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3 **Dominance-diversity relationships in ant communities differ with invasion**

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5 Running head: global dominance-diversity relationships

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99 ABSTRACT

100 The relationship between levels of dominance and species richness is highly
101 contentious, especially in ant communities. The dominance-impoverishment rule states
102 that high levels of dominance only occur in species-poor communities, but there appear
103 to be many cases of high levels of dominance in highly diverse communities. The extent
104 to which dominant species limit local richness through competitive exclusion remains
105 unclear, but such exclusion appears more apparent for non-native rather than native
106 dominant species. Here we perform the first global analysis of the relationship between
107 behavioral dominance and species richness. We used data from 1293 local assemblages
108 of ground-dwelling ants distributed across five continents to document the generality of
109 the dominance-impoverishment rule, and to identify the biotic and abiotic conditions
110 under which it does and does not apply. We found that the behavioral dominance –
111 diversity relationship varies greatly, and depends on whether dominant species are
112 native or non-native, whether dominance is considered as occurrence or relative
113 abundance, and on variation in mean annual temperature. There were declines in
114 diversity with increasing dominance in invaded communities, but diversity increased
115 with increasing dominance in native communities. These patterns occur along the global
116 temperature gradient. However, positive and negative relationships are strongest in the
117 hottest sites. We also found that climate regulates the degree of behavioral dominance,
118 but differently from how it shapes species richness. Our findings imply that, despite
119 strong competitive interactions among ants, competitive exclusion is not a major driver
120 of local richness in native ant communities. Although the dominance-impoverishment
121 rule applies to invaded communities, we propose an alternative dominance-
122 diversification rule for native communities.

123

124 **Keywords:** ants, behavioral dominance, coexistence, dominance-impoverishment rule,

125 global scale, invasive species, precipitation, species richness, temperature

126

127 INTRODUCTION

128 Understanding the factors that drive variation in local species richness at different
129 spatial and temporal scales remains a fundamental challenge to community ecology
130 (Ricklefs, 1987; Chesson, 2000; Kneitel & Chase, 2004). Regional species pools are
131 determined by evolutionary and historical factors, while environmental filtering and
132 dispersal barriers set the limit on the species that might potentially occur in a local
133 community (Cornell & Harrison, 2014). The final realized diversity of communities
134 then depends on local biotic interactions such as competition (Silvertown et al., 2006).
135 The relative importance of competition is thought to vary predictably with
136 environmental stress and disturbance, both of which constrain the capacity of dominant
137 species to achieve levels of resource monopolization that lead to the exclusion of other
138 species (Connell, 1978; Grime, 1979).

139 The stress-disturbance-competition framework was originally developed for
140 communities of plants (Grime, 1979) and other sessile organisms (Connell, 1978), but
141 has also been applied to macro-scale analyses of the dynamics of ant communities
142 (Andersen, 1995; 1997a). Like plants, ants are principally central-place foragers whose
143 foraging modules ramify in the environment to an extent that allows resource
144 monopolization, leading to higher levels of competition than is the case for many other
145 faunal groups (Andersen, 1991). Behavioral dominant species are aggressive species
146 that are capable of exerting a strong influence on other species (Cerdá et al., 2013). The
147 primary factors limiting ant productivity and the abundance of behaviorally dominant
148 species are considered to be temperature (including a requirement of direct solar
149 radiation), a structurally simple foraging environment, and the supply of liquid
150 carbohydrates, particularly honeydew (Andersen 2010; Dunn et al., 2009). These factors

151 combine in two highly contrasting environments, the canopies of lowland tropical
152 rainforest, and on the ground in warm open habitats where honeydew is readily
153 available (Andersen, 2000; 2003; 2010). The abundance of behaviourally dominant
154 species is likewise highest in these environments (Andersen, 1995; 1997a; Davidson et
155 al., 2003; Blüthgen & Fiedler, 2004).

156 Despite competition being regarded as the ‘hallmark of ant ecology’ (Hölldobler &
157 Wilson, 1990), its role as a driver of community assembly and species richness remains
158 somewhat contentious (Cerdá et al., 2013; Stuble et al., 2017). Hölldobler & Wilson
159 (1990) proposed the ‘dominance-impoverishment rule’ to describe a negative
160 relationship between local ant species richness and the abundance of behaviorally
161 dominant species: “the fewer the ant species in a local community, the more likely the
162 community is to be dominated behaviorally by one or a few species with large,
163 aggressive colonies that maintain absolute territories”. This tenet was based on studies
164 across a wide variety of environments, ranging from temperate and boreal forests of
165 Europe (e.g., Vepsäläinen & Pisarski, 1982) to the canopies of tropical Africa and
166 Australia (e.g., Room, 1971; Hölldobler, 1983). Hölldobler & Wilson (1990) argued
167 that the high abundance of behaviorally dominant ants was due to the low diversity of
168 the sites in which they were found, rather than the cause of the low diversity. Both
169 mechanisms, however, are possible. Here we use the term ‘dominance-impoverishment
170 rule’ to describe the pattern generally, regardless of its mechanism.

171 There have been many studies showing that behaviourally dominant ants exclude other
172 species from near their nests (Savolainen et al., 1989; Parr, 2008; Cerdá et al., 2013)
173 and from high-value food resources (Andersen, 1992; Parr et al., 2005). The presence of
174 behaviourally dominant non-native (i.e., invasive) species often reduces local species

175 richness through competitive exclusion (Hoffmann et al., 1999; Holway et al., 2002;
176 Lach & Hooper-Bùi, 2010). However, there is only limited evidence that competitive
177 exclusion by native species can be an important driver of patterns of local species
178 richness (Andersen, 1992; Parr, 2008), and this does not typically appear to be the case
179 (Albrecht & Gotelli, 2001; Gibb & Hochuli, 2004; Baccaro et al., 2012; Stuble et al.,
180 2017) and may be conditional on environmental disturbance (Gibb, 2011). Many
181 examples of high levels of competitive dominance co-occur with high ant diversity,
182 especially in Australia (Andersen, 2008; 2016; Arnan et al., 2011).

183 We perform the first global analysis of the relationship between behavioral dominance
184 and species richness in any faunal group, using data from 1,293 local ant assemblages
185 distributed across five continents. In local communities, competitive exclusion is often
186 expressed as a humped relationship between the abundance of dominant species and
187 local species richness, conforming to general models of the control of local diversity in
188 relation to resource availability (Grime, 1973; Cardinale et al., 2009), productivity
189 (Tilman, 1982) and disturbance (Connell, 1978; MacKey & Currie, 2001). Few species
190 occur under hostile environmental conditions, where the abundance of behaviorally
191 dominant species will likewise be very low. Both species richness and the abundance of
192 dominant species can be expected to increase as environmental favorability improves,
193 forming the ascending side of the humped diversity curve (Andersen, 1992; Parr et al.,
194 2005). For example, local species richness increases with temperature up to a point
195 (Dunn et al., 2009; Jenkins et al., 2011), and this also appears to be the case for the
196 abundance of dominant ants (Andersen, 1995; 1997a). If competitive exclusion occurs,
197 an inflection point will be reached where a continued increase in the abundance of
198 dominant species is associated with declining species richness, creating the descending
199 side of the humped diversity curve (Andersen, 1992; Parr et al., 2005). In such a case,

200 an extremely high abundance of dominant species would be associated with very low
201 species richness, conforming with the dominance-impoverishment rule.

202 However, humped diversity models in relation to environmental stress and disturbance
203 apply to assemblages of species from clearly circumscribed environments (Chase &
204 Leibold, 2002), and such patterns cannot be expected to emerge from broader scale
205 analyses, where local processes are often overwhelmed by regional factors such as
206 variation in climate (Andersen, 1997b). A more robust global test of the relationship
207 between dominant species and species richness is to compare species richness with and
208 without dominant species under matched climates.

209 The objective of our study is to examine the global relationship between behavioral
210 dominance and diversity in ant communities, in the context of testing the generality of
211 the dominance-impoverishment rule and its environmental drivers. Our specific aims
212 are to: (1) compare species richness with and without the occurrence of dominant
213 species; (2) document the global relationship between species richness and the
214 abundance of dominant species; and (3) analyze the interactions between climate, the
215 abundance and identity (native or non-native) of dominant species and ant richness. We
216 predict that whereas high levels of behavioural dominance are associated with low
217 diversity in invaded communities, this is not the case when dominant species are native.
218 We therefore predict that the dominance-impoverishment rule applies to communities
219 dominated by non-native species, but not by native species.

220

221 MATERIALS AND METHODS

222 *Ant assemblage database*

223 We assembled species composition data from 1,293 local ground-dwelling ant
224 communities around the world (Fig. 1). The database includes primary data collected
225 during the authors' own field work and data derived from an exhaustive search of the
226 scientific literature. The data are compiled in the Global Ants Database (GLAD,
227 <http://globalants.org/>), a collaboration among ant ecologists worldwide bringing
228 together data on the abundance and traits of ants in local assemblages worldwide (Dunn
229 et al., 2009; Gibb et al., 2017; Parr et al., 2017). Ant assemblages included in this study
230 met the following criteria: (1) the ground-foraging ant assemblage was sampled using
231 pitfall trapping. We wanted to ensure that sampling was standardized, and pitfall traps
232 were the most commonly used sampling technique in GLAD. If Winkler, Berlese funnel
233 or bait sampling were conducted in addition to pitfall trapping, then such supplementary
234 data were also used; (2) sampling was not trophically or taxonomically limited (for
235 example, the study was not focused only on seed-harvesting ants); (3) study sites had
236 not undergone habitat transformation due to intensive land use, such as cropping or
237 clear-cut forestry (we included moderately disturbed sites, such as those affected by fire
238 or grazing; such disturbance did not affect the presence of invasive ant species in our
239 data set: Generalized linear mixed model, $\chi_1^2=0.96$, $p=0.326$); and (4) we had
240 information on factors such as sampling intensity and habitat type that might confound
241 the behavioral dominance – diversity relationship, and which were included as
242 covariates in statistical models (see below). Assemblage data came from all continents
243 where ants occur: Oceania (41.0% of sites), North America (18.6%), Europe (16.6%),
244 Africa (11.8%), South America (8.2%), and Asia (3.8%). GLAD includes data sets for
245 regions that are not well-represented in our analyses, but unfortunately these did not
246 meet our selection criteria, especially relating to the use of pitfall traps.

247

248 *Defining behavioral dominance and invasive (non-native) species*

249 We focused on the relationship between diversity and behavioral dominance, rather than
250 simply numerical dominance, because this is specified in the dominance-
251 impoverishment rule. At any rate, in those sites where behaviorally dominant species
252 occurred, the abundance of behaviorally dominant species was highly correlated to the
253 abundance of the most abundant species (Spearman $r = 0.96$, $p < 0.0001$, $n = 645$), i.e.
254 behavioral and numerical dominance was highly correlated. We considered a species to
255 be behaviorally dominant based on both aggressive behavior and effects on other
256 species by excluding them from near their nests and from high-value food resources
257 (Vepsäläinen & Pisarski, 1982; Savolainen et al., 1989; Andersen, 1992; Cerdá et al.,
258 2013). Behaviorally dominant species are thus defined as highly aggressive species that
259 usually predominate numerically, occupy large territories, and have mutually exclusive
260 distribution patterns at local scales. Given the large number of studies use, data are not
261 available to demonstrate impact by dominant species in each of our study communities,
262 and so we had to rely on a priori classifications of taxa based on the literature and our
263 combined expert knowledge. The following taxa were thus classified as behaviorally
264 dominant (Appendix S1): *Anonychomyrma*, *Anoplolepis*, *Azteca*, *Dorymyrmex* (except
265 *insana* group), *Formica* (only *exsecta* and *rufa* groups), *Froggattella*, *Iridomyrmex*,
266 *Linepithema*, *Liometopum*, *Oecophylla*, *Papyrius*, *Pheidole* (only *megacephala* and
267 *fallax* groups), *Philidris*, *Solenopsis* (sub-genus *Solenopsis*, i.e. “fire ants”), *Tapinoma*
268 (*nigerrimum* group), and *Wasmannia auropunctata*. There is considerable empirical
269 evidence that species in these taxa are behaviorally dominant and influence the structure
270 and dynamics of local ant communities (e.g., Andersen, 1995; 1997a; Savolainen et al.,

271 1989; Lach & Hooper-Bùi, 2010; Arnan et al., 2011; Cerdá et al., 2013; Bertelsmeier et
272 al., 2015a). Some species from other genera (e.g., *Crematogaster*) might also be good
273 candidates, but the distribution of behavioural dominance among constituent species
274 groups is poorly known, and so they have not been included. Army-ants (subfamily
275 Dorylinae) were also not included. These species are behavioural dominant species, but
276 their effects on other ant species are temporally limited given their nomadic life style.

277 Our pool of behaviorally dominant species included five invasive species occurring in
278 our communities outside their native ranges: the yellow crazy ant (*Anoplolepis*
279 *gracilipes*), the Argentine ant (*Linepithema humile*), the big-headed ant (*Pheidole*
280 *megacephala*), fire ants (*Solenopsis* spp., subgenus *Solenopsis*) and the electric ant
281 (*Wasmannia auropunctata*) (Lach & Hooper-Bùi, 2010; Bertelsmeier et al., 2015a;
282 2015b; 2016). These species are considered the five top invasive ants (Bertelsmeier et
283 al., 2016) and are on the list of the “100 of the world’s worst invasive alien species”
284 (Lowe et al., 2000).

285

286 *Climatic characterization of sites*

287 We selected two climatic variables that are consistently related to variation in ant
288 communities globally (e.g., Dunn et al., 2009; Jenkins et al., 2011; Arnan et al., 2014;
289 Gibb et al., 2015): mean annual temperature (hereafter, temperature) and annual
290 precipitation (hereafter, precipitation). We acknowledge that other aspects of climate
291 such as seasonality can have an important influence on ant communities, but there is no
292 evidence that they are key drivers of ant diversity at a global scale. For each locality,
293 temperature and precipitation information was obtained for the period 1950 - 2000 from
294 the WORLDCLIM database (<http://www.worldclim.org/bioclim>) using rasters with the

295 highest available resolution (30 arc-s, approx. 1 x 1 km). Such a resolution provides
296 climatic data that are directly applicable to the scale of sampling in our study
297 communities (approximately 1 ha).

298

299 *Data analyses*

300 All analyses were performed in R v.3.2.4 statistical environment (R Core Team, 2016).

301 We initially determined that temperature and precipitation were significantly but not
302 highly correlated (Spearman $r = 0.27$, $p < 0.0001$), so both variables were retained for
303 analyses.

304 We considered behavioral dominance at two levels: the (1) occurrence (presence-
305 absence) and (2) abundance of dominant species in a site. Occurrence data were
306 considered for all 1,293 sites, whereas abundance data were considered only for those
307 645 sites where behaviorally dominant species occurred and where abundance data were
308 available, in order to remove the effects of a high proportion of zeros. Abundance of
309 behaviorally dominant species was computed as a proportion of total individuals
310 sampled for all species combined.

311 We used two general linear mixed models (GLMMs) to test how behavioral dominance
312 and climate relate to ant species richness. The first model used occurrence of dominant
313 species (sites with vs sites without dominants), temperature and precipitation as
314 explanatory variables with ln-transformed species richness as the response variable
315 ('Global occurrence model', Table 1). The second model used abundance of dominant
316 species, temperature and precipitation as explanatory variables with ln-transformed
317 species richness as the response variables ('Global abundance model', Table 1). The
318 abundance model also included the quadratic term of abundance, in case the relationship

319 was unimodal (Andersen, 1992; Parr et al., 2005; Parr, 2008). To compare dominance-
320 diversity relationships under native vs non-native dominant species and along climate
321 gradients, we first classified sites into three categories: “sites without dominants”, “sites
322 with native dominants” and “sites with non-native dominants” (our data set included no
323 sites with both native and non-native dominants). We then tested the relationship
324 between the interaction of dominant type (no dominants, native dominants, non-native
325 dominants) and the climatic variables (temperature and precipitation) on species
326 richness (ln-transformed) by using a GLMM (‘Dominants type x climate model’, Table
327 1). We also analyzed the relationship between the abundance of native and non-native
328 dominant ants and species richness (ln-transformed) in separate GLMM models
329 (‘Native dominants x climate model’; and ‘Non-native dominants x climate model’;
330 Table 1). Both models included the interaction of the abundance of dominant ants and
331 its quadratic term with the climatic variables (temperature and precipitation) as
332 explanatory variables.

333 Finally, we analyzed how climate variables shape the relative abundance of native and
334 non-native dominant species in two separate models where only the sites where
335 dominants occurred and with available abundance data were used (‘Climate model of
336 native dominants’ and ‘Climate model of non-native dominants’, Table 1). In both
337 models, the explanatory variables were temperature, precipitation and their interaction,
338 and the abundance of native and non-native dominants species (logit transformed) were
339 the response variables, respectively. All models included a set of covariates as fixed
340 variables that were used to control for variation in sampling effort (number of trap days
341 and transect length), region (continent and hemisphere) and habitat structural type
342 (forest or open habitat).

343 We used mixed-effects models because sites were spatially clustered. Thus, clusters of
344 sites separated by no more than 100 km from each other were represented by a single
345 random effect to control for potential autocorrelation between localized sites (see Gibb
346 et al., 2015) while allowing the direct comparison between sites from nearby locations.
347 The mixed-effect models (GLMMs) were fitted with the *lme* function in *lme4* package
348 in R. Akaike's Information Criterion with a correction for finite sample sizes (AICc)
349 was used to select the best-supported models (Burnham & Anderson, 2002). In each
350 analysis, models were constructed using all combinations of explanatory variables. The
351 best-supported models for each analysis were selected based on the AICc weights,
352 which reveal the relative likelihood of a given model—based on the data and the fit—
353 scaled to one; thus, models with a delta (AICc difference) < 2 were selected (Burnham
354 & Anderson, 2002). We selected as relevant variables those that were included in the
355 best-supported models. The model selection procedure was conducted using the *dredge*
356 function in the MuMIn package in R. Both marginal and conditional R^2 values of the
357 best-supported models (which give the variation explained by fixed as well as fixed +
358 random effects, respectively) were reported (Nakagawa & Schielzeth, 2013).

359

360 RESULTS

361 Mean species richness was significantly higher at sites with than without dominant
362 species (Table 1, 'Global occurrence model', Fig. 2; Appendix S2 for more details on
363 outputs from model selection procedure), a pattern that was consistent between
364 temperate latitudes and subtropical and tropical latitudes. Species richness increased
365 linearly with mean annual temperature ($R^2_{\text{marginal/conditional}}=0.23/0.65$), but not with
366 annual precipitation (Table 1, 'Global occurrence model'). These relationships varied

367 according to whether dominant species occurred at a site, and whether the dominant
368 species were native or non-native, such that species richness tended to be lowest at sites
369 with non-native dominant species, and highest at sites with native dominant species
370 (Table 1, 'Dominants type x climate model', Fig. 3a). Mean species richness was 31.9%
371 higher at sites with dominant species than those without only when the dominant
372 species were native, but was 4.6% lower when the dominant species were non-native.
373 The difference between sites dominated by non-native species and sites without
374 dominant species varied markedly with temperature: there was no difference in species
375 richness at low temperatures (temperature <15°C), but as temperature increased, the
376 difference between the two increased such that by 27°C, there were 27.5% more species
377 in sites without dominants than in sites with non-native dominants (Fig. 3a). In
378 contrast, species richness at sites dominated by native species tended to be higher than
379 at sites without dominant species, although the difference increased with increasing
380 temperature (Fig. 3a). Moreover, whereas native dominant species occurred across the
381 full temperature gradient, non-native dominant species were absent from the coldest
382 sites (temperature <7°C; Fig. 3A). Notably, all sites in the very hottest environments
383 (temperature >27°C) had dominant species, and they were mostly native rather than
384 non-native (Fig. 3a).

385 At sites where dominant species occurred and where abundance data were available,
386 there was a unimodal relationship between species richness and the abundance of
387 behaviorally dominant species (Table 1, 'Global abundance model'), with a very
388 shallow ascending side of the curve but steeper descent (Fig. 3b,
389 $R^2_{\text{marginal/conditional}}=0.20/0.72$). Species richness was not only lower when non-native
390 species were present relative to when they were absent, but it declined at a faster rate as
391 their relative abundance increased (Table 1, 'Native dominants x climate' and 'Non-

392 native dominants x climate' models, Fig. 3b). In both cases there was no interaction
393 between relative abundance of dominant species and either temperature or precipitation
394 (Table 1, 'Native dominants x climate' and 'Non-native dominants x climate' models).
395 The relative abundance of non-native dominant species was not related to either
396 temperature or precipitation, whereas that of native dominant species was related to
397 both (Table 1, 'Climate model of non-native dominants' and 'Climate model of native
398 dominants'). There was a very shallow U-shaped relationship between the relative
399 abundance of native dominants and temperature (Fig. 4a), with the relative abundance
400 of dominants tending to be highest at the lowest and highest temperatures. The relative
401 abundance of native dominant ants was negatively related to precipitation (Fig. 4b).

402

403 DISCUSSION

404 In nearly 1,300 local ant assemblages distributed across five continents, we found that
405 where dominant species occurred and abundance data were available, the relationship
406 between dominance and richness is humped-shaped. Such a relationship parallels
407 models of the control of diversity in communities of plants and sessile intertidal
408 organisms along gradients of resource availability (Grime, 1973), productivity (Tilman,
409 1982), or disturbance (Connell, 1978). A premise in these models is that diversity
410 initially increases with environmental favorability but then decreases as conditions
411 allow highly competitive species to become so dominant that they exclude other
412 species. Such a unimodal relationship has been documented in ants sampled at very
413 localized food resources in a variety of local communities (Andersen, 1992; Parr et al.,
414 2005; Campbell et al., 2015). However, there is only limited evidence that competitive

415 exclusion from local food resources scales up to exclusion at the site level (e.g., Gibb &
416 Hochuli, 2004; Baccaro et al., 2012; Parr, 2008).

417 What causes the descending side of the dominance-diversity curve? It cannot
418 necessarily be attributed to competitive exclusion because the humped model applies
419 specifically to local communities, and at larger scales there are confounding effects of
420 climatic drivers of ant diversity. For example, if communities corresponding to very
421 high levels of behavioural dominance associated with very low levels of species
422 richness are from low-diversity systems (e.g. *Formica*-dominated communities from
423 boreal forests), then this is not evidence of competitive exclusion in highly diverse
424 systems. Indeed, our analysis shows many examples of very high diversity occurring
425 with very high levels of behavioural dominance, and when native dominant species
426 were present, species richness was actually higher than at sites without dominant
427 species. The dominance-impoverishment 'rule' is clearly not a general one.

428 The shape of the dominance-diversity relationship depended on whether the dominant
429 species were native or non-native. In contrast to the situation with native dominant
430 species, when the dominant species were non-native, species richness was 4.6% lower
431 at sites with dominant species than those without. We thus found a positive relationship
432 between the occurrence of dominant ants and species richness when the dominant
433 species were native, but a negative relationship when they were non-native. There were
434 also different relationships between species richness and the *abundance* of dominant
435 species depending on whether the dominant species were native or non-native, with the
436 negative slope being much steeper in the latter. Ant richness increased with temperature
437 regardless of whether dominant species were present, or whether dominant species were
438 native or non-native. However, its interaction with behavioural dominance varied

439 markedly with temperature. At lower temperature, sites with non-native dominant
440 species had the same richness as those without dominant species, but had progressively
441 lower richness with increasing temperature. Sites with native dominant species had
442 higher richness than those without dominant species across the full temperature range,
443 but slightly more so at higher temperature. Moreover, native dominant species occurred
444 across the full temperature range, but non-native dominant species did not occur at
445 either the coldest or hottest sites. The relative abundance of native dominant ants was
446 lowest at moderate temperature, being greater at lower and higher temperature, and was
447 highest at driest sites, whereas the relative abundance of non-native species was not
448 related to climate.

449 The extent to which the dominance-diversity relationships that we have reported are
450 causal is unclear. The association between the occurrence of non-native dominant
451 species and lower species richness can at least partly be explained by competitive
452 exclusion, given that the elimination of native species by invasive invaders has been
453 well demonstrated (Holway et al., 2002; Lach & Hooper-Bùi 2010; Stuble et al., 2013).
454 This is consistent with our finding that the association of non-native dominant ants with
455 lower diversity increased with temperature, given that the effects of competition
456 typically increase with increasing productivity (Grime, 1979; Andersen, 1995; 1997a;
457 Rees, 2013), and productivity in ants is strongly related to temperature (Andersen,
458 1995).

459 There are alternative explanations for the association of native dominant species with
460 higher species richness. The most parsimonious explanation is that species richness and
461 the abundance of native dominant species show parallel responses to increasing climatic
462 favourability (Andersen, 1995). We found a positive relationship between temperature

463 and ant species richness, and native dominant species occupy sites with higher
464 temperature compared to sites without dominant species. However, we found that
465 species richness tends to be higher in sites with dominant species than those without
466 dominant species, regardless of temperature. Moreover, if habitat favorability alone is at
467 work, we would expect parallel responses of species richness and the abundance of
468 native dominants to mean annual temperature, but this was not the case (species
469 richness increased linearly along the temperature gradient, but the abundance of
470 dominant species followed a U-shaped relationship with temperature). The best-
471 supported climate model of native dominants kept most covariates, suggesting that
472 native dominants may be responding differently depending on the continent, hemisphere
473 and habitat type.

474 An alternative explanation is that dominant species actually promote species richness.
475 Such facilitation might be through increased heterogeneity and resource availability, as
476 suggested by Gibb (2011) for northern Europe in a study at the regional scale in boreal
477 forests. Although Gibb (2001) found facilitation by dominant ants in the most disturbed
478 (least productive) sites, we found that the presence of native dominant species had the
479 greatest impact on species richness at warm (i.e. more productive) sites. Our results are
480 consistent with the finding that facilitation occurs primarily at the most productive sites
481 (Golberg et al., 1999). An alternative mechanism for facilitation of species richness by
482 dominant species is that they moderate the suppressive effect of subdominant species on
483 subordinate species (Arnan et al., 2011). Further experimental work (see below) is
484 required to clarify the causal mechanism(s) behind the positive relationship between
485 species richness and the abundance of dominant species.

486 Why might non-native dominant species have a negative effect on local species richness
487 when native dominant species do not? One explanation is a lack of co-evolution
488 between invasive and native species, such that native species lack the particular
489 compensatory mechanisms (e.g. niche partitioning, thermal tolerance-behavioral
490 dominance trade-offs) that would allow coexistence (Cerdá et al., 2013). In non-invaded
491 areas, dominant and non-dominant species have evolved together and different
492 compensatory mechanisms that allow coexistence have arisen; facilitation processes
493 might even promote stable coexistence among species (Hart & Marshall, 2013). It is
494 also worth mentioning that invasion and species richness suppression by invasive ant
495 species has not been recorded for high-diversity systems with high levels of behavioral
496 dominance of native species, that is, invasion and exclusion might only occur in
497 communities that are 'naïve' to dominance. Another explanation relates to differences in
498 social structure between native and non-native dominants: unlike many native species,
499 invasive populations are often unicolonial (a population of ants inhabiting a single
500 large polydomous colony), and so there is little or no aggression between workers from
501 different nests (Passera, 1994; Holway et al., 2002; Robinson, 2014). Notably,
502 *Linepithema humile* is entirely unicolonial in its introduced range, but often is not in its
503 native range (Giraud et al., 2002). Such a difference in social structure might have a
504 major role in shifting competition for resources from intraspecific (in multicolonial
505 species of native dominant species) to interspecific (in unicolonial species of invasive
506 dominant species), and thus potentially exerting a greater effect on local species
507 richness.

508 The mechanisms underlying the dominance-diversity relationships we have reported are
509 best tested through experimental manipulation of dominant ants (Gibb & Johansson,
510 2011). However, experimental removals or additions of dominant species (either native

511 or non-native) have shown conflicting results, variably showing positive (Gibb, 2011),
512 negative (King & Tschinkel, 2008; Blinova, 2011; Gibb, 2011) or neutral (Andersen &
513 Patel, 1994; Gibb & Hochuli, 2004; King & Tschinkel, 2006; 2013; Gibb & Johansson,
514 2011) effects on species richness. This suggests the effects of dominant species on
515 species richness might depend on biotic (e.g., whether dominant species are native or
516 non-native) and abiotic conditions (e.g., climate or habitat structure), as well as the
517 interaction between them.

518 If our results really are caused by interactions between dominant ants and the rest of the
519 community, then this implies that biotic interactions (competition and possibly also
520 facilitation) can be important drivers of diversity patterns at macro-ecological as well as
521 local scales (Stubbs & Wilson, 2004; Slingsby & Verboom, 2006). We call for
522 revisiting macro-ecological studies that present environmental constraints as drivers of
523 spatial patterns of diversity at large spatial scales when these studies were unable to
524 distinguish environmental filtering from the outcome of biotic interactions. For
525 instance, the effects of environmental favorability on species richness might be severely
526 under- or overestimated in areas where non-native or native dominant species occur,
527 respectively. Our results also raise serious concerns relating to some key drivers of
528 global change. Economic globalization is triggering an exponential increase in the
529 number of introductions of exotic species (Butchart et al., 2010; Essl et al., 2011), and
530 climate change is predicted to promote a proliferation of several non-native dominant
531 ant species (Bertelsmeier et al., 2015b). Our findings suggest that reductions in ant
532 diversity by dominant species will be greatest under a combination of highest
533 temperatures with highest occurrence of non-native ant species, and the frequency of
534 this scenario is likely to increase under global change.

535 In conclusion, we have shown that dominance-diversity relationships in ant
536 communities vary markedly depending on whether dominant species are native or non-
537 native. In particular, the association of high levels of behavioural dominance with low
538 species richness that is often observed in invaded communities does not typically occur
539 in native communities. Indeed, species richness in communities with native dominant
540 species is consistently higher than in communities lacking dominant species. The
541 dominance-impoverishment rule appears to be restricted to invaded communities, and
542 we propose a ‘dominance-diversification rule’ for native communities.

543 Such dominance-diversification appears to be peculiar to ants. Although ants have many
544 parallels with plants in that both are central-place foragers with complex foraging
545 modules, in plant communities both native and non-native dominant species exert
546 negative influences on species diversity (Grime, 1973, Pyšek et al., 2012). As central
547 place foragers, dominant ants cannot persistently monopolize key resources within their
548 foraging territories in the comprehensive way that dominant plants can. Canopy trees,
549 for instance, can comprehensively monopolize key plant resources such as light,
550 providing no opportunity for the sort of temporal or fine-scale spatial niche
551 differentiation, variable outcomes of competition, or forager priority effects that
552 facilitate species co-existence in ant communities (Andersen, 2008). However, the
553 dominance-diversification rule might apply to other mobile animal groups that, like
554 ants, are organized in complex behavioral dominance hierarchies (i.e., hummingbirds,
555 fishes, lizards) (Werner, 1976, Des Granges, 1979), and further research is needed to
556 test the applicability of this rule among other faunal taxa.

557

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757 Row.
- 758

759 **Table 1.** Summary of the best-supported models analyzing the dominance-diversity
 760 relationship as well as the relationship between climate and behavioral dominance from
 761 different datasets. A reference name for each complete model, the variables included in
 762 each complete model, the variables included within the best-fitted models, the range of
 763 the marginal and conditional R^2 values for the best-fitted models and the number of
 764 sites used for each analysis are shown. All complete models included a set of covariates
 765 (cov: Continent, Hemisphere, Habitat type, Pitfall days and Transect length).
 766 Abbreviations: BD, Behavioral dominance (two levels: sites without dominants and
 767 sites with dominants); DT, Dominance type (three levels: sites without dominants, sites
 768 with native dominants, and sites with non-native dominants); MAT, Mean annual
 769 temperature; AP, Annual precipitation; RAB, Relative abundance of dominant ants; and
 770 S, Species richness.

Model name	Complete model	Variables selected	$R^2_{\text{marginal/conditional}}$	N sites
<i>Effects on species richness</i>				
Global occurrence model	S = BD + MAT + AP + cov	BD + MAT + Hemisphere	0.29-0.34 / 0.66-0.68	1293
Global abundance model	S = RAB + RAB ² + MAT + AP + cov	RAB + RAB ² + Hemisphere	0.12-0.20 / 0.72	645
Dominants type x climate model	S = DTxMAT + DTxAP + DTxMATxAP + cov	DTxMAT	0.35 / 0.69	1293
Native dominants x climate model	S = RABxMAT + RABxAP + RABxMATxAP + RAB ² xMAT + RAB ² xAP + RAB ² xMATxAP + cov	RAB ² + Continent + Hemisphere	0.04-0.17 / 0.72-0.74	523

Non-native dominants x climate model	S = RABxMAT + RABxAP + RABxMATxAP + RAB ² xMAT + RAB ² xAP + RAB ² xMATxAP + cov	RAB + RAB ² + Habitat type + Hemisphere	0.17–0.21 / 0.80– 0.84	122
<i>Effects on relative abundance of dominant species</i>				
Climate model of native dominants	RAB = MAT + MAT ² + AP + MATxAP + cov	MAT + MAT ² + AP + Continent + Habitat type + Hemisphere	0.31–0.37 / 0.54– 0.59	523
Climate model of non-native dominants	RAB = MAT + MAT ² + AP + MATxAP + cov	Continent + Habitat type + Hemisphere	0.11–0.12 / 0.41– 0.44	122

771

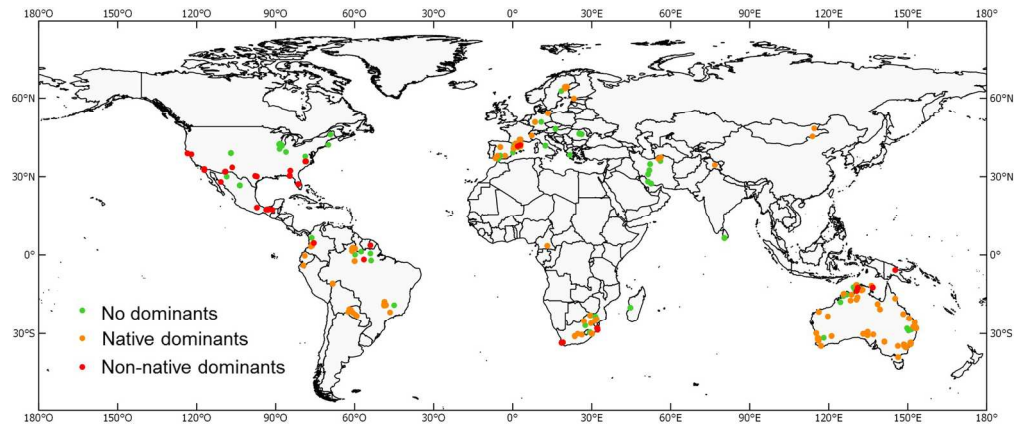
772 FIGURE LEGENDS

773 **Figure 1.** World map showing the 1293 independent study plots with no dominant ants
774 (green circles), native (yellow circles), or non-native dominants (red circles). Many of
775 the study plots were conducted in independent locations in relatively close proximity, so
776 appear as a single plot.

777 **Figure 2.** Relationship between ant species richness and the presence or absence of
778 behaviorally dominant species in the world, and separated by temperate and subtropical
779 and tropical latitudes.

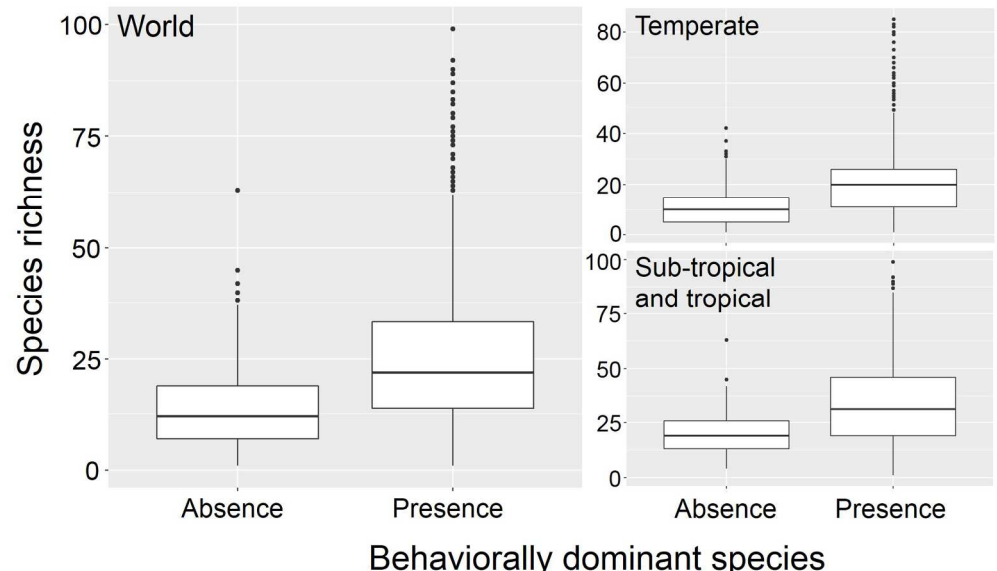
780 **Figure 3.** Interaction effects of dominants type (sites without dominants, sites with
781 native dominants and sites with non-native dominants) and mean annual temperature on
782 species richness (ln-transformed) (a), and unimodal relationships between the relative
783 abundance of behaviorally dominant species and ant species richness (ln-transformed)
784 in sites with native or non-native dominant species (blue line), with only native
785 dominants (green line) and sites with only non-native dominants (red line) (b). Shaded
786 area represents the standard error. Circle size is proportional to sample size.

787 **Figure 4.** Relationships between mean annual temperature (a) and annual precipitation
788 (b) with the relative abundance (logit transformed) of native dominant species. Shaded
789 area represents the standard error.



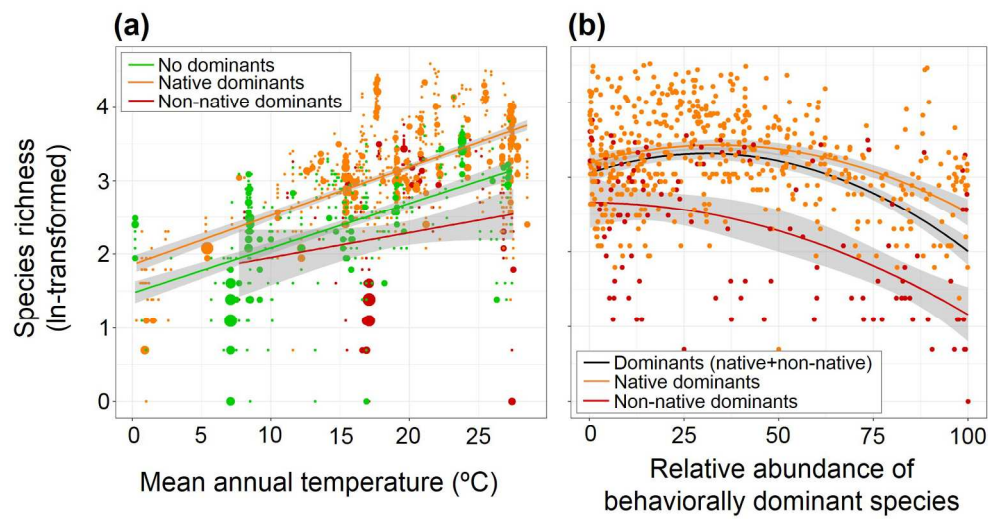
World map showing the 1293 independent study plots with no dominant ants (green circles), native (yellow circles), or non-native dominants (red circles). Many of the study plots were conducted in independent locations in relatively close proximity, so appear as a single plot.

173x72mm (300 x 300 DPI)



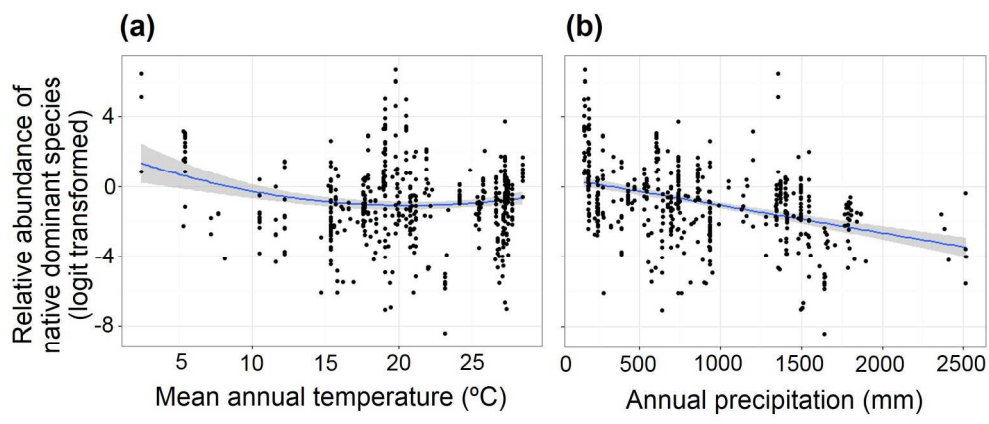
Relationship between ant species richness and the presence or absence of behaviorally dominant species in the world, and separated by temperate and subtropical and tropical latitudes.

187x113mm (300 x 300 DPI)



Interaction effects of dominants type (sites without dominants, sites with native dominants and sites with non-native dominants) and mean annual temperature on species richness (ln-transformed) (a), and unimodal relationships between the relative abundance of behaviorally dominant species and ant species richness (ln-transformed) in sites with native or non-native dominant species (blue line), with only native dominants (green line) and sites with only non-native dominants (red line) (b). Shaded area represents the standard error. Circle size is proportional to sample size.

186x100mm (300 x 300 DPI)



Relationships between mean annual temperature (a) and annual precipitation (b) with the relative abundance (logit transformed) of native dominant species. Shaded area represents the standard error.

379x164mm (150 x 150 DPI)