

1 **Intransitive competition is widespread in plant communities and maintains their**
2 **species richness**

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41 **Keywords:** aridity, biodiversity, coexistence, drylands, land use, mesic grasslands,
42 rock-paper-scissors game

43

44 **Number of words in the Abstract:** 149

45 **Number of words in the main text:** 4978

46 **Number of cited references:** 50

47 **Number of tables:** 1

48 **Number of figures:** 4

49 **AUTHORSHIP**

50 SS, EA and FTM conceived the study, SS and WU analyzed the data, SS, MF, FTM,
51 DP, MB, SB, JLQ, IS, MDB, WW, VO, PM, SAS and JM gathered data, SS wrote the
52 first draft and all co-authors significantly contributed to improve it.

53

54 **Short running title:** Intransitivity in plant communities

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56 **Type of article:** Letter

57 **Abstract**

58 Intransitive competition networks, those in which there is no single best competitor,
59 may ensure species coexistence. However, their frequency and importance in
60 maintaining diversity in real-world ecosystems remains unclear. We used two large
61 datasets from drylands and agricultural grasslands to assess: 1) the generality of
62 intransitive competition, 2) intransitivity-richness relationships, and 3) effects of two
63 major drivers of biodiversity loss (aridity and land-use intensification) on intransitivity
64 and species richness. Intransitive competition occurred in >65% of sites and was
65 associated with higher species richness. Intransitivity increased with aridity, partly
66 buffering its negative effects on diversity, but was decreased by intensive land use,
67 enhancing its negative effects on diversity. These contrasting responses likely arise
68 because intransitivity is promoted by temporal heterogeneity, which is enhanced by
69 aridity but may decline with land-use intensity. We show that intransitivity is
70 widespread in nature and increases diversity, but it can be lost with environmental
71 homogenization.

72 **INTRODUCTION**

73 Species coexistence is made possible by a range of mechanisms including differential
74 resource uptake, frequency-dependent enemy attack or limited dispersal (Chesson 2000;
75 HilleRisLambers *et al.* 2012). Most of these mechanisms reduce competitive exclusion;
76 however, such reduction is not required for species coexistence because the absence of a
77 competitive hierarchy may allow species coexistence even if they compete strongly
78 (Gilpin 1975; Wootton 2001). This lack of competitive hierarchy within a community is
79 nature's equivalent to the rock-paper-scissors game: species A excludes B ($A > B$), B
80 excludes C ($B > C$) but C excludes A ($C > A$; e.g., Kerr *et al.* 2002). Such networks of
81 interactions are termed intransitive competition networks and may enhance species
82 coexistence because no species is a universally weak competitor (Laird & Schamp
83 2006, Rojas-Echenique & Allesina 2010).

84 Intransitivity can emerge and allow species coexistence via different
85 mechanisms. Niche differentiation can generate intransitivity if species compete for the
86 same nutrients but have differential competitive abilities depending on their balance
87 (e.g., N/P ratios) or on the presence of a third species (e.g., Huisman *et al.* 2001; Borer
88 *et al.* 2007). Such intransitivity can be enhanced by temporal resource heterogeneity
89 and/or spatial heterogeneity among different interaction neighborhoods (Allesina &
90 Levine 2011). Alternatively, intransitivity may arise if the hierarchy in species' ability
91 to exploit resources differs from their ability to prevent resource uptake by others (Buss
92 1980; Laird & Schamp 2006). Intransitive competition networks may be common in
93 nature, although studies empirically demonstrating them have generally focused on
94 species-poor assemblages of, e.g., bacteria (Kerr *et al.* 2002), lizards (Sinervo & Lively
95 1996), or intertidal organisms (Buss 1980).

96 Mathematical models have provided further insights into the underlying
97 mechanisms and ecological implications of intransitive competition networks (Gilpin
98 1975; Laird & Schamp 2006; Allesina & Levine 2011). However, modelling studies
99 alone cannot reveal how frequent intransitivity is or how many species in natural
100 communities are maintained by it. Indeed, the role of intransitive competition in
101 structuring plant communities remains unclear despite years of research devoted to
102 answering this question. Some studies have found that intransitivity is an important
103 mechanism structuring plant communities (e.g., Freckleton *et al.* 2000), but others have
104 suggested the opposite (e.g., Grace *et al.* 1993). A potential explanation for these
105 contrasting results is that the degree of intransitivity depends on the species pool
106 considered. As with many measures of community organization, considering an overall
107 metric for all species in the community can render very different results than more
108 detailed analyses of a particular subset of species (e.g., Stone & Roberts 1992; Ulrich &
109 Gotelli 2007). Similarly, if competition is intransitive amongst dominant or amongst
110 rare species, but strongly hierarchical (i.e., transitive) between such groups,
111 communities would be organized by nested intransitive networks. Such nestedness
112 could increase coexistence, but would result in no overall signal of intransitivity for the
113 whole community. To test this idea field assessments quantifying intransitivity for
114 different groups of species within a community are necessary.

115 The degree of intransitivity in plant communities might also be altered by two
116 of the major global change drivers (GCDs hereafter) threatening biodiversity in
117 terrestrial ecosystems: land-use intensification and climate change (Sala *et al.* 2000).
118 Both GCDs alter heterogeneity and productivity, which in turn are likely to affect
119 intransitive competition networks. Intransitivity might be more common and important
120 for coexistence in productive environments, because environmental filtering is relaxed

121 and competition may be more important than disturbance or abiotic stress in structuring
122 communities (e.g., Gilpin 1975; Bowker *et al.* 2010). Productivity increases with
123 fertilization (Suding *et al.* 2005; Manning 2013), which would suggest more
124 intransitivity at higher land-use intensity. Modelling and empirical evidence suggest
125 that intransitive competition is more likely to occur in heterogeneous environments
126 (Huisman *et al.* 2001). In these cases, niche specialization coupled with different
127 limiting resources across local interaction neighbourhoods can generate, or interact
128 with, intransitive competition enhancing species coexistence (Allesina & Levine 2011).
129 In this regard, GCDs can modify the level of intransitivity in a community by altering
130 not only the spatial, but also the temporal heterogeneity in resources. High land-use
131 intensity (fertilization or overgrazing) can reduce variation in biomass over time (Osem
132 *et al.* 2002; Grman *et al.* 2010), suggesting that temporal heterogeneity is reduced at
133 high land use intensity. On the other hand, climate change could increase temporal
134 heterogeneity, especially in drylands, where water availability is often more variable in
135 drier than wetter environments (Whitford 2002). The well-known negative effects of
136 GCDs on diversity may therefore be buffered or enhanced depending on their indirect
137 effects on the degree of intransitivity (Fig. 1). However, the interrelationship between
138 GCDs and the competitive hierarchy amongst coexisting species is poorly understood.

139 To address these research gaps we used a recently developed method to measure
140 the degree of intransitivity from observational data (Ulrich *et al.* 2014a) using two large
141 datasets describing plant diversity responses to changes in land use or aridity. We tested
142 the following hypotheses: i) intransitive competition is frequent in plant communities,
143 ii) intransitive networks are more common amongst species similar in dominance, but
144 transitive competition (i.e., strong hierarchy among competitors) prevails between
145 species with contrasting dominance levels (i.e., intransitive competition networks are

146 nested), iii) the degree of intransitivity in plant communities is positively related to their
147 species richness, and iv) increases in intransitivity in response to more temporally
148 heterogeneous or fertile environments mitigate the impact of increasing aridity and
149 intensive land uses on plant richness.

150

151 **MATERIALS AND METHODS**

152 **Study sites**

153 We used two large-scale datasets: the occurrence of plant species in European
154 grasslands along land-use intensity gradients (the German Biodiversity Exploratories;
155 Fischer *et al.*, 2010), and the occurrence of plant species along aridity gradients in
156 global dryland ecosystems (the BIOCOM project; Maestre *et al.*, 2012). These two
157 datasets complement each other and allow us to assess the overall frequency and drivers
158 of intransitivity across a wide range of communities varying in habitat type, species
159 pool and environmental conditions as well as across datasets with different sampling
160 methods (see details below).

161 The Biodiversity Exploratories include 1500 grassland plots, varying in land use
162 and situated in three regions of Germany (Fischer *et al.*, 2010; Blüthgen *et al.* 2012;
163 Socher *et al.* 2013). In each of these 4 m × 4 m grassland plots, the relative cover of all
164 plant species was recorded. In the center of each plot, a 10 cm-depth soil sample was
165 taken to measure total soil nitrogen and soil organic carbon concentrations (Fischer *et*
166 *al.* 2010). Information on land use was obtained via questionnaires sent to land owners;
167 these asked about grazing type (permanent, rotational, none), livestock type (sheep,
168 cattle or other), fertilization (fertilized or unfertilized), mowing (number of cuts per
169 year), and the presence of water drainage or water retention structures (see Fischer *et*
170 *al.*, 2010; Blüthgen *et al.* 2012 for full methodological details). This classification

171 resulted in 40 different levels of land-use intensity and management types. Hereafter,
172 we refer to this dataset as “grasslands”.

173 Data from the BIOCOM project were gathered in 224 dryland sites (all with
174 aridity index values [precipitation/potential evapotranspiration] < 0.65) scattered across
175 all continents except Antarctica. These sites include a variety of habitat types
176 (grasslands, shrublands and open woodlands). In each habitat type, the sites were placed
177 spanning a natural gradient of aridity (full details in Maestre *et al.* 2012). At each site
178 plant species and their relative cover were recorded in four 30m-long quadrats, divided
179 into 80 1.5 m × 1.5 m quadrats. Climatic variables were extracted from the WorldClim
180 database (Hijmans *et al.* 2005), and were used to derive an aridity index
181 (precipitation/potential evapotranspiration). To ease interpretation, we use the
182 complement of the aridity index (1-aridity index) so that higher levels of this metric
183 indicate drier environments (Delgado-Baquerizo *et al.* 2013). Hereafter, we refer to this
184 dataset as “drylands”.

185

186 **Data organization and measurement of the degree of intransitivity**

187 We measured the degree of intransitivity in the grassland and dryland datasets by using
188 the Markov chain approach of Ulrich *et al.* (2014a). Under the assumption that observed
189 species abundances represent the equilibrium abundances of the species forming the
190 community, the method allows us to assess 1) to what degree competition predicts
191 observed species abundances, and 2) the degree of intransitivity within a given
192 competition network. As a measure of species abundances, we used the cover of each
193 species within each quadrat (drylands) or plot within a cluster (grasslands; see how
194 clusters were assembled below). Thus a single metric of intransitivity was calculated by
195 each site (drylands) or cluster (grasslands). At equilibrium, observed species

196 abundances should be equal to the dominant eigenvector of a hypothetical species \times
 197 species transition matrix (i.e., the matrix that contains the probability that one species
 198 replaces another in a given quadrat [drylands] or plot [grasslands]); as used in Markov
 199 chain models. 100,000 patch-transition species by species matrices are randomly
 200 generated, of which the 100 best fitting ones (i.e. matrices where the dominant
 201 eigenvector is closest to the observed species abundances) are chosen. The match (R^2)
 202 between simulated and observed abundances informs about the importance of
 203 competition, with higher values meaning higher importance of competition for
 204 community assembly. We used for further analyses those sites or clusters with match
 205 levels (R^2) > 0.60, as their metrics of intransitivity are reliable. Results using a higher
 206 threshold (R^2 > 0.70) were qualitatively similar to those presented here and are not
 207 shown.

208 If competition is fully transitive then one species will always have a higher
 209 probability of displacing the rest (represented as high transition coefficients between
 210 species in the matrix columns vs those in the matrix rows; Fig. 1). If however, there are
 211 competitive reversals (species in the rows displace species in the columns, blue numbers
 212 in Fig. 1) then this indicates intransitivity. The degree of intransitivity can be measured
 213 as the number of competitive reversals found in the best-fitting matrices (see also Laird
 214 & Schamp 2006). Our intransitivity metric (I) is the normalized count of these
 215 competitive reversals in the patch-transition matrix (equation 1; Ulrich *et al.* 2014a):

$$216 \quad I = 1 - \tau_P = \frac{2N(p_{ij} < p_{kj})}{m(m-1)(m-2)} \quad (i < k \text{ and } i, k \neq j) \quad (1)$$

217 where p_{ij} is the probability that species i (in the column) replaces species j (in the row)
 218 in a given patch; j ranges from 1 to m (total number of species), i from m to $m-1$, and k
 219 from $i+1$ to m . Increasing values of I indicate higher levels of intransitivity within the

220 community. Our metric (I), therefore, ranges from 1 (fully intransitive community) to 0
221 (fully transitive community; Fig. 1).

222 Although spatial heterogeneity between local neighbourhoods may enhance
223 intransitive competition by providing more opportunities for niche differentiation, it
224 may also complicate its measurement and make competition ranks more difficult to
225 estimate from the observed abundances (e.g., Ulrich *et al.* 2014a). Thus, for our method
226 to yield reliable results, quadrats within a given site (drylands) or plots within a given
227 cluster (grasslands) should be as homogeneous as possible. To meet this requirement,
228 and according to their different structure, the two datasets were organized differently
229 (henceforth we refer to them as grassland clusters and dryland sites). As the grasslands
230 dataset lacked within-plot replication, we organized the 1500 plots into 190 plot clusters
231 with the same land-use type and region to have enough replication to calculate I . The
232 high number of species found in the grasslands (318–365, depending on the region;
233 Socher *et al.* 2013) made it impossible to produce clusters of plots which were relatively
234 homogenous in their environmental conditions and contained a sufficient number of
235 plots to analyze all possible interactions between species pairs. Therefore, we only
236 considered the five dominant species within each cluster and divided the dataset in
237 clusters of ~ 6–10 plots (always greater than 5, the number of species considered).
238 When 12 or more plots were found within the same land-use type and region, we
239 divided them into two clusters according to total soil nitrogen and organic carbon
240 concentrations to create the most environmentally homogeneous, and the highest
241 number, of clusters possible.

242 To allow comparison between both datasets, we also considered the five
243 dominant species within each site in drylands. Using this database we assessed changes
244 in our intransitivity metric as a function of the number of species considered,

245 progressively including a larger number of subordinate species. This allowed us to
246 determine if the probability of detecting intransitive competition varied depending on
247 the target species pool, and therefore if intransitive competition networks were nested
248 (present only amongst the dominant species) or not (see full results in Appendix S1).

249 The methodology used here has three important assumptions to which our results
250 are reasonably robust. First, it assumes that the sampled communities are at equilibrium.
251 The high match between observed and predicted abundances (see results), and the
252 consistency of match levels across all land-use intensities (Appendix S2) suggest that
253 violations of this assumption have not affected the results. Second, we assume that
254 species are not dispersal limited within our sites or clusters. Dispersal limitation is
255 unlikely because the selected species are abundant across the three regions (grasslands;
256 see also Appendix S3), and sampling quadrats were close to each other (drylands).
257 Third, we assumed our sites to be environmentally homogeneous. To further determine
258 that environmental variation between sites did not drive intransitivity measures, we
259 recalculated intransitivity whilst correcting for environmental conditions and this led to
260 similar values (see Appendix S2).

261 Separating intransitive competition from other processes enhancing coexistence
262 is difficult from observational, or even manipulative, studies. The main distinguishing
263 characteristic between these mechanisms is that intransitivity relies on strong
264 competition, i.e., it reduces co-occurrence of plant species within local interaction
265 neighbourhoods (i.e., quadrat [drylands] or plot [grasslands] scale; Laird & Schamp
266 2006). The latter should lead to segregation of species between sampling quadrats.
267 Those coexistence mechanisms relying on reduced competition (e.g., differential
268 resource uptake), instead, should allow co-occurrence of different plant species at the
269 local interaction neighbourhood scale. When applied to the matrices of the drylands

270 dataset, our intransitivity metric was positively correlated with the level of species
271 spatial segregation between quadrats (Spearman's $\rho = 0.59$; Appendix S4). These
272 results suggest that a high level of competitive exclusion within these local interaction
273 neighbourhoods took place in the studied plots, and thus a strong confounding effect of
274 other local-scale coexistence mechanisms that reduce competition in our results is
275 unlikely.

276

277 **Statistical analyses**

278 *-Extent of intransitive competition in nature and its relationship with species richness*

279 We evaluated whether average values of our intransitivity metric (I) differed from 0.05
280 (indicating fully transitive communities) by using Wilcoxon's matched pairs test. The
281 threshold of 0.05 was obtained from simulated matrices; those with intransitive loops
282 always had predicted values of $I > 0.05$, whereas the 95% confidence limits of I in test
283 matrices with no intransitivity always included the value of 0 (Ulrich *et al.* 2014a).
284 Separate tests were performed to assess whether or not metrics calculated for each
285 dataset (clusters in grasslands or sites in drylands) differed from this threshold. To
286 compare the level of intransitivity between the two datasets, we used Mann-Whitney
287 rank tests because the data departed from a normal distribution. The relationship
288 between intransitivity and species richness was evaluated by performing OLS model II
289 regressions using the `lmodel2` package (Legendre 2008) for R version 3.0.2 (R
290 Development Core Team 2013). Wilcoxon and Mann-Whitney rank tests were
291 conducted with SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA).

292

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294

295 - *Relationship between intransitivity, global change drivers and diversity*

296 We used structural equation modeling (SEM; Grace 2006) to analyze the relationships
297 between land use (grasslands) or aridity (drylands), intransitivity and species richness.
298 Our *a priori* model followed the rationale stated in the introduction (see also Fig. 1):
299 aridity and land use affect both species richness and intransitivity, and intransitivity
300 affects species richness (see Appendix S5 for full details and rationale). Both datasets
301 have strong spatial clustering (sites were sampled within regions in the grasslands and
302 within countries in the drylands). To account for this, we introduced the geographic
303 coordinates in the SEMs. Latitude sufficed to represent the spatial distribution of the
304 grassland dataset (the three regions were distributed along a North-South axis) whereas
305 both latitude and longitude were necessary to represent the spatial distribution of the
306 dryland sites, which were globally distributed.

307 The different land-use categories (grazing and livestock types, number of cuts
308 per year, fertilization or water management) from the grasslands dataset were simplified
309 with a non-metric multidimensional scaling (NMDS), which can handle categorical and
310 continuous variables (McCune & Grace 2002). A two-dimensional NMDS solution was
311 sufficient to represent the data. High values along axis 1 indicated the more intense
312 land-use practices of water drainage and permanent grazing (rather than rotational
313 grazing). High values along axis 2 were associated with grazing by livestock other than
314 sheep (mostly cattle, which have a larger impact in terms of biomass removal and plant
315 diversity than sheep; Blüthgen *et al.* 2012; Socher *et al.* 2013) and more frequent
316 mowing (axis 2; details in Appendix S5).

317 An additional set of analyses were performed as an alternative to data reduction
318 with NMDS in the grasslands dataset. Land-use factors could vary in their effects (e.g.,
319 grazing vs. fertilization) and also in their effect within regions (Socher *et al.* 2013).

320 Thus, separate SEMs using grazing, fertilization, number of cuts and water management
321 as different land-use predictors were performed, and the same *a priori* model structure
322 was used to analyze each region separately (details and results in Appendix S6). SEM
323 analyses were performed using AMOS for windows (SPSS Inc., Chicago, IL, USA).

324

325 **RESULTS**

326 **Extent of intransitive competition in nature and its relationship with species**

327 **richness**

328 Intransitive competition networks (those in which $I > 0.05$) were detected at most study
329 sites (Wilcoxon's test: $z < -8.9$; $P < 0.001$; $N > 150$ in both datasets; Fig. 2). The
330 simulated matrices satisfactorily reflected observed abundances in 92% of the grassland
331 and 78% of the dryland sites ($R^2 \geq 0.70$ in both cases, although these percentages were
332 smaller when including environmental variables; Appendix S2). Although the average
333 degree of intransitivity did not change across the two datasets (Fig. 2), the frequency of
334 sites displaying some degree of intransitivity did: 82% of grassland clusters had I values
335 higher than 0.05, while this was the case in 68% of the dryland sites.

336 Furthermore, the strength of intransitivity (I value) was positively related to
337 plant richness in both datasets (Fig. 3). The presence of intransitivity increased species
338 richness by 6 species in the grasslands and by 4 in the drylands, based on comparing the
339 lowest ($I < 0.05$) and highest ($0.4 < I < 0.8$) levels of intransitivity within the studied
340 communities (Fig. 3). Although the overall relationship between intransitivity and
341 richness was consistent across datasets (Fig. 3), within both datasets the level of
342 intransitivity and its relationship with richness varied geographically. The degree of
343 intransitivity decreased with increasing latitude in both grasslands and drylands (Fig. 4).
344 Intransitivity-richness relationships were either positive (Central), neutral (North-east)

345 or negative (South-west) depending on the grassland region considered (Fig. 3A;
346 Appendix S6).

347 We found an exponential decay in I values as more subordinate species were
348 considered in our calculations (Appendix S1). This suggests strong nestedness of
349 intransitive networks caused by high intransitivity amongst the dominant species, and
350 strong competitive exclusion of rarer species by dominant ones. It must be noted that
351 the positive relationship between intransitivity and species richness remained
352 consistently positive regardless of the number of species considered (Appendix S1).

353

354 **Effects of global change drivers on intransitivity and diversity**

355 Land-use intensification and aridity reduced species richness, but had contrasting effects
356 on intransitivity (Fig. 4). Aridity increased intransitivity in dryland communities (Fig.
357 4B), and this indirectly ameliorated the negative effects of aridity on species richness. In
358 contrast, increasing land-use intensification reduced intransitivity, and this slightly
359 enhanced the direct negative effects of land-use intensity on diversity. More detailed
360 analysis of the land-use effects revealed that both fertilization and mowing decreased
361 species richness and the degree of intransitivity (Table 1). Increased grazing intensity
362 had a similar effect: switching from rotational to permanent grazing, or from sheep to
363 cattle grazing, substantially reduced species richness and intransitivity. Nevertheless, a
364 clear result was that the intransitivity-mediated effect of land use intensification on
365 species richness was much weaker and variable than its direct negative effects (Table 1).

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369

370 **DISCUSSION**

371 **Extent of intransitive competition networks in natural plant communities**

372 Intransitive competition networks have previously only been demonstrated in simple
373 three-species systems (e.g., Buss 1980; Sinervo & Lively 1996; Kerr *et al.* 2002) and in
374 mathematical models (Gilpin 1975; Wootton 2001; Laird & Schamp 2006; Allesina &
375 Levine 2011). To date there has been little empirical evidence to suggest that they are
376 widespread in nature (but see Bowker *et al.* 2010; Allesina & Levine 2011; Soliveres *et*
377 *al.* 2011). Using field data from two large datasets and a novel methodology, we
378 provide strong evidence that intransitive competition networks are both common in
379 natural plant communities and are associated with higher species richness. This general
380 pattern was robust and not influenced by the biome, sampling methodology or spatial
381 scale considered.

382 Previous studies assessing the degree of intransitivity in plant communities have
383 generated contrasting results and substantial debate (Aarsen 1988; Keddy & Shipley
384 1989; Silvertown & Dale 1991; Grace *et al.* 1993; Freckleton *et al.* 2000). Generally,
385 these studies concluded that intransitivity is uncommon in plant communities and,
386 therefore, sharply contrast with our results (Grace *et al.* 1993; but see Aarsen 1988;
387 Freckleton *et al.* 2000; Allesina & Levine 2011). This contrast may be explained by the
388 differences in the methodology used and the species pool considered. Pairwise
389 competition experiments are often performed in the greenhouse, and do not consider
390 multispecies assemblages or the context-dependency of competition under natural and
391 changing environments (Herben & Krahulec 1990; Silvertown & Dale 1991;
392 Chamberlain *et al.* 2014). Thus, the pairwise approach to estimating competition could
393 underestimate the occurrence of intransitive loops (Grace *et al.* 1993; Laird & Schamp
394 2008; Allesina & Levine 2011). Indeed, competitive hierarchies identified using

395 pairwise approaches fail to predict observed abundances in the field (Aarsen 1989;
396 Weigelt *et al.* 2007; Engel & Wetzin 2008). In contrast, the patch-transition matrices
397 used here implicitly account for competition under natural conditions and in multiple
398 species assemblages (Ulrich *et al.* 2014a and references therein), and thus provide a
399 truer reflection (according to the high match levels found between simulated and
400 observed data) of competitive hierarchies and more accurate assessments of
401 intransitivity in natural communities.

402 Regarding the role of the species pool when estimating intransitivity, and in
403 agreement with our second hypothesis, we found strong nestedness in intransitive
404 competition networks. Our results suggest high levels of intransitivity among the
405 dominant species, but not between dominant and rare species (Appendix S1). Studies
406 focusing on dominant species will, therefore, likely find high levels of intransitivity
407 (e.g., Freckleton *et al.* 2000), whereas those including broader species pools will likely
408 find the opposite pattern. While these contradictory results have fueled strong debate
409 (e.g., Aarsen 1988; Grace *et al.* 1993), only by analyzing real-world data were we able
410 to cast some light on the potential explanation for these contradictions. Our nestedness
411 hypothesis requires experimental confirmation, but it suggests that coexistence of
412 similarly abundant (or co-dominant) species could be promoted by nested intransitive
413 competition networks.

414

415 **The relationship between intransitivity and species richness**

416 Our study is, to the best of our knowledge, the first to empirically show a positive
417 relationship between the strength of intransitivity and species richness in natural
418 communities, thus supporting previous mathematical and conceptual models (Huisman
419 *et al.* 2001; Laird & Schamp 2006; Wootton 2001; Rojas-Echenique & Allesina 2010).

420 This relationship suggests that the degree of intransitivity among the dominant species
421 alone could explain 4–9% of the variance observed in plant species richness, which,
422 given the wide range of environmental conditions, habitats and sampling procedures in
423 our study, suggests that intransitivity is an important driver of species richness. We also
424 find that intransitive competition boosted species richness considerably (Fig. 3). Future
425 work is needed to fully integrate intransitive competition with coexistence theory
426 (Chesson 2000; HilleRisLambers *et al.* 2012) and to determine whether intransitive
427 loops equalize fitness between species (e.g., Laird & Schamp 2006) and/or stabilize
428 niche differences (Rojas-Echenique & Allesina 2010). However, these first empirical
429 results on the relationship between intransitivity and diversity suggest that it may be an
430 important, but largely overlooked, coexistence mechanism. Our results also suggest that
431 incorporating multi-species (rather than multiple pairwise) competition dynamics and
432 nested competition networks, which have been largely neglected before, can contribute
433 explaining species coexistence. More studies are needed to confirm whether the patterns
434 we find are consistent across ecosystem types and different groups of organisms; our
435 results and the methodology employed (Ulrich *et al.* 2014a) pave the way for such
436 future research.

437

438 **Effects of global change drivers on intransitivity and diversity**

439 Could an increase in intransitivity offset the negative effects of global change drivers
440 (GCDs) on diversity? This would require three conditions: i) GCDs (here, aridity or
441 land-use intensity) directly decrease richness, ii) intransitivity increases richness, and
442 iii) GCDs increase intransitivity. While i) and ii) were supported by our results, we
443 found that iii) was largely dependent on the GCD studied (Table 1).

444 We speculate that the contrasting effects of aridity and land-use intensity on
445 intransitivity are related to their different effects on temporal heterogeneity. We
446 minimized the role of spatial heterogeneity on our intransitivity metric. Thus, although
447 spatial heterogeneity across local interaction neighbourhoods would normally be an
448 important driver of intransitivity and plant coexistence (Huisman *et al.* 2001; Sears &
449 Chesson 2007; Allesina & Levine 2011), it should not affect intransitivity here.
450 However temporal heterogeneity is still expected to increase opportunities for
451 intransitivity. Temporal heterogeneity could enhance intransitivity in competition
452 networks through temporal storage effects (Chesson 1983) as a given species will
453 experience higher intra- than inter-specific competition during favorable time periods
454 and this may hinder its ability to compete with others, enhancing the chances to form
455 intransitive competition loops. It may also provide more opportunities for niche
456 differentiation, where slightly different environmental conditions across time can
457 generate different competition hierarchies and therefore enhance community-level
458 intransitivity and allow coexistence (Allesina & Levine 2011). In this regard, aridity is
459 known to increase temporal heterogeneity in water availability (e.g., Whitford 2002)
460 which might explain the more pronounced effects of intransitivity in drylands. Land-use
461 intensification (grazing and fertilization) instead, reduces temporal heterogeneity in
462 biomass (Osem *et al.* 2002; Grman *et al.* 2010) and also asynchrony of species
463 fluctuations in diverse communities (Hautier *et al.* 2014). Additionally, both grazing
464 and mowing can compromise potential trade-offs between competition abilities (e.g.,
465 those between resource uptake and pollinator attraction) and reduce the chances for
466 intransitive competition (Aarsen 1992). Overall, more intensive land uses can reduce
467 temporal niche dimensionality (similarly as it does with spatial niche dimensionality;
468 Harpole & Tilman 2007) and therefore shifts in competition hierarchy across time,

469 preventing intransitive competition. This may explain why increasing temporal
470 heterogeneity in land use has been shown to increase diversity (Allan *et al.* 2014) as it
471 might also increase intransitivity and other coexistence mechanisms. Overall, our results
472 point to another means by which GCDs alter competition between plants (see Tilman &
473 Lehman 2001 for a review) and suggest that the effects of such GCDs depend on how
474 they impact upon the temporal heterogeneity of resources. The unique nature of our data
475 also allowed us to shed some light on other drivers of intransitivity within natural
476 communities, which have been largely overlooked by previous studies and also are
477 likely to be linked to changes in temporal heterogeneity. For example, the strong
478 latitudinal gradient in intransitivity found in the drylands could be due to rainfall
479 variability, which decreases from north to south in the studied sites (Ulrich *et al.*
480 2014b).

481 Our results provide weak support for the notion that intransitive competition
482 networks should prevail in more productive environments (Gilpin 1975; Bowker *et al.*
483 2010). We found a higher frequency of intransitive communities in the more productive
484 grasslands (~81%) than in the drylands (~67%; but see Appendix S2). However,
485 productivity may not positively affect intransitivity at smaller scales: the more heavily
486 fertilized grasslands had lower intransitivity (Table 1), as did those in the northern
487 region in Germany, which is also the most productive (Fischer *et al.* 2010). Thus, it is
488 unlikely that the negative effects of fertilization on diversity (Suding *et al.* 2005; Socher
489 *et al.* 2013) will be counterbalanced by increased intransitivity associated with overall
490 productivity (see Table 1). The latter result might be explained by a shift towards light
491 competition with increased fertility and an increased dominance by some fast-growing
492 species (Tilman & Lehman 2001; Suding *et al.* 2005). This is likely to increase fitness

493 differences between species which would be expected to result in more asymmetric and
494 therefore more transitive competition.

495

496 **Conclusions**

497 We found that intransitive competition networks are widespread in natural plant
498 communities and explained 4-9% of the variance in species richness across a wide
499 variety of habitat-types and environmental conditions. Additionally, different global
500 change drivers had contrasting effects on intransitivity: aridity increased it, while land-
501 use intensification generally reduced intransitivity. These differences are probably
502 explained by their contrasting effects on temporal environmental heterogeneity. Thus,
503 more intransitive competition could partially buffer diversity loss in natural
504 communities, where the drivers of diversity loss increase this heterogeneity, but it is
505 unlikely to buffer diversity loss resulting from environmental homogenization. Finally,
506 we identified two properties of intransitive networks that have been previously
507 overlooked: a strong geographical gradient and a nested structure in intransitive
508 competition networks, both undetectable with previous modelling or local empirical
509 studies. The latter suggests that intransitivity is prevalent between dominant species, but
510 not between dominant and rarer species, and this could explain contrasting results
511 between studies of differing species pool size. Forty years after its inclusion in ecology,
512 we assessed for the first time the extent of intransitive competition in real-world plant
513 communities. Our approach and findings pave the way for wider empirical evaluation of
514 intransitivity in a range of systems, and highlight the links between intransitivity and
515 other well-studied coexistence mechanisms.

516

517

518 **ACKNOWLEDGEMENTS**

519 We thank three anonymous reviewers for comments on a previous version of this
520 manuscript. We thank the managers of the Biodiversity Exploratories, Swen Renner,
521 Sonja Gockel, Kerstin Wiesner, and Martin Gorke for their work in maintaining the plot
522 and project infrastructure; Simone Pfeiffer and Christiane Fischer giving support
523 through the central office, Michael Owonibi for managing the central data base, and
524 Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, François Buscot and the
525 late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project.
526 We thank all the member of the EPES-BIOCOM network for their involvement in data
527 collection. The work has been partly funded by the DFG Priority Program 1374
528 "Infrastructure-Biodiversity-Exploratories" (DFG- FI1246/6-1, DFG-FI1246/9-1) and
529 by the BIOCOM project, funded by the European Research Council under the European
530 Community's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement
531 242658. Field work permits were issued by the responsible state environmental offices
532 of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).
533 WU was supported by the Polish National Science Centre (grant
534 2014/13/B/NZ8/04681).

535

536 **REFERENCES**

537 1.

538 Aarssen, L.W. (1988). 'Pecking order' of four plant species from pastures of different
539 ages. *Oikos*, 51, 3-12.

540 2.

541 Aarssen, L.W. (1992). Causes and consequences of variation in competitive ability in
542 plant communities. *J. Veg. Sci.*, 3, 165-174.

- 543 3.
- 544 Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tschardtke, T., *et al.*
545 (2014). Interannual variation in land-use intensity enhances grassland
546 multidiversity. *Proc. Natl. Acad. Sci. USA*, 111, 308-303.
- 547 4.
- 548 Allesina, S. & Levine, J.M. (2011). A competitive network theory of species diversity. -
549 *Proc. Natl. Acad. Sci. USA*, 108, 5638-5642.
- 550 5.
- 551 Blüthgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Kleinebecker, T., Hölzel, N. *et al.*
552 (2012). A quantitative index of land-use intensity in grasslands: Integrating
553 mowing, grazing and fertilization. *Basic Appl. Ecol*, 13, 207-220.
- 554 6.
- 555 Borer, E.T., Hosseini, P.R., Seabloom, E.W. & Dobson, A.P. (2007). Pathogen-induced
556 reversal of native dominance in a grassland community. *Proc. Natl. Acad. Sci. USA*,
557 104, 5473-5478.
- 558 7.
- 559 Bowker, M.A., Soliveres, S. & Maestre, F.T. (2010). Competition increases with abiotic
560 stress and regulates the diversity of biological soil crusts. *J. Ecol.*, 98, 551-560.
- 561 8.
- 562 Buss, L.W. (1980). Competitive intransitivity and size-frequency distributions of
563 interacting populations. *Proc. Natl. Acad. Sci. USA*, 77, 5355-5359.
- 564 9.
- 565 Chamberlain, S.A., Bronstein, J.L. & Rudgers, J.A. (2014). How context dependent are
566 species interactions? *Ecol. Lett.*, 17, 881–890
- 567 10.

568 Chesson, P. (1983). Coexistence of competitors in a stochastic environment: The
569 storage effect. *Pop. Biol.*, 52, 188-198.

570 11.

571 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol.*
572 *Syst.*, 31, 343-366.

573 12.

574 Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D.,
575 Quero, J.L., *et al.* (2013). Aridity decouples soil C, N and P biogeochemical cycles
576 in global drylands. *Nature*, 502, 672-676.

577 13.

578 Engel, E.C. & Wetzin, J.F. (2008). Can community composition be predicted from
579 pairwise species interactions? *Plant Ecol.*, 195, 77-85.

580 14.

581 Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., *et al.*
582 (2010). Implementing large-scale and long-term functional biodiversity research:
583 The biodiversity exploratories. *Basic Appl. Ecol.*, 11, 473–485.

584 15.

585 Freckleton, R.P., Watkinson, A.R., Dowling, P.M. & Ley, A.R. (2000). Determinants of
586 the abundance of invasive annual weeds: community structure and non-equilibrium
587 dynamics. *Proc. R. Soc. B*, 267, 1153-1161

588 16.

589 Gilpin, M.E. (1975). Limit cycles in competition communities. *Am. Nat.*, 109, 51–60.

590 17.

591 Grace, J.B. (2006). Structural Equation Modeling and Natural Systems. *Cambridge*
592 *Univ. Press.*

- 593 18.
- 594 Grace, J.B., Guntenspergen, G.R. & Keough, J. (1993). The examination of a
595 competition matrix for transitivity and intransitive loops. *Oikos*, 68, 91-98.
- 596 19.
- 597 Grman, E., Lau, J. A., Schoolmaster, D. R. & Gross, K. L. (2010). Mechanisms
598 contributing to stability in ecosystem function depend on the environmental
599 context. *Ecol. Lett.*, 13, 1400-1410.
- 600 20.
- 601 Harpole, W. S. & Tilman, D. (2007). Grassland species loss resulting from reduced
602 niche dimension. *Nature*, 446, 791-793.
- 603 21.
- 604 Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H.,
605 *et al.* (2014). Eutrophication weakens stabilizing effects of diversity in natural
606 grasslands. *Nature*, 508, 521-525.
- 607 22.
- 608 Herben, T. & Krahulec, F. (1990). Competitive hierarchies, reversals of rank order and
609 the de Wit approach: are they compatible? *Oikos*, 58, 254-265.
- 610 23.
- 611 Hijmans, R.J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005). Very high
612 resolution interpolated climate surfaces for global land areas. *Internatl J. Climatol.*,
613 25, 1965-1978.
- 614 24.
- 615 HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M.
616 (2012). Rethinking community assembly through the lens of coexistence theory.
617 *Ann. Rev. Ecol. Evol. Syst.*, 43, 227-248.

- 618 25.
- 619 Huisman, J., Johansson, A.M., Folmer, E.O. & Weissing, F.J. (2001). Towards a
620 solution of the plankton paradox: the importance of physiology and life history.
621 *Ecol. Lett.*, 4: 408–411
- 622 26.
- 623 Keddy, P.A. & Shipley, B. (1989). Competitive hierarchies in herbaceous plant
624 communities. *Oikos*, 54, 234-241.
- 625 27.
- 626 Kerr, B., Riley, M.A., Feldman, M.W. & Bohannan, B.J. (2002). Local dispersal
627 promotes biodiversity in a real-life game of rock–paper–scissors. *Nature*, 418, 171-
628 174.
- 629 28.
- 630 Laird, R.A. & Schamp, B.S. (2006). Competitive intransitivity promotes species co-
631 existence. *Am. Nat.*, 168, 182-193.
- 632 29.
- 633 Laird, R.A. & Schamp, B.S. (2008). Does local competition increase the coexistence of
634 species in intransitive networks? *Ecology*, 89, 237-247.
- 635 30.
- 636 Legendre, P. 2008. lmodel2: Model II Regression. Available: [http://www.cran.r-](http://www.cran.r-project.org)
637 [project.org](http://www.cran.r-project.org)
- 638 31.
- 639 Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo,
640 M., *et al.* (2012). Plant species richness and ecosystem multifunctionality in global
641 drylands. *Science*, 335, 214-218.
- 642 32.

643 Manning, P. (2012). The impact of nitrogen enrichment on ecosystems and their
644 services. In: Wall, D.H. (Ed.). The Oxford handbook of soil ecology and ecosystem
645 services. Oxford University Press, UK
646 33.

647 McCune, B. & Grace, J.B. (2002). Analysis of ecological communities. MjM Software
648 Design.
649 34.

650 Osem, Y., Perevolotsky, A. & Kigel, J. (2002). Grazing effect on diversity of annual
651 plant communities in a semi-arid rangeland: interactions with small-scale spatial
652 and temporal variation in primary productivity. *J. Ecol.*, 90, 936-946.
653 35.

654 Rojas-Echenique, J.R. & Allesina, S. (2011). Interaction rules affect species coexistence
655 in intransitive networks. *Ecology*, 92, 1174-1180.
656 36.

657 Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., et al.
658 (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.
659 37.

660 Sears, A.L.W. & Chesson, P. (2007). New methods for quantifying the spatial storage
661 effect: an illustration with desert annuals. *Ecology* 88, 2240-2247.
662 38.

663 Silvertown, J. & Dale, P. (1991). Competitive hierarchies and the structure of
664 herbaceous plant communities. *Oikos*, 61, 441-444.
665 39.

666 Sinervo, B. & Lively, C.M. (1996). The rock–paper–scissors game and the evolution of
667 alternative male strategies. *Nature*, 380, 240-243.

668 40.

669 Stone, L. & Roberts, A. (1992). Competitive exclusion, or species aggregation?
670 *Oecologia*, 91, 419-424.

671 41.

672 Socher, S.A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., *et al.* (2013).
673 Interacting effects of fertilization, mowing and grazing on plant species diversity of
674 1500 grasslands in Germany differ between regions. *Basic Appl. Ecol.*, 14: 126-
675 136.

676 42.

677 Soliveres, S., Eldridge, D.J., Maestre, F.T., Bowker, M.A., Tighe, M., Escudero, A.
678 (2011). Microhabitat amelioration and reduced competition among understorey
679 plants as drivers of facilitation across environmental gradients: towards a unifying
680 framework. *Persp. Plant Ecol. Evol. Syst.*, 13, 247-258.

681 43.

682 Suding, K.N., Collins, S. L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., *et al.*
683 (2005). Functional- and abundance-based mechanisms explain diversity loss due to
684 N fertilization. *Proc. Natl. Acad. Sci. USA*, 102, 4387-4392.

685 44.

686 Tilman, D. & Lehman, C. (2001). Human-caused environmental change: impacts on
687 plant diversity and evolution. *Proc. Natl. Acad. Sci. USA*, 98, 5433-5440.

688 45.

689 Ulrich, W. & Gotelli, N.J. (2007). Null model analysis of species nestedness patterns.
690 *Ecology*, 88, 1824-1831.

691 46.

692 Ulrich, W., Soliveres, S., Kryszeński, W., Maestre, F.T. & Gotelli, N.J. (2014a). Matrix
693 models for quantifying competitive intransitivity from species abundance data.
694 *Oikos*, 123, 1057–1070.
695 47.

696 Ulrich, W., Soliveres, S., Maestre, F.T., Gotelli, N.J., Quero, J.L., Delgado-Baquerizo,
697 M., *et al.* (2014b). Climate and soil attributes determine plant species turnover in
698 global drylands. *J. Biogeogr.*, doi:10.1111/jbi.12377.
699 48.

700 Weigelt, A., Schumacher, J., Walther, T., Bartelheimer, M., Steinlein, T. & Beyschlag,
701 W. (2007). Identifying mechanisms of competition in multi-species communities. *J.*
702 *Ecology*, 95, 53–64
703 49.

704 Whitford, W.G. (2002). Ecology of desert systems. *Academic Press*, California, USA.
705 50.

706 Wootton, J.T. (2001). Causes of species diversity differences: a comparative analysis of
707 Markov models. *Ecol. Lett.*, 4, 46-56.

708

709

710 **SUPPORTING INFORMATION**

711 Additional Supporting Information may be downloaded via the online version of this
712 article at Wiley Online Library (www.ecologyletters.com).

713 **Table 1.** Summary results of the structural equation models performed with the
714 different environmental factors (in rows) separately. Standardized total effects (STE;
715 sum of direct and indirect effects) and standardized direct effects (SDE; equivalent to
716 the path coefficient from the predictor to the response variable) for richness are shown.
717 For intransitivity STE = SDE. Environmental factors were introduced as: Mowing
718 (number of cuts per year), grazing (sheep/other, permanent/rotational/none) fertilization
719 (yes/no), and water management (drainage/retention/none). Significant path coefficients
720 are highlighted in bold.

	Intransitivity	Richness	
	SDE	SDE	STE
Mowing	-0.16	-0.29	-0.31
Grazing	0.20	0.50	0.51
Fertilization	-0.09	-0.44	-0.45
Water management (only NE region)	0.15	-0.46	-0.45
Aridity	0.20	-0.28	-0.23

721

722 **FIGURE LEGENDS**

723 **Figure 1.** Conceptual model outlining our theoretical framework. We address here the
724 direct and indirect relationships between 1) global change drivers (GCDs), 2)
725 intransitive competition networks and 3) species richness. Intransitivity is expected to
726 increase richness. GCDs are expected to decrease species richness and have variable
727 effects (positive = green, negative = red, unimodal = black) on intransitivity. Species-
728 by-species transition matrices with different levels of intransitivity are shown. These
729 matrices have an associated competition network (arrow pointing from winner to loser)
730 and their changes in abundance across time or space (represented in different columns
731 within the grid boxes). Competitive reversals from perfect hierarchical competition are
732 in blue (numbers and arrows) and the changes expected in our intransitivity metric (I)
733 are shown.

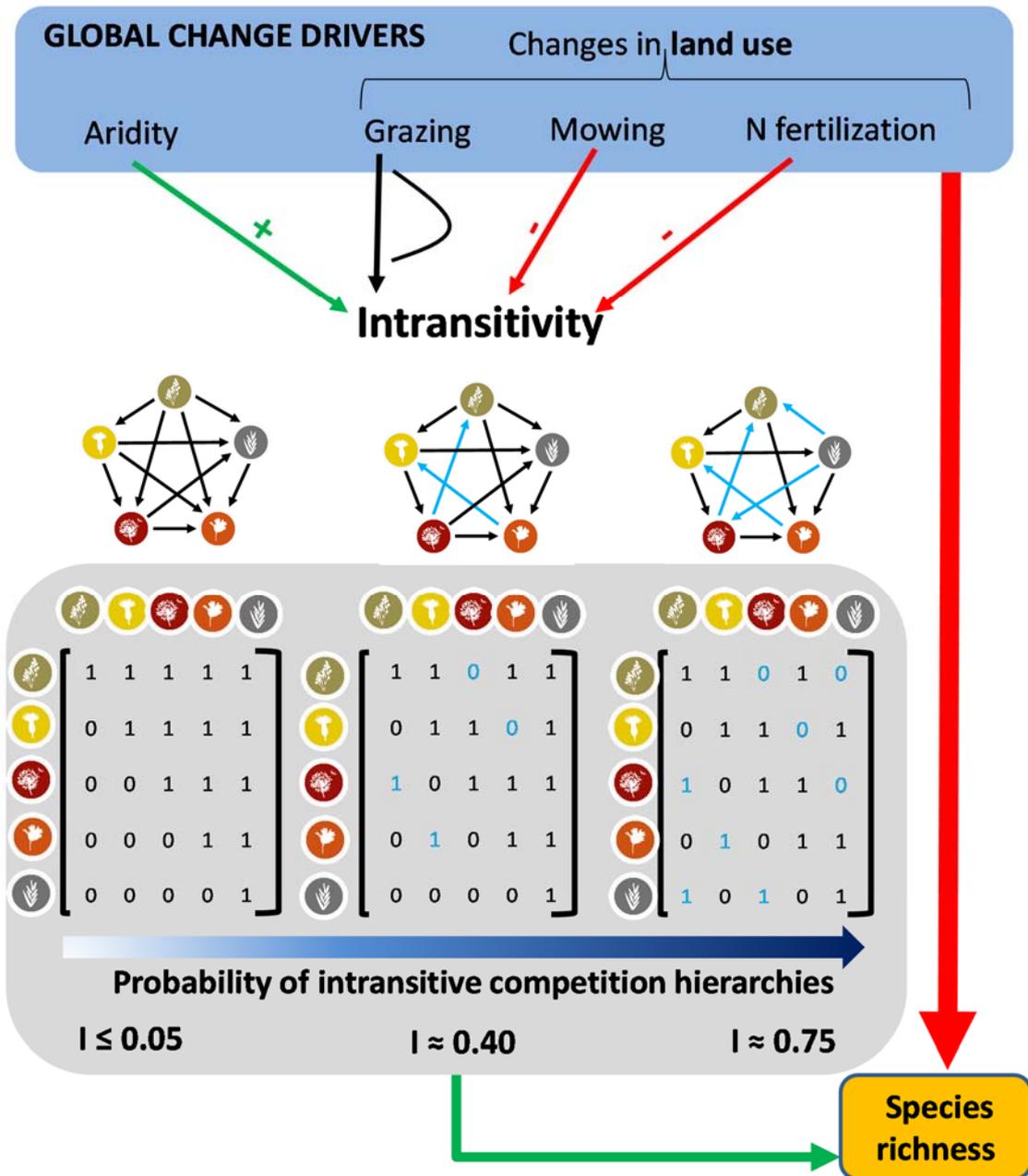
734

735 **Figure 2.** Intransitivity (measured as metric I) observed in grasslands ($n = 175$ clusters
736 of environmentally similar grasslands out of a set of 1500 sites) and drylands ($n = 151$,
737 sites). Box plots show the median, 25% and 75% quartiles. The intransitivity metric was
738 not significantly different between the two datasets (Mann-Whitney's $U = 12030$; $P =$
739 0.16).

740

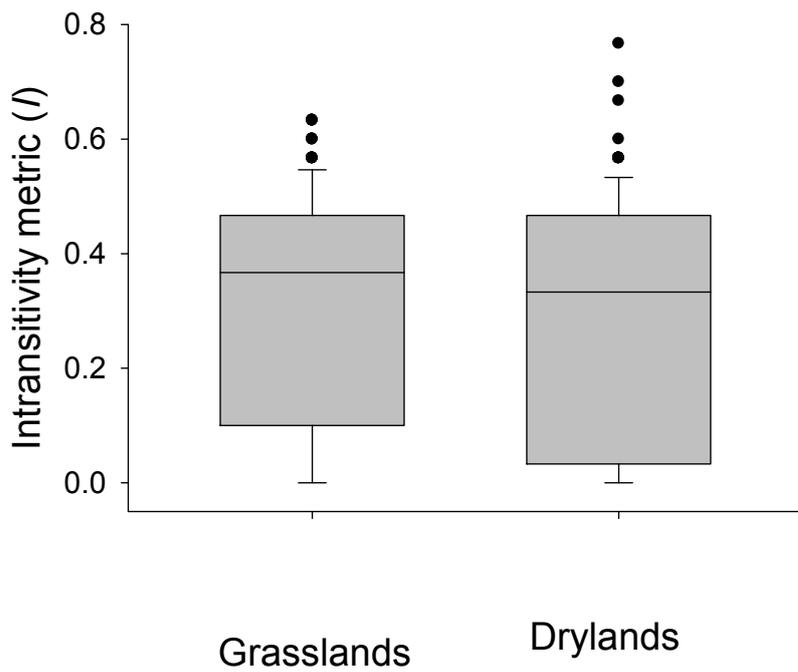
741 **Figure 3.** Relationships between intransitivity (measured as metric I) and species
742 richness in grasslands (A; mean for each cluster of sites) and drylands (B). Model II
743 OLS regression results are shown. The different colors in the upper panel show the three
744 different study regions: Southwest (red, $n = 50$), Central (blue, $n = 54$) and Northeast
745 (green, $n = 71$).

746 **Figure 4.** Structural equation models depicting effects of geographic factors (region or
747 latitude/longitude) and global change drivers (land-use or aridity) on intransitivity and
748 species richness for grasslands (A) and drylands (B). Composite variables are shown
749 with the variables forming them inside. The width of arrows is proportional to the
750 standardized path coefficient, with green and red lines for positive and negative
751 relationships, respectively. The overall goodness-of-fit test and the R^2 for each variable
752 introduced are given. *P*-values are: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ° = P
753 < 0.1. Lat = latitude, lon = longitude, mds= non-metric multi-dimensional ordination
754 axes performed with the land-use variables.
755
756



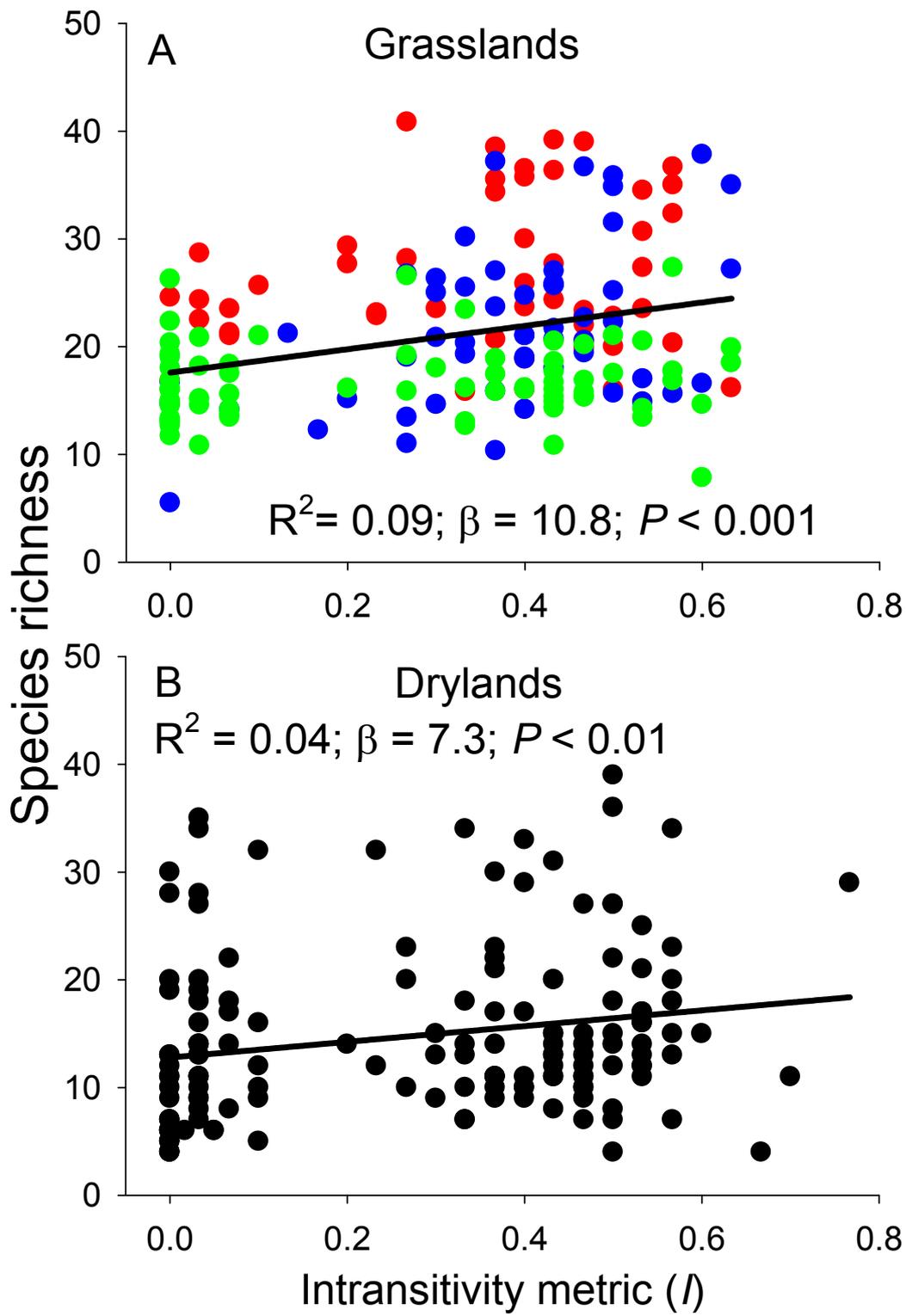
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758 **Figure 1**



759

760 **Figure 2**



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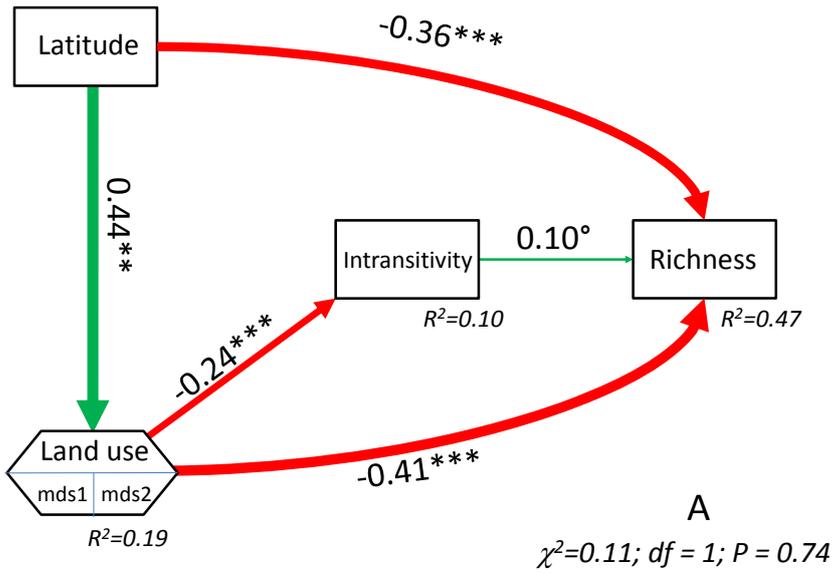
762 **Figure 3**

763

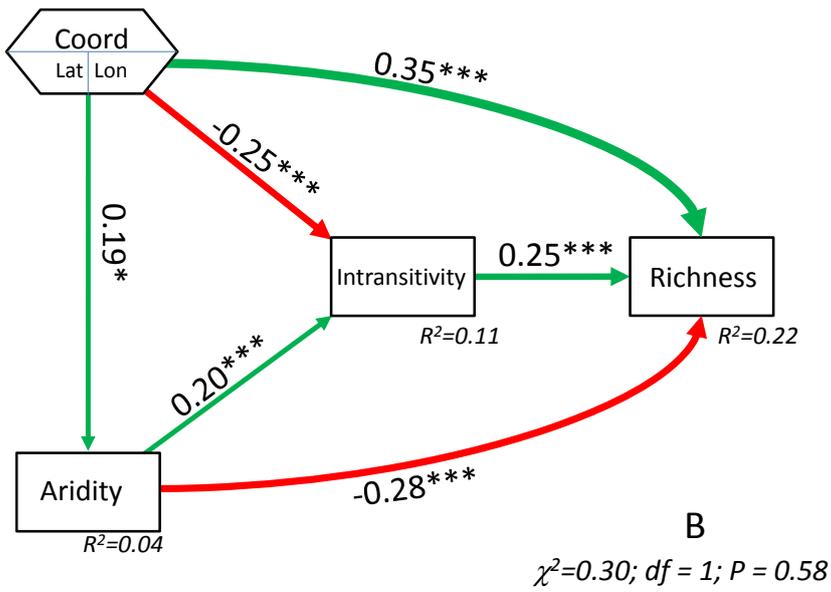
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768

769 **Figure 4**

770 **Supporting Information**

771 **Appendix S1.** Results with the five dominant species vs. other subsets of species within
772 the community for the dryland dataset.

773 **Appendix S2.** Results controlling for environmental variation across sites and other
774 assumptions of the method.

775 **Appendix S3.** Results using the five dominant species within each region instead of
776 cluster in the grassland database.

777 **Appendix S4.** Differentiating between intransitivity and other drivers of the observed
778 patterns.

779 **Appendix S5.** Methodological details of the SEM analyses conducted.

780 **Appendix S6.** Results of the interrelationships between land use, intransitivity and
781 richness for the grassland dataset divided by each region.