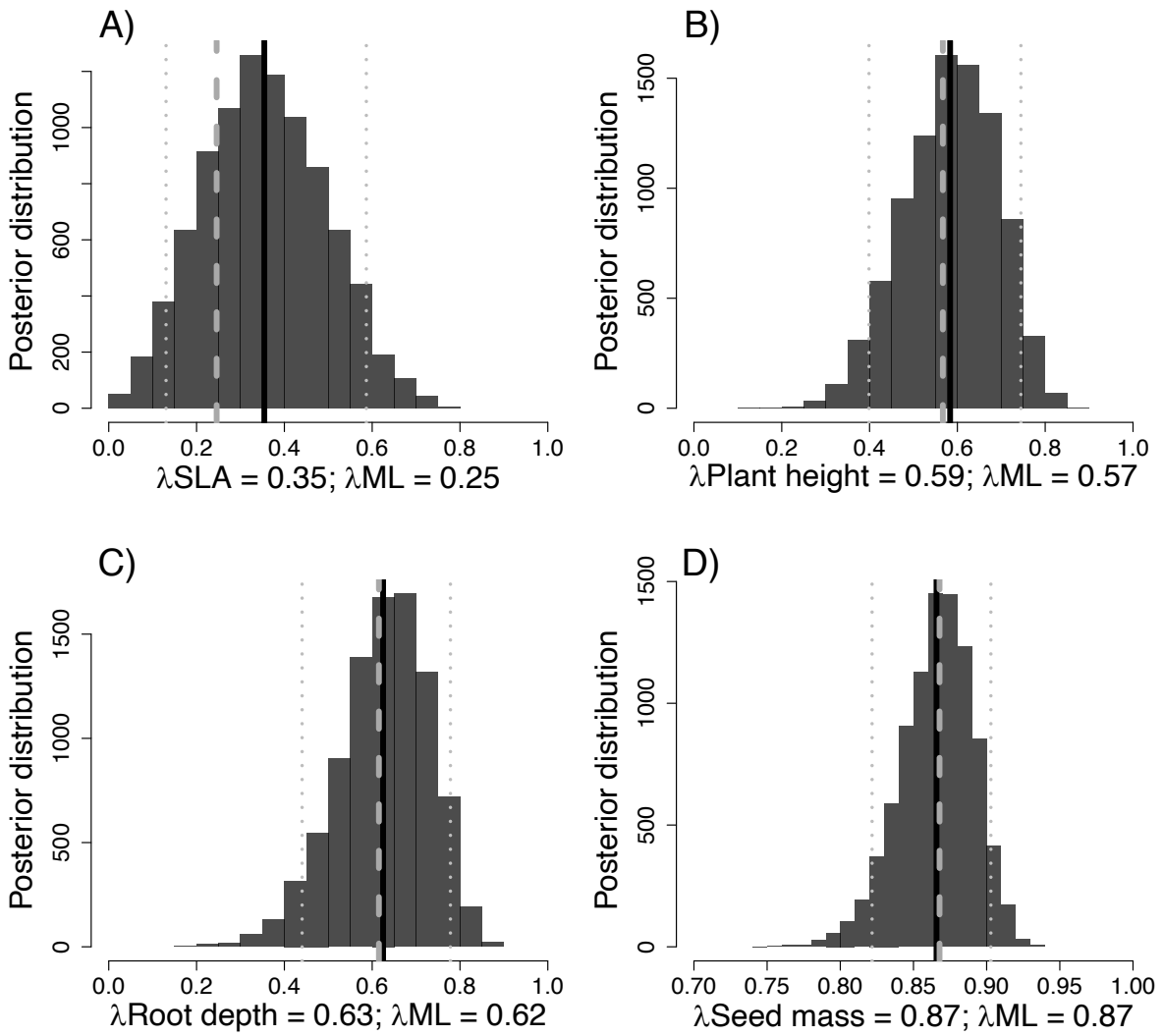


1049 **Fig. 5**



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1054 *Note:* We did not evaluate the phylogenetic signal of functional trait combinations (i.e., LHS and
 1055 LHS + root depth) given the expectation that traits evolve independently of one another.

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