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

2 **species richness**

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53

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

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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.

INTRODUCTION

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

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

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

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

293

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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DISCUSSION

Extent of intransitive competition networks in natural plant communities

Intransitive competition networks have previously only been demonstrated in simple

three-species systems (e.g., Buss 1980; Sinervo & Lively 1996; Kerr *et al.* 2002) and in

mathematical models (Gilpin 1975; Wootton 2001; Laird & Schamp 2006; Allesina &

Levine 2011). To date there has been little empirical evidence to suggest that they are

widespread in nature (but see Bowker *et al.* 2010; Allesina & Levine 2011; Soliveres *et*

al. 2011). Using field data from two large datasets and a novel methodology, we

provide strong evidence that intransitive competition networks are both common in

natural plant communities and are associated with higher species richness. This general

pattern was robust and not influenced by the biome, sampling methodology or spatial

scale considered.

Previous studies assessing the degree of intransitivity in plant communities have

generated contrasting results and substantial debate (Aarsen 1988; Keddy & Shipley

1989; Silvertown & Dale 1991; Grace *et al.* 1993; Freckleton *et al.* 2000). Generally,

these studies concluded that intransitivity is uncommon in plant communities and,

therefore, sharply contrast with our results (Grace *et al.* 1993; but see Aarsen 1988;

Freckleton *et al.* 2000; Allesina & Levine 2011). This contrast may be explained by the

differences in the methodology used and the species pool considered. Pairwise

competition experiments are often performed in the greenhouse, and do not consider

multispecies assemblages or the context-dependency of competition under natural and

changing environments (Herben & Krahulec 1990; Silvertown & Dale 1991;

Chamberlain *et al.* 2014). Thus, the pairwise approach to estimating competition could

underestimate the occurrence of intransitive loops (Grace *et al.* 1993; Laird & Schamp

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

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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

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)
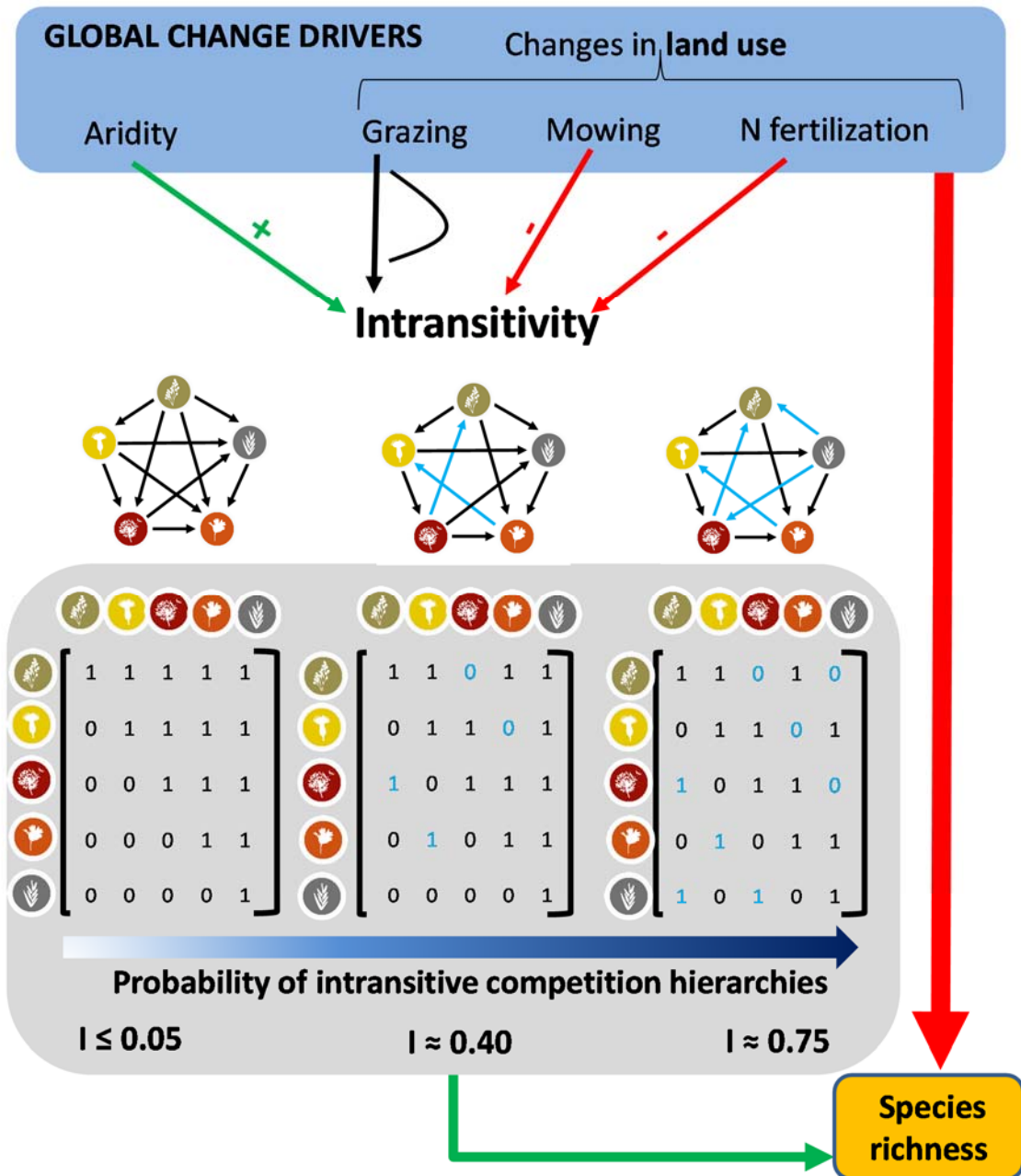
733 are shown.

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; $P =$
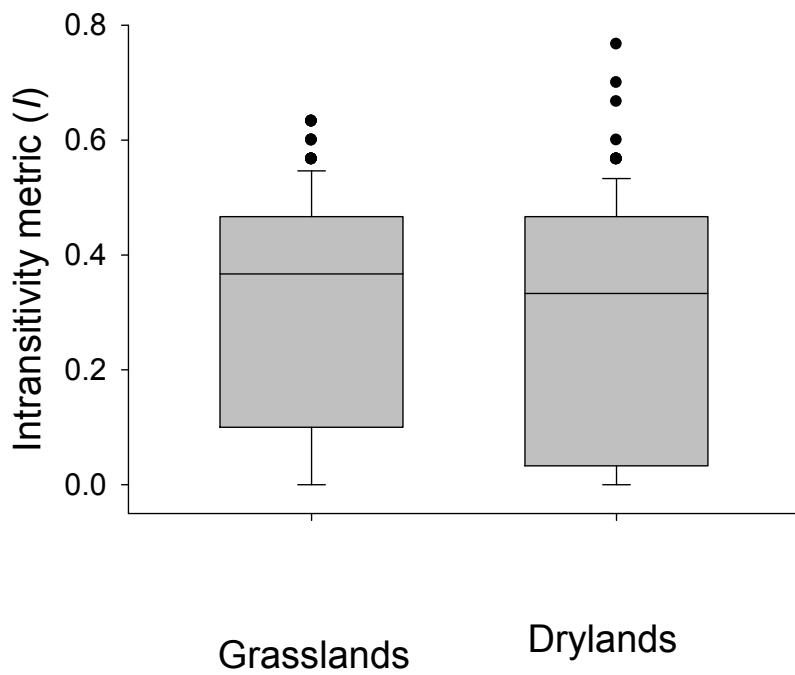
739 0.16).

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: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; º = *P*

753   < 0.1. Lat = latitude, lon = longitude, mds= non-metric multi-dimensional ordination

754   axes performed with the land-use variables.
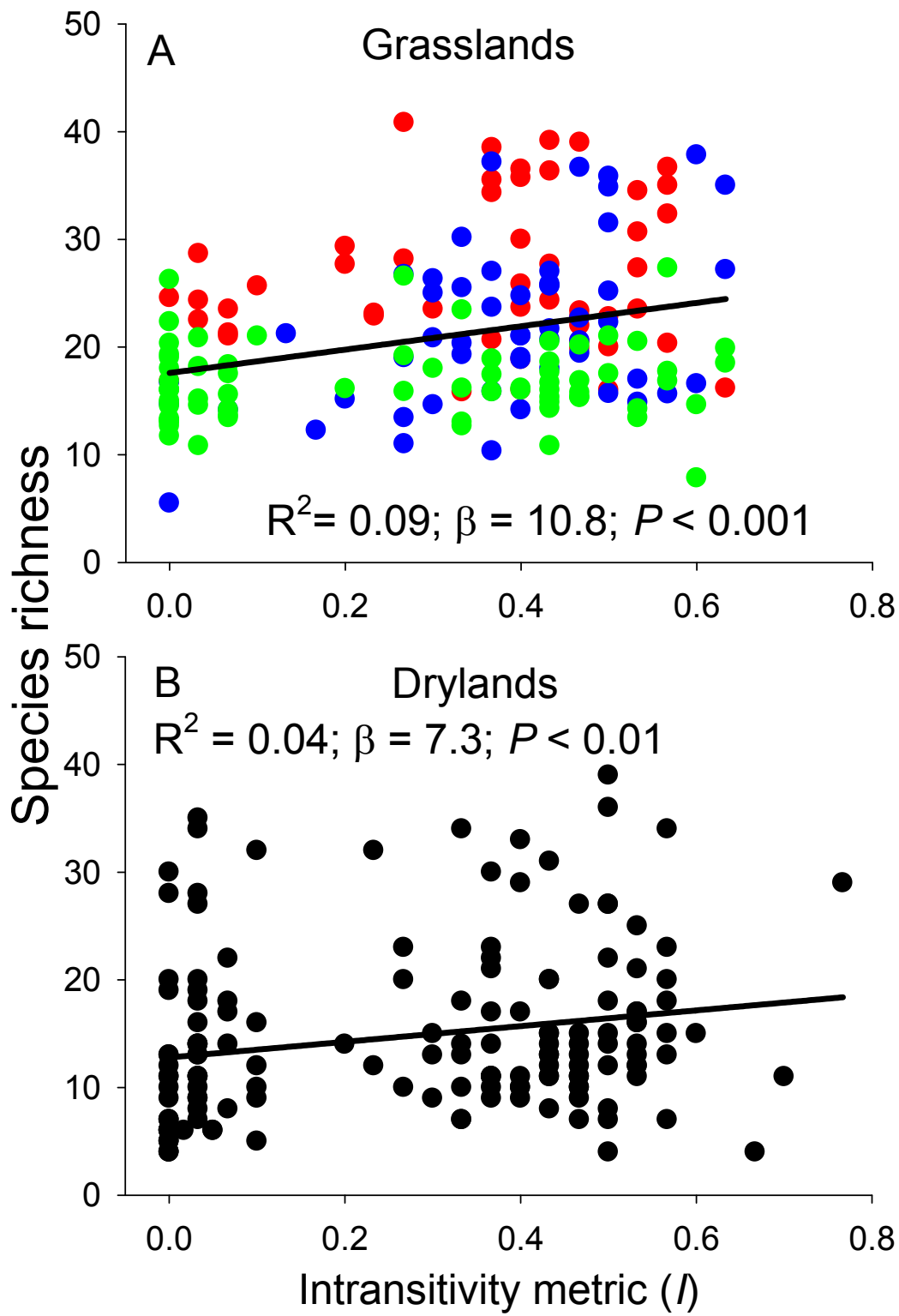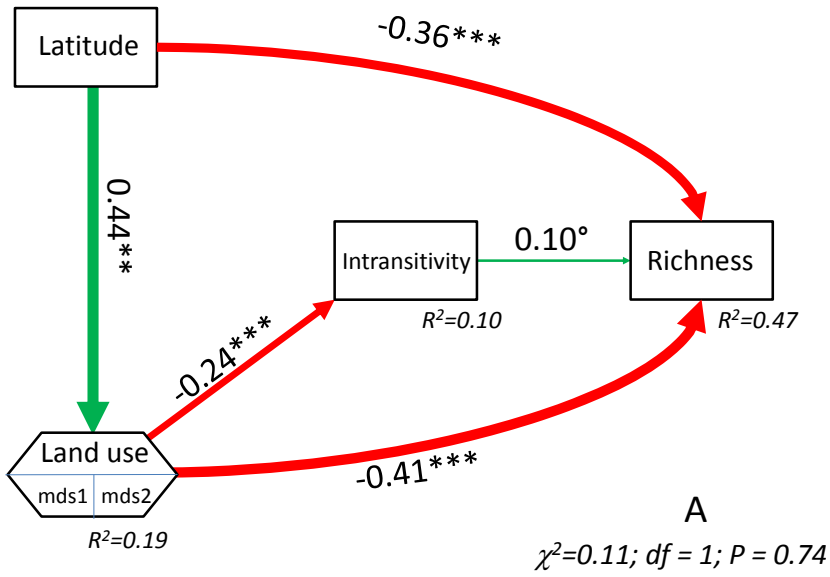
755

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757

758 **Figure 1**

759

760 **Figure 2**

Species richness

$R^2 = 0.09$; $\beta = 10.8$; $P < 0.001$

$R^2 = 0.04$; $\beta = 7.3$; $P < 0.01$

Intransitivity metric (I)

761

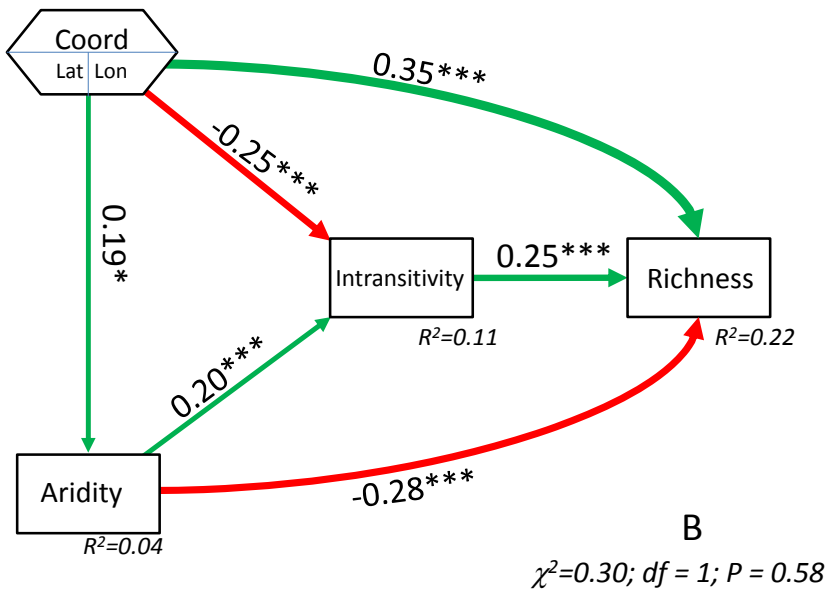**Figure 3**

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Figure 4

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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.