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Dominance–diversity relationships in ant communities differ with invasion

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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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98

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

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, χ_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

Defining behavioral dominance and invasive (non-native) species

We focused on the relationship between diversity and behavioral dominance, rather than

simply numerical dominance, because this is specified in the dominance-

impoverishment rule. At any rate, in those sites where behaviorally dominant species

occurred, the abundance of behaviorally dominant species was highly correlated to the

abundance of the most abundant species (Spearman $r = 0.96$, $p<0.0001$, $n=645$), i.e.

behavioral and numerical dominance was highly correlated. We considered a species to

be behaviorally dominant based on both aggressive behavior and effects on other

species by excluding them from near their nests and from high-value food resources

(Vepsäläinen & Pisarski, 1982; Savolainen et al., 1989; Andersen, 1992; Cerdá et al.,

2013). Behaviorally dominant species are thus defined as highly aggressive species that

usually predominate numerically, occupy large territories, and have mutually exclusive

distribution patterns at local scales. Given the large number of studies use, data are not

available to demonstrate impact by dominant species in each of our study communities,

and so we had to rely on a priori classifications of taxa based on the literature and our

combined expert knowledge. The following taxa were thus classified as behaviorally

dominant (Appendix S1): *Anonychomyrma, Anoplolepis, Azteca, Dorymyrmex* (except

insana group), *Formica* (only *exsecta* and *rufa* groups), *Froggattella, Iridomyrmex,*

Linepithema, Liometopum, Oecophylla, Papyrius, Pheidole (only *megacephala* and

fallax groups), *Philidris, Solenopsis* (sub-genus *Solenopsis*, i.e. "fire ants"), *Tapinoma*

(*nigerrimum* group), and *Wasmannia auropunctata*. There is considerable empirical

evidence that species in these taxa are behaviorally dominant and influence the structure

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 ($R^2_{marginal/conditional}$=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    $R^2_{marginal/conditional}$=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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570

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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	$R^2_{marginal/conditional}$	N sites
Effects on species richness				
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	$S = RAB \times MAT + RAB \times AP + RAB \times MAT \times AP + RAB^2 \times MAT + RAB^2 \times AP + RAB^2 \times MAT \times AP + cov$	$RAB + RAB^2 +$ Habitat type + Hemisphere	0.17–0.21 / 0.80-0.84	122

Effects on relative abundance of dominant species

|				
Climate model of native dominants	$RAB = MAT + MAT^2 + AP + MAT \times AP + cov$	$MAT + MAT^2 + AP +$ Continent + Habitat type + Hemisphere	0.31-0.37 / 0.54-0.59	523
Climate model of non-native dominants	$RAB = MAT + MAT^2 + AP + MAT \times AP + cov$	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
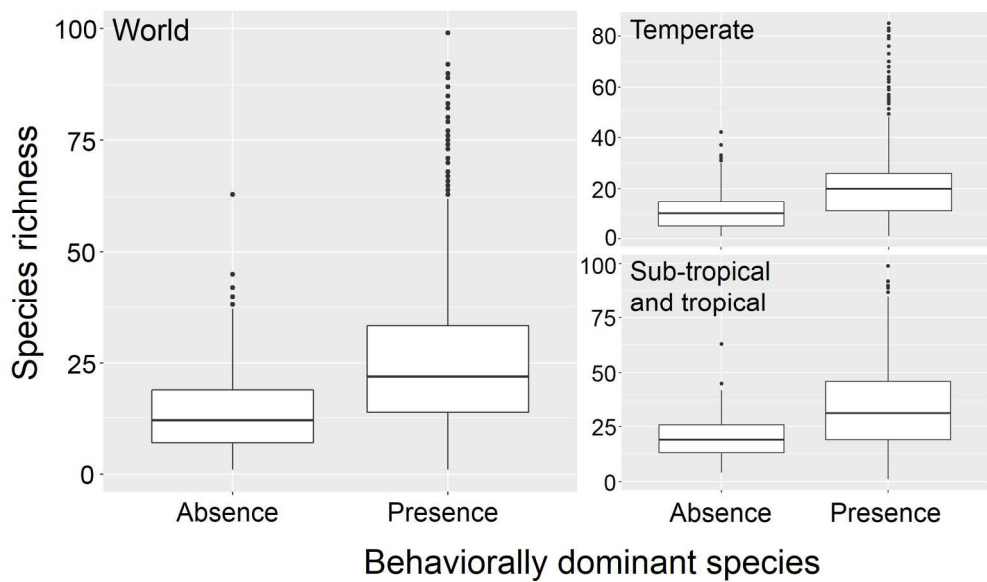
779   and tropical latitudes.

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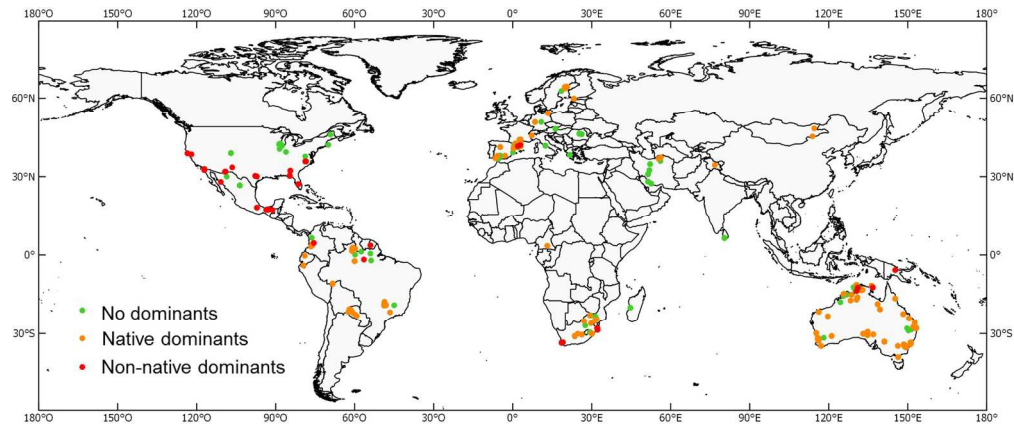
World map showing the 1293 independent study plots with no dominant ants (green circles), native (yellow circles), or non-native dominants (red circles). Many of the study plots were conducted in independent locations in relatively close proximity, so appear as a single plot.

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)
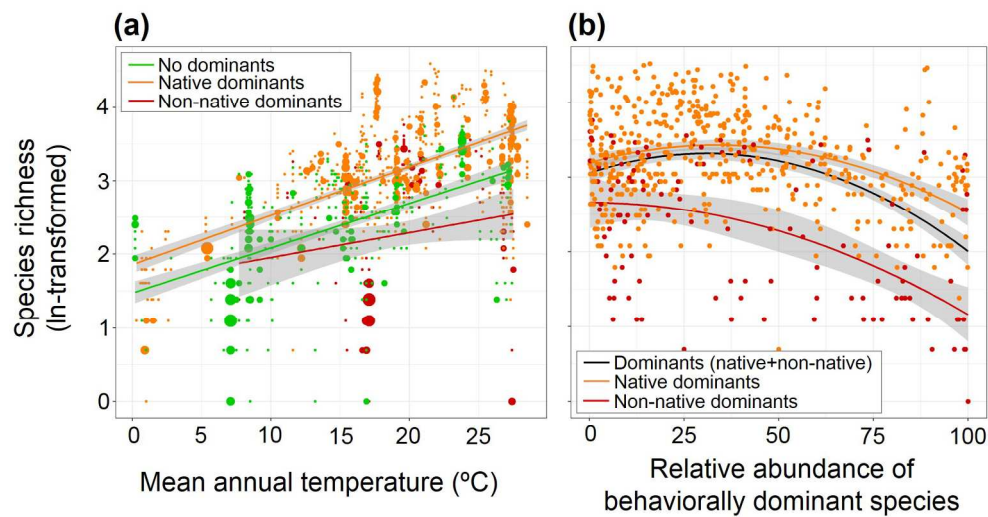
Interaction effects of dominants type (sites without dominants, sites with native dominants and sites with non-native dominants) and mean annual temperature on species richness (ln-transformed) (a), and unimodal relationships between the relative abundance of behaviorally dominant species and ant species 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)
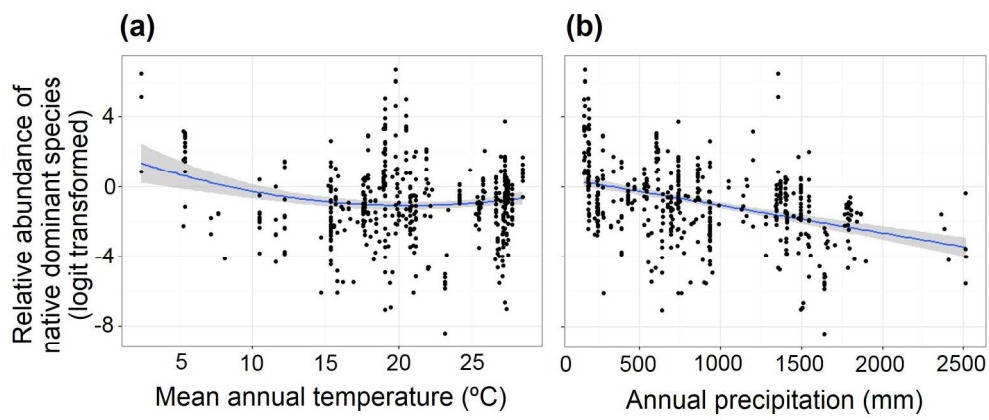
Relationships between mean annual temperature (a) and annual precipitation (b) with the relative abundance (logit transformed) of native dominant species. Shaded area represents the standard error.

379x164mm (150 x 150 DPI)