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Dominance-diversity relationships in ant communities differ with invasion

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1	Paper type: Primary Research Article
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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

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

- 124 *Keywords:* ants, behavioral dominance, coexistence, dominance-impoverishment rule,
- 125 global scale, invasive species, precipitation, species richness, temperature

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, 10

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	

220

221 MATERIALS AND METHODS

222 Ant assemblage database

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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.

2	247	
2	248	Defining behavioral dominance and invasive (non-native) species
2	249	We focused on the relationship between diversity and behavioral dominance, rather than
2	250	simply numerical dominance, because this is specified in the dominance-
2	251	impoverishment rule. At any rate, in those sites where behaviorally dominant species
2	252	occurred, the abundance of behaviorally dominant species was highly correlated to the
2	253	abundance of the most abundant species (Spearman $r = 0.96$, p<0.0001, n=645), i.e.
2	254	behavioral and numerical dominance was highly correlated. We considered a species to
2	255	be behaviorally dominant based on both aggressive behavior and effects on other
2	256	species by excluding them from near their nests and from high-value food resources
2	257	(Vepsäläinen & Pisarski, 1982; Savolainen et al., 1989; Andersen, 1992; Cerdá et al.,
2	258	2013). Behaviorally dominant species are thus defined as highly aggressive species that
2	259	usually predominate numerically, occupy large territories, and have mutually exclusive
2	260	distribution patterns at local scales. Given the large number of studies use, data are not
2	261	available to demonstrate impact by dominant species in each of our study communities,
2	262	and so we had to rely on a priori classifications of taxa based on the literature and our
2	263	combined expert knowledge. The following taxa were thus classified as behaviorally
2	264	dominant (Appendix S1): Anonychomyrma, Anoplolepis, Azteca, Dorymyrmex (except
2	265	insana group), Formica (only exsecta and rufa groups), Froggattella, Iridomyrmex,
2	266	Linepithema, Liometopum, Oecophylla, Papyrius, Pheidole (only megacephala and
2	267	fallax groups), Philidris, Solenopsis (sub-genus Solenopsis, i.e. "fire ants"), Tapinoma
2	268	(nigerrimum group), and Wasmannia auropunctata. There is considerable empirical
2	.69	evidence that species in these taxa are behaviorally dominant and influence the structure
2	270	and dynamics of local ant communities (e.g., Andersen, 1995; 1997a; Savolainen et al.,

1989; Lach & Hooper-Bùi, 2010; Arnan et al., 2011; Cerdá et al., 2013; Bertelsmeier et 271 272 al., 2015a). Some species from other genera (e.g., Crematogaster) might also be good candidates, but the distribution of behavioural dominance among constituent species 273 274 groups is poorly known, and so they have not been included. Army-ants (subfamily Dorylinae) were also not included. These species are behavioural dominant species, but 275 276 their effects on other ant species are temporally limited given their nomadic life style. Our pool of behaviorally dominant species included five invasive species occurring in 277 our communities outside their native ranges: the yellow crazy ant (Anoplolepis 278 279 gracilipes), the Argentine ant (Linepithema humile), the big-headed ant (Pheidole 280 megacephala), fire ants (Solenopsis spp., subgenus Solenopsis) and the electric ant (Wasmannia auropunctata) (Lach & Hooper-Bùi, 2010; Bertelsmeier et al., 2015a; 281 282 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*

We selected two climatic variables that are consistently related to variation in ant 287 communities globally (e.g., Dunn et al., 2009; Jenkins et al., 2011; Arnan et al., 2014; 288 289 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 evidence that they are key drivers of ant diversity at a global scale. For each locality, 292 temperature and precipitation information was obtained for the period 1950 - 2000 from 293 the WORLDCLIM database (http://www.worldclim.org/bioclim) using rasters with the 294

295	highest available resolution	(30 arc-s, approx.	1 x 1 km). Such a	resolution	provides
		(,				

- climatic data that are directly applicable to the scale of sampling in our study
- 297 communities (approximately 1 ha).

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299 Data analyses
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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

highly correlated (Spearman r = 0.27, p<0.0001), so both variables were retained for

303 analyses.

We considered behavioral dominance at two levels: the (1) occurrence (presence-

absence) and (2) abundance of dominant species in a site. Occurrence data were

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

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.

We used two general linear mixed models (GLMMs) to test how behavioral dominance and climate relate to ant species richness. The first model used occurrence of dominant species (sites with vs sites without dominants), temperature and precipitation as explanatory variables with ln-transformed species richness as the response variable ('Global occurrence model', Table 1). The second model used abundance of dominant species, temperature and precipitation as explanatory variables with ln-transformed species, temperature and precipitation as explanatory variables with ln-transformed 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 (In-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 (In-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 <i>lme</i> function in <i>lme4</i> 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 <i>dredge</i>
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

temperate latitudes and subtropical and tropical latitudes. Species richness increased

linearly with mean annual temperature ($R^2_{marginal/conditional}=0.23/0.65$), but not with

annual precipitation (Table 1, 'Global occurrence model'). These relationships varied

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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

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 between dominance and richness is humped-shaped. Such a relationship parallels 406 models of the control of diversity in communities of plants and sessile intertidal 407 408 organisms along gradients of resource availability (Grime, 1973), productivity (Tilman, 1982), or disturbance (Connell, 1978). A premise in these models is that diversity 409 initially increases with environmental favorability but then decreases as conditions 410 allow highly competitive species to become so dominant that they exclude other 411 species. Such a unimodal relationship has been documented in ants sampled at very 412 localized food resources in a variety of local communities (Andersen, 1992; Parr et al., 413 414 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

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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

462 favourability (Andersen, 1995). We found a positive relationship between temperature

the abundance of native dominant species show parallel responses to increasing climatic

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

(least productive) sites, we found that the presence of native dominant species had the 478

greatest impact on species richness at warm (i.e. more productive) sites. Our results are

consistent with the finding that facilitation occurs primarily at the most productive sites 480

(Golberg et al., 1999). An alternative mechanism for facilitation of species richness by 481

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

required to clarify the causal mechanism(s) behind the positive relationship between 484

485 species richness and the abundance of dominant species.

479

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

or non-native) have shown conflicting results, variably showing positive (Gibb, 2011), 511 negative (King & Tschinkel, 2008; Blinova, 2011; Gibb, 2011) or neutral (Andersen & 512 Patel, 1994; Gibb & Hochuli, 2004; King & Tschinkel, 2006; 2013; Gibb & Johansson, 513 2011) effects on species richness. This suggests the effects of dominant species on 514 species richness might depend on biotic (e.g., whether dominant species are native or 515 516 non-native) and abiotic conditions (e.g., climate or habitat structure), as well as the interaction between them. 517 If our results really are caused by interactions between dominant ants and the rest of the 518 community, then this implies that biotic interactions (competition and possibly also 519 520 facilitation) can be important drivers of diversity patterns at macro-ecological as well as local scales (Stubbs & Wilson, 2004; Slingsby & Verboom, 2006). We call for 521 revisiting macro-ecological studies that present environmental constraints as drivers of 522 523 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 instance, the effects of environmental favorability on species richness might be severely 525 under- or overestimated in areas where non-native or native dominant species occur, 526 527 respectively. Our results also raise serious concerns relating to some key drivers of global change. Economic globalization is triggering an exponential increase in the 528 number of introductions of exotic species (Butchart et al., 2010; Essl et al., 2011), and 529 climate change is predicted to promote a proliferation of several non-native dominant 530 ant species (Bertelsmeier et al., 2015b). Our findings suggest that reductions in ant 531 532 diversity by dominant species will be greatest under a combination of highest

temperatures with highest occurrence of non-native ant species, and the frequency of

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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571 REFERENCES

- 572 Albrecht, M. & Gotelli, N.J. (2001) Spatial and temporal niche partitioning in grassland
- 573 ants. *Oecologia*, *126*, 134–141.
- Andersen, A.N. (1991) Parallels between ants and plants: implications for community
- ecology. In C.R. Huxley & D.F. Cutler (Eds.), *Ant Plant interactions* (pp. 539-538).
- 576 Oxford, UK: Oxford University Press.
- 577 Andersen, A.N. (1992) Regulation of "momentary" diversity by dominant species in
- 578 exceptionally rich ant communities of the Australian seasonal tropics. American
- 579 *Naturalist*, *140*, 401–420.
- 580 Andersen, A.N. (1995) A classification of Australian ant communities, based on
- 581 functional groups which parallel plant life-forms in relation to stress and disturbance.
- *Journal of Biogeography*, *22*, 15–29.

- 583 Andersen, A.N. (1997a) Functional groups and patterns of organization in North
- American ant communities: a comparison with Australia. Journal of Biogeography, 24,
- **585 433–460**.
- 586 Andersen, A.N. (1997b) Using ants as bioindicators: multi-scale issues in ant
- 587 community ecology. *Conservation Ecology*, 1, 8.
- 588 Andersen, A.N. (2000) A global ecology of rain forest ants: functional groups in
- relation to stress and disturbance. In D. Agosti, J.D. Majer, L. Alonso & T. Shultz
- 590 (Eds.), Ants: Standard Methods for Measuring and Monitoring Biodiversity (pp. 25-34).
- 591 Washington D.C., USA: Smithsonian Institution Press.
- 592 Andersen, A.N. (2008) Not enough niches: non-equilibrial processes promoting species
- 593 coexistence in diverse ant communities. *Austral Ecology*, *33*, 211–20.
- Andersen, A.N. (2010) Functional groups in ant community ecology. In L. Lach, C.L.
- 595 Parr & K. Abbott (Eds.), Ant Ecology (pp. 142-144). Oxford, UK: Oxford University
- 596 Press.
- 597 Andersen, A.N. & Patel, A.D. (1994) Meat ants as dominant members of Australian ant
- 598 communities: an experimental test of their influence on the foraging success and forager
- abundance of other species. *Oecologia*, 98, 15–24.
- Arnan, X., Cerdá, X. & Retana, J. (2014) Ant functional responses along environmental
- 601 gradients. Journal of Animal Ecology, 83, 1398-1408.
- Arnan, X., Gaucherel, C. & Andersen, A.N. (2011) Dominance and species co-
- occurrence in highly diverse ant communities: a test of the interstitial hypothesis and
- discovery of a competition cascade. *Oecologia*, *166*, 783-794.

- Baccaro, F.B., de Souza, J.L.P., Franklin, E., Landeiro, V.L. & Magnusson, W.E.
- 606 (2012) Limited effects of dominant ants on assemblage species richness in three
- 607 Amazon forests. *Ecological Entomology*, *37*, 1-12.
- Bertelsmeier, C., Avril, A., Blight, O., Confais, A., Diez, L., Jourdan, H. et al. (2015a)
- 609 Different behavioural strategies among seven highly invasive ant species. *Biological*
- 610 *Invasions*, *17*, 2491.
- 611 Bertelsmeier, C., Luque, G.M., Hoffmann, B.D. & Courchamp, F. (2015b) Worldwide
- ant invasions under climate change. *Biodiversity and Conservation*, 24, 117-128.
- Bertelsmeier, C., Blight, O. & Courchamp, F. (2016) Invasions of ants (hymenoptera:
- formicidae) in light of global climate change. *Myrmecological News*, 22, 25-43.
- Blinova, S.V. (2011) Changes in the ant assemblage of pine-birch forest upon removal
- of the nests of dominant species. *Russian Journal of Ecology*, 42, 525-528.
- 617 Blüthgen, N. & Fiedler, K. (2004) Competition for composition: Lessons from nectar-
- feeding ant communities. *Ecology*, 85, 1479–1485.
- 619 Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference: A
- 620 Practical Information-Theoretic Approach. New York, NY: Springer-Verlag.
- 621 Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W.,
- 622 Rosamunde, E.A., et al. (2010). Global biodiversity: indicators of recent declines.
- 623 *Science*, *328*, 1164-1168.
- 624 Campbell, H., Fellowes, M.D.E. & Cook, J.M. (2015) Species diversity and dominance-
- richness relationships for ground and arboreal ant (Hymenoptera: Formicidae)
- assemblages in Namibian desert, saltpan, and savannah. *Myrmecological News*, 21, 37-
- **627** 47.

- 628 Cardinale, B.J., Hillebrand, H., Harpole, W.S., Gross, K. & Ptacnik, R. (2009)
- 629 Separating the influence of resource 'availability' from resource 'imbalance' on
- 630 productivity-diversity relationships. *Ecology Letters*, *12*, 475-487.
- 631 Cerdá, X., Arnan, X. & Retana, J. (2013) Is competition a significant hallmark of ant
- 632 (Hymenoptera: Formicidae) ecology? *Myrmecological News*, 18, 131-147.
- 633 Chasse, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity-biodiversity
- 634 relationship. *Nature*, *416*, 427-430.
- 635 Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review*
- 636 *of Ecology, Evolution, and Systematics, 31*, 343-66.
- 637 Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, 199,
- **638** 1302-1310.
- 639 Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A trait-based test for habitat
- 640 filtering: convex hull volume. *Ecology*, 87, 1465–1471.
- 641 Davidson, D.W., Cook, S.C., Snelling, R.R. & Chua T.H. (2003) Explaining the
- abundance of ants in lowland tropical rainforest canopies. *Science*, *300*, 969–973.
- 643 Des Granges, J.L. (1979) Organization of a tropical nectar feeding bird guild in a
- 644 variable environment. *Living Bird*, *17*, 199–236.
- Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerdá, X. et al. (2009)
- 646 Climatic drivers of hemispheric asymmetry in global patterns of ant species richness.
- 647 *Ecology Letters*, *12*, 324–333.
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarosik, V. et al. (2011)
- 649 Socioeconomic legacy yelds an invasion debt. *Proceedings of the National Academy of*
- 650 *Sciences of the United States of America*, 108, 203-207.

- 651 Gibb, H. (2011) Experimental evidence for mediation of competition by habitat
- 652 succession. *Ecology*, *92*, 1871-1878.
- 653 Gibb, H., Dunn, R.R., Sanders, N.J., Grossman, B.F., Photakis, M., Abril, S., et al.
- (2017) A global database of ant species abundances. *Ecology*, *98*, 883-884.
- Gibb, H. & Hochuli, D.F. (2004) Removal experiment reveals limited effects of a
- behaviorally dominant species on ant assemblages. *Ecology*, *85*, 648–657.
- 657 Gibb, H. & Johansson, T. (2011) Field tests of interspecific competition in ant
- assemblages: revisiting the dominant red wood ants. *Journal of Animal Ecology*, 80,
- **659 548-557**.
- Gibb, H., Sanders, N.J., Dunn, R.R., Photakis, M., Andersen, A.N., Angulo, E. et al.
- 661 (2015) Climate regulates the effects of anthropogenic disturbance on ant assemblage
- structure. *Proceedings of the Royal Society of London B: Biological Sciences*, 282,

663 20150418.

- 664 Giraud, T., Pedersen, J.S. & Keller, J. (2002) Evolution of supercolonies: The Argentine
- ants of southern Europe. *Proceedings of the National Academy of Sciences of the United*
- 666 *States of America*, *99*, 6075-6079.
- 667 Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, *242*, 244–
 668 247.
- 669 Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley, Chichester.
- Golberg, D.H., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical
- approaches to quantifying interaction intensity: competition and facilitation along
- 672 productivity gradients. *Ecology*, *80*, 1118-1131.

- 673 Hart, S.P. & Marshall, D.J. (2013) Environmental stress, facilitation, competition, and
- 674 coexistence. *Ecology*, *94*, 2719-2731.
- Hoffmann, B.D., Andersen, A.N. & Hill, G.J.E. (1999) Impact of an introduced ant on
- 676 native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia.
- 677 *Oecologia*, *120*, 595-604.
- Hölldobler, B. (1983) Chemical manipulation, enemy specification and intercolony
- 679 *communication in ant communities.* In F. Huber & H. Markl (Eds.), *Neuroethology and*
- 680 Behavioral Physiology (pp. 354-365). Berlin: Springer-Verlag.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Belknap Press, Cambridge, MA.
- Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D. & Case, T.J. (2002) The causes
- and consequences of ant invasions. *Annual Review of Ecology, Evolution, and*
- 684 *Systematics*, *33*, 181–233.
- Jenkins, C.N., Sanders, N.J., Andersen, A.N., Arnan, X., Brühl, A., Cerdá, X. et al.
- 686 (2011) Global diversity in light of climate change: the case of ants. *Diversity and*
- 687 *Distributions*, 17, 652-662.
- 688 King, J.R. & Tschinkel, W.R. (2006) Experimental evidence that the introduced fire ant,
- 689 Solenopsis invicta, does not competitively suppress co-occurring ants in a disturbed
- habitat. Journal of Animal Ecology, 75, 1370-1378.
- 691 King, J.R. & Tschinkel, W.R. (2008) Experimental evidence that human impacts drive
- 692 fire ant invasions and ecological change. *Proceedings of the National Academy of*
- 693 *Sciences of the United States of America*, *105*, 20339–20343.

- 694 King, J.R. & Tschinkel, W.R. (2013) Experimental evidence for weak effects of fire
- ants in a naturally invaded pine-savanna ecosystem in north Florida. *Ecological*
- 696 *Entomology*, *38*, 543–545.
- 697 Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial
- scales and species coexistence. *Ecology Letters*, 7, 69–80.
- Lach, L. & Hooper-Bùi, L.M. (2010) Consequences of Ant Invasions. In L. Lach, C.L.
- 700 Parr & K. Abbott (Eds.), Ant Ecology (pp. 261-286). Oxford, UK: Oxford University
- 701 Press.
- Lowe, S., Browne, M., Boudjelas, S. & Poorter, M. de (2000) 100 of the world's worst
- invasive alien species a selection from the global invasive species database.
- 704 http://www.issg.org/database/species/reference_files/100English.pdf
- 705 MacKey, R.L. & Currie, D.J. (2001) The diversity-disturbance relationship: is it
- generally strong and peaked? *Ecology*, *82*, 3479-3492.
- 707 Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2
- from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4,
- 709 133-142.
- 710 Parr, C.L. (2008) Dominant ants can control assemblages species richness in a South
- 711 African savanna. *Journal of Animal Ecology*, 77, 1191-1198.
- 712 Parr, C.L., Sinclair, B.J., Andersen, A.N., Gaston, K.J. & Chown, S.L. (2005)
- 713 Constraint and competition in assemblages: a cross-continental and modeling approach
- for ants. *American Naturalist*, *165*, 481-494.

- Parr, C.L., Dunn, R.R., Sanders, N.J., Weiser, M.D., Photakis, M., Fitzpatrick, M.C. et
- 716 *al.* (2017) GLobal Ants trait Database (GLAD): a new database on the geography of ant
- traits (Hymenoptera: Formicidae). Insect Conservation and Diversity, 10, 5-20.
- 718 Passera, L. (1994) Characteristics of tramp species. In D. Williams (Ed.), *Exotic ants:*
- *biology, impact and control of introduced species* (pp. 23-43). Boulder, CO: Westview
- 720 Press.
- 721 Pyšek, P., Jarošík, V., Hulme, P.E., Perg, IJ., Hejda, M., Schaffner, U. & Vilà. M.
- 722 (2012). A global assessment of invasive plant impacts on resident species, communities
- and ecosystems: The interaction of impact measures, invading species' traits and
- environment. *Global Change Biology*, 18, 1725–1737.
- 725 R Core Team (2016). R: A language and environment for statistical computing. R
- 726 Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-
- 727 project.org/.
- Rees, M. (2013) Competition on productivity gradients what do we expect? *Ecology Letters*, *16*, 291-298.
- 730 Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional
- 731 processes. *Science*, *235*, 167–71.
- Room, P.M. (1971) The relative distribution of ant species in Ghana's cocoa farms.
- 733 Journal of Animal Ecology, 40, 735–751.
- Robinson, E.J.H. (2014) Polydomy: the organisation and adaptive function of complex
- nest systems in ants. *Current Opinion In Insect Science*, 5, 37–43.
- 736 Savolainen, R., Vepsäläinen, K. & Wuorenrinne, H. (1989) Ant assemblages in the taiga
- biome: testing the role of territorial wood ants. *Oecologia*, *81*, 481-486.

- 738 Silvertown, J., Dodd, M., Gowing, D., Lawson, C. & McConway, K. (2006) Phylogeny
- and the hierarchical organization of plant diversity. *Ecology*, 87, S39–S49.
- 740 Slingsby, J.A. & Verboom, G.A. (2006) Phylogenetic relatedness limits co-occurrence
- at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of
- the Cape Floristic Region, South Africa. *American Naturalist*, 168, 14–27.
- 743 Stuble, K.L., Chick, L.D., Rodriguez-Cabal, M.A., Lessard, J-P. & Sanders, N.J. (2013)
- Fire ants are drivers of biodiversity loss: a reply to King and Tschinkel (2013).
- *Ecological Entomology*, *38*, 540-542.
- 746 Stuble, K.L., Juric, I., Cerdá, X., Sanders, N.J. (2017) Dominance hierarchies are a
- dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be?
- And what is a dominance hierarchy anyways? *Myrmecological News*, 24, 71-81.
- 749 Stubbs, W.J. & Wilson, J.B. (2004) Evidence for limiting similarity in a sand dune
- community. Journal of Ecology, 92, 557–567.
- 751 Tilman. D. (1982) *Resource competition and community structure*. Princeton University
- 752 Press, Princeton, N.J.
- 753 Vepsäläinen, K. & Pisarski, B. (1982) Assembly of island ant communities. Annales
- 754 Zoologici Fennici, 19, 327-335.
- 755 Werner, E.E. (1976) Species interactions in freshwater fish communities. In J. Diamond
- and T.J. Case (Eds.), Community ecology (pp. 344-357). New York, NY: Harper and
- 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 marginal/conditional	Ν	
				sites	
Effects on species richness					
Global occurrence	S = BD + MAT + AP +	BD + MAT +	0.29-0.34 / 0.66-	1293	
model	COV	Hemisphere	0.68		
Global abundance	$S = RAB + RAB^2 + MAT$	$RAB + RAB^2 +$	0.12-0.20 / 0.72	645	
model	+ AP + cov	Hemisphere			
Dominants type x	S = DTxMAT + DTxAP	DTxMAT	0.35 / 0.69	1293	
climate model	+ DTxMATxAP + cov				
Native dominants x	S = RABxMAT +	$RAB^2 + Continent +$	0.04-0.17 / 0.72-	523	
climate model	RABxAP +	Hemisphere	0.74		
	RABxMATxAP +				
	$RAB^{2}xMAT + RAB^{2}xAP$				
	$+ RAB^{2}xMATxAP + cov$				

Non-native dominants	S = RABxMAT +	$RAB + RAB^2 + Habitat$	0.17-0.21 / 0.80-	122
x climate model	RABxAP +	type + Hemisphere	0.84	
	RABxMATxAP +			
	$RAB^{2}xMAT + RAB^{2}xAP$			
	$+ RAB^{2}xMATxAP + cov$			
Effects on relative abu	ndance of dominant			
species				
Climate model of	$RAB = MAT + MAT^2 +$	$MAT + MAT^2 + AP +$	0.31-0.37 / 0.54-	523
native dominants	AP + MATxAP + cov	Continent + Habitat type	0.59	
		+ Hemisphere		
Climate model of	$RAB = MAT + MAT^2 +$	Continent + Habitat type	0.11-0.12 / 0.41-	122
non-native dominants	AP + MATxAP + cov	+ Hemisphere	0.44	
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 (In-transformed) (a), and unimodal relationships between the relative
783	abundance of behaviorally dominant species and ant species richness (In-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 (In-transformed) (a), and unimodal relationships between the relative abundance of behaviorally dominant species and ant species richness (In-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)