

LETTER

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

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Abstract

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

Keywords

Aridity, biodiversity, coexistence, drylands, land use, mesic grasslands, rock-paper-scissors game.

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INTRODUCTION

Species coexistence is made possible by a range of mechanisms including differential resource uptake, frequency-dependent enemy attack or limited dispersal (Chesson 2000; HilleRis-Lambers *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 to coexist 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 2011).

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 neighbourhoods (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).

Mathematical models have provided further insights into the underlying mechanisms and ecological implications of intransitive competition networks (Gilpin 1975; Laird & Schamp 2006; Allesina & Levine 2011). However, modelling studies alone cannot reveal how frequent intransitivity is or

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how many species in natural communities are maintained by it. Indeed, the role of intransitive competition in structuring plant communities remains unclear despite years of research devoted to answering this question. Some studies have found that intransitivity is an important mechanism structuring plant communities (e.g. Freckleton *et al.* 2000), but others have suggested the opposite (e.g. Grace *et al.* 1993). A potential explanation for these contrasting results is that the degree of intransitivity depends on the species pool considered. As with many measures of community organisation, considering an overall metric for all species in the community can produce very different results than more detailed analyses of a particular subset of species (e.g. Stone & Roberts 1992; Ulrich & Gotelli 2007). Similarly, if competition is intransitive amongst dominant or amongst rare species, but strongly hierarchical (i.e. transitive) between such groups, communities would be organised by nested intransitive networks. Such nestedness could increase coexistence, but would result in no overall signal of intransitivity for the whole community. To test this idea, field assessments quantifying intransitivity for different groups of species within a community are necessary.

The degree of intransitivity in plant communities might also be altered by two of the major global change drivers (GCDs hereafter) threatening biodiversity in terrestrial ecosystems: land-use intensification and climate change (Sala *et al.* 2000). Both GCDs alter heterogeneity and productivity, which in turn are likely to affect intransitive competition networks. Intransitivity could be more common and important for coexistence in productive environments, because here environmental filtering is relaxed and competition may be more important than disturbance or abiotic stress in structuring communities (e.g. Gilpin 1975; Bowker *et al.* 2010). Productivity increases with fertilisation (Suding *et al.* 2005; Manning 2012), which would suggest more intransitivity at higher land-use intensity. Modelling and empirical evidence suggests that intransitive competition is more likely to occur in heterogeneous environments (Huisman *et al.* 2001). In these environments, variation in limiting resources between local interaction neighbourhoods, coupled with niche specialisation, can generate, or interact with, intransitive competition, thereby enhancing species coexistence (Allesina & Levine 2011). In this regard, GCDs can modify the level of intransitivity in a community by altering not only the spatial but also the temporal heterogeneity in resources. High land-use intensity (fertilisation or overgrazing) can reduce variation in biomass over time (Osem *et al.* 2002; Grman *et al.* 2010), suggesting that temporal heterogeneity is reduced at high land-use intensity. On the other hand, climate change could increase temporal heterogeneity, especially in drylands, where water availability is often more variable in drier than in wetter environments (Whitford 2002). The well-known negative effects of GCDs on diversity may therefore be buffered or enhanced depending on their indirect effects on the degree of intransitivity (Fig. 1). However, the interrelationship between GCDs and the competitive hierarchy amongst coexisting species is poorly understood.

To address these research gaps, we applied a recently developed method to measure the degree of intransitivity from

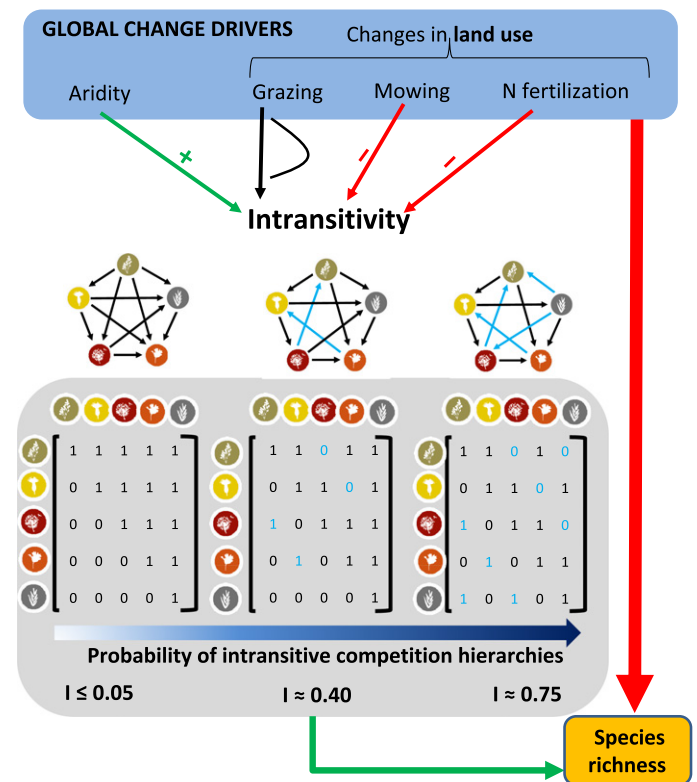


Figure 1 Conceptual model outlining our theoretical framework. We address here the direct and indirect relationships between (1) global change drivers (GCDs), (2) intransitive competition networks and (3) species richness. Intransitivity is expected to increase richness. GCDs are expected to decrease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

observational data (Ulrich *et al.* 2014a) on two large data sets describing plant diversity responses to changes in land use or aridity. We tested the following hypotheses: (1) intransitive competition is frequent in plant communities, (2) intransitive networks are more common amongst species similar in dominance, but transitive competition (i.e. strong hierarchy among competitors) prevails between species with contrasting dominance levels (i.e. intransitive competition networks are nested), (3) the degree of intransitivity in plant communities is positively related to their species richness and (4) increases in intransitivity in response to more temporally heterogeneous or fertile environments mitigate the impact of increasing aridity and intensive land uses on plant richness.

MATERIALS AND METHODS

Study sites

We used two large-scale data sets: the occurrence of plant species in European grasslands along land-use intensity gradients

(the German Biodiversity Exploratories; Fischer *et al.* 2010), and the occurrence of plant species along aridity gradients in global dryland ecosystems (the BIOCUM project; Maestre *et al.* 2012). These two data sets complement each other and allow us to assess the overall frequency and drivers of intransitivity across a wide range of communities varying in habitat type, species pool and environmental conditions as well as across data sets with different sampling methods (see details below).

The Biodiversity Exploratories include 1500 grassland plots, varying in land use and situated in three regions of Germany (Fischer *et al.* 2010; Blüthgen *et al.* 2012). In each of these 4×4 m grassland plots, the relative cover of all plant species was recorded. In the centre of each plot, a 10-cm depth soil sample was taken to measure total soil nitrogen and soil organic carbon concentrations (Fischer *et al.* 2010). Information on land use was obtained via questionnaires sent to land owners; these asked about grazing type (permanent, rotational, none), livestock type (sheep, cattle or other), fertilisation (fertilised or unfertilised), mowing (number of cuts per year) and the presence of water drainage or water retention structures (see Fischer *et al.* 2010; Blüthgen *et al.* 2012 for methodological details). This classification resulted in 40 different levels of land-use intensity and management types. Hereafter, we refer to this data set as 'grasslands'.

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

Data organisation and measurement of the degree of intransitivity

We measured the degree of intransitivity in the grassland and dryland data sets by using the Markov chain approach of Ulrich *et al.* (2014a). Under the assumption that observed species abundances represent the equilibrium abundances of the species forming the community, the method allows us to assess (1) to what degree competition predicts observed species abundances, and (2) the degree of intransitivity within a given competition network. As a measure of species abundances, we used the cover of each species within each quadrat (drylands) or plot within a cluster (grasslands; see how clusters were assembled below). Thus, a single metric of intransitivity was calculated by each site (drylands) or cluster (grasslands). At equilibrium, observed species abundances should be equal to the dominant eigenvector of a hypothetical species \times species transition matrix [i.e. the matrix that

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

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

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

where p_{ij} is the probability that species i (in the column) replaces species j (in the row) in a given patch; j ranges from 1 to m (total number of species), i from m to $m-1$ and k from $i+1$ to m . Increasing values of I indicate higher levels of intransitivity within the community. Our metric (I), therefore, ranges from 1 (fully intransitive community) to 0 (fully transitive community; Fig. 1).

Although spatial heterogeneity between local neighbourhoods may enhance intransitive competition by providing more opportunities for niche differentiation, it may also complicate its measurement and make competition ranks more difficult to estimate from the observed abundances (e.g. Ulrich *et al.* 2014a). Thus, for our method to yield reliable results, quadrats within a given site (drylands) or plots within a given cluster (grasslands) should be as homogeneous as possible. To meet this requirement, and according to their different structure, the two data sets were organised differently (henceforth we refer to them as grassland clusters and dryland sites). As the grasslands data set lacked within-plot replication, we organised the 1500 plots into 190 plot clusters with the same land-use type and region to have enough replication to calculate I . The high number of species found in the grasslands (318–365, depending on the region; Socher *et al.* 2013) made it impossible to produce clusters of plots which were relatively homogenous in their environmental conditions and contained a sufficient number of plots to analyse all possible interactions between species pairs. Therefore, we only considered the five dominant species within each cluster and divided the data set in clusters of *c.* 6–10 plots (always > 5 , the number of species

considered). When 12 or more plots were found within the same land-use type and region, we divided them into two clusters according to total soil nitrogen and organic carbon concentrations to create the most environmentally homogeneous, and the highest number, of clusters possible.

To allow comparison between both data sets, we also considered the five dominant species within each site in drylands. Using this database, we assessed changes in our intransitivity metric as a function of the number of species considered, progressively including a larger number of subordinate species. This allowed us to determine if the probability of detecting intransitive competition varied depending on the target species pool, and therefore if intransitive competition networks were nested (present only amongst the dominant species) or not (see full results in Appendix S1).

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

Separating intransitive competition from other processes enhancing coexistence is difficult from observational, or even manipulative, studies. The main distinguishing characteristic between these mechanisms is that intransitivity relies on strong competition, i.e. it reduces co-occurrence of plant species within local interaction neighbourhoods [i.e. quadrat (drylands) or plot (grasslands) scale; Laird & Schamp 2006]. The latter should lead to segregation of species between sampling quadrats. Those coexistence mechanisms relying on reduced competition (e.g. differential resource uptake), instead, should allow co-occurrence of different plant species at the local interaction neighbourhood scale. When applied to the matrices of the drylands data set, our intransitivity metric was positively correlated with the level of species spatial segregation between quadrats (Spearman's $\rho = 0.59$; Appendix S4). These results suggest that a high level of competitive exclusion within these local interaction neighbourhoods took place in the studied plots, and thus it is unlikely that our results are confounded by the operation of local-scale coexistence mechanisms that reduce competition.

Statistical analyses

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

We evaluated whether average values of our intransitivity metric (I) differed from 0.05 (indicating fully transitive

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

Relationship between intransitivity, global change drivers and diversity

We used structural equation modelling (SEM; Grace 2006) to analyse the relationships between land use (grasslands) or aridity (drylands), intransitivity and species richness. Our *a priori* model followed the rationale stated in the introduction (see also Fig. 1): aridity and land use affect both species richness and intransitivity, and intransitivity affects species richness (see Appendix S5 for full details and rationale). Both data sets have strong spatial clustering (sites were sampled within regions in the grasslands and within countries in the drylands). To account for this, we introduced the geographic coordinates in the SEMs. Latitude sufficed to represent the spatial distribution of the grassland data set (the three regions were distributed along a North–South axis), whereas both latitude and longitude were necessary to represent the spatial distribution of the dryland sites, which were globally distributed.

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

An additional set of analyses were performed as an alternative to data reduction with NMDS in the grasslands data set. Land-use factors could vary in their effects (e.g. grazing vs. fertilisation) and also in their effect within regions (Socher *et al.* 2013). Thus, separate SEMs using grazing, fertilisation, number of cuts and water management as different land-use predictors were performed, and the same *a priori* model structure was used to analyse each region separately (details and results in Appendix S6). SEM analyses were performed using AMOS for windows (SPSS Inc., Chicago, IL, USA).

RESULTS

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

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

Furthermore, the strength of intransitivity (I value) was positively related to plant richness in both data sets (Fig. 3). The presence of intransitivity increased species richness by six species in the grasslands and by four in the drylands, based on comparing the lowest ($I < 0.05$) and highest ($0.4 < I < 0.8$) levels of intransitivity within the studied communities (Fig. 3). Although the overall relationship between intransitivity and richness was consistent across data sets (Fig. 3), within both data sets the level of intransitivity and its relationship with richness varied geographically. The degree of intransitivity decreased with increasing latitude in both grasslands and drylands (Fig. 4). Intransitivity–richness relationships were either positive (Central), neutral (Northeast) or negative (Southwest) depending on the grassland region considered (Fig. 3a; Appendix S6).

We found an exponential decay in I values as more subordinate species were considered in our calculations (Appendix S1). This suggests strong nestedness of intransitive networks caused by high intransitivity amongst the dominant species, and strong competitive exclusion of rarer species by dominant ones. The relationship between intransitivity and species richness remained consistently positive

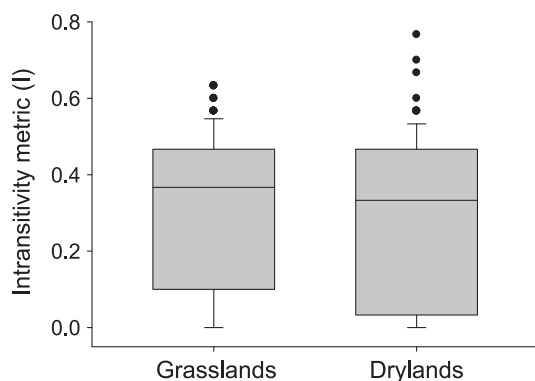


Figure 2 Intransitivity (measured as metric I) observed in grasslands ($n = 175$ clusters of environmentally similar grasslands out of a set of 1500 sites) and drylands ($n = 151$, sites). Box plots show the median, 25 and 75% quartiles. The intransitivity metric was not significantly different between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

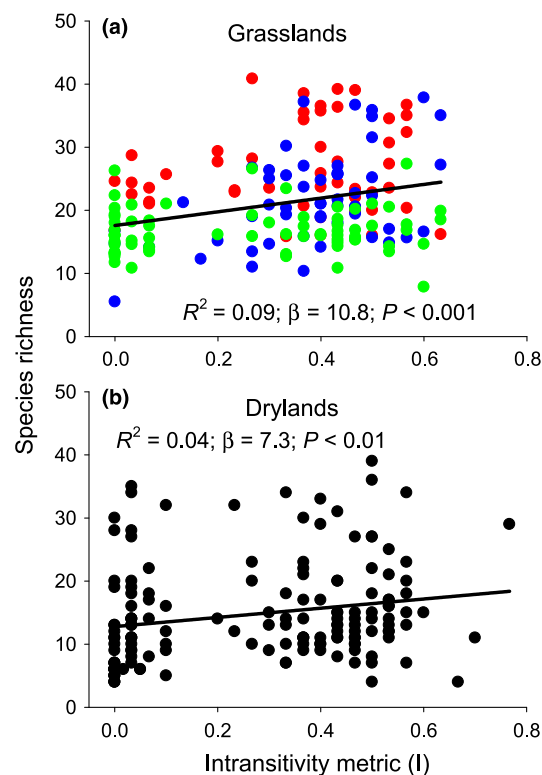


Figure 3 Relationships between intransitivity (measured as metric I) and species richness in grasslands (a; mean for each cluster of sites) and drylands (b). Model II OLS regression results are shown. The different colours in the upper panel show the three different study regions: Southwest (red, $n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

regardless of the number of species considered, however, it became non-significant if all subordinate species were combined and treated as a single species, suggesting that subordinate species differ in their response to the dominants (Appendix S1).

Effects of global change drivers on intransitivity and diversity

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

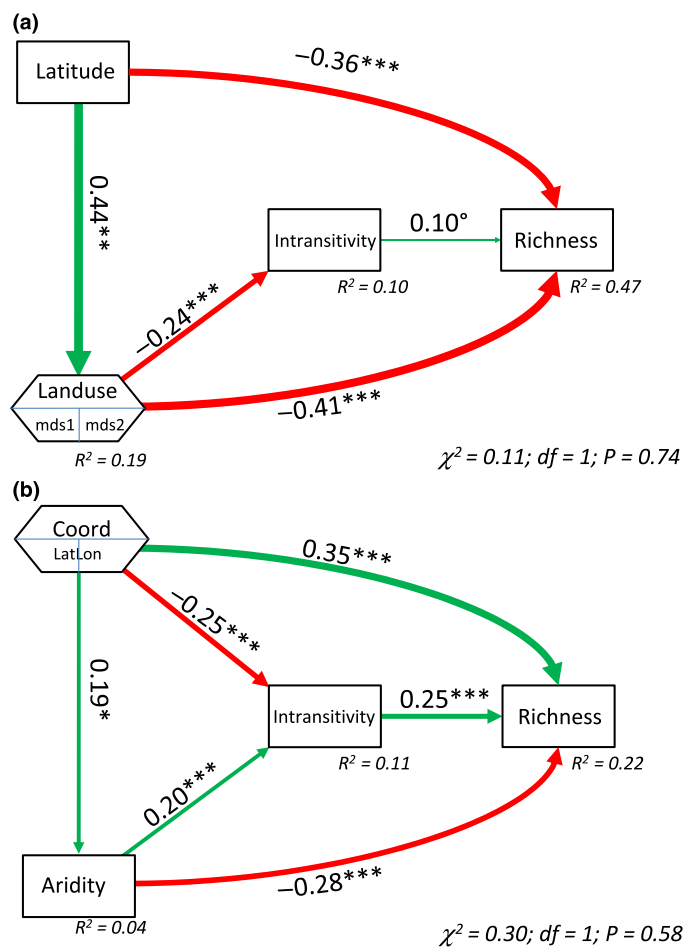


Figure 4 Structural equation models depicting effects of geographic factors (region or latitude/longitude) and global change drivers (GCD) (land use or aridity) on intransitivity and species richness for grasslands (a) and drylands (b). Composite variables are shown with the variables forming them inside. The width of arrows is proportional to the standardised path coefficient, with green and red lines for positive and negative relationships respectively. The overall goodness-of-fit test and the R^2 for each variable introduced are given. P -values are: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$; $^{\circ}P < 0.1$. Lat = latitude, Lon = longitude, mds = non-metric multi-dimensional ordination axes performed with the land-use variables.

Table 1 Summary results of the structural equation models performed with the different environmental factors (in rows) separately

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

Standardised total effects (STE; sum of direct and indirect effects) and standardised direct effects (SDE; equivalent to the path coefficient from the predictor to the response variable) for richness are shown. For intransitivity STE = SDE. Environmental factors were introduced as: Mowing (number of cuts per year), grazing (sheep/other, permanent/rotational/none) fertilisation (yes/no) and water management (drainage/retention/none). Significant path coefficients are highlighted in bold.

DISCUSSION

Frequency 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 data sets 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 the spatial scale considered.

Previous studies assessing the degree of intransitivity in plant communities have generated contrasting results and substantial debate (Aarssen 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 Aarssen 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 pairwise approaches fail to predict observed abundances in the field (Aarssen 1989; Weigelt *et al.* 2007; Engel & Wetzel 2008). In contrast, the patch-transition matrices used here implicitly account for competition under natural conditions and in multiple species assemblages (Ulrich *et al.* 2014a and references therein), and thus provide a truer reflection (according to the high match levels found between simulated and observed data) of competitive hierarchies and a more accurate assessment of intransitivity in natural communities.

Regarding the role of the species pool when estimating intransitivity, and in agreement with our second hypothesis, we found strong nestedness in intransitive competition networks. Our results suggest high levels of intransitivity among the dominant species, but not between dominant and rare species (Appendix S1). Studies focusing on dominant species will, therefore, likely find high levels of intransitivity (e.g. Freckleton *et al.* 2000), whereas those including broader species pools will likely find the opposite pattern. While these contradictory results have fuelled strong debate (e.g. Aarssen 1988; Grace *et al.* 1993), only by analysing real-world data were we able to cast some light on the potential explanation for these contradictions. Our nestedness hypothesis requires experimental confirmation, but it suggests that coexistence of

similarly abundant (or co-dominant) species could be promoted by nested intransitive competition networks.

The relationship between intransitivity and species richness

Our study is, to the best of our knowledge, the first to empirically show a positive relationship between the strength of intransitivity and species richness in natural communities, thus supporting previous mathematical and conceptual models (Huisman *et al.* 2001; Wootton 2001; Laird & Schamp 2006; Rojas-Echenique & Allesina 2011). This relationship suggests that the degree of intransitivity among the dominant species could explain 4–9% of the variance in plant species richness, which, given the wide range of environmental conditions, habitats and sampling procedures in our study, suggests that intransitivity may be an important driver of species richness. We also find that intransitive competition boosted species richness considerably (Fig. 3). Future work is needed to fully integrate intransitive competition with coexistence theory (Chesson 2000; HilleRisLambers *et al.* 2012) and to determine whether intransitive loops equalise fitness between species (e.g. Laird & Schamp 2006) and/or stabilise niche differences (Rojas-Echenique & Allesina 2011). However, these first empirical results on the relationship between intransitivity and diversity suggest that it may be an important, but largely overlooked, coexistence mechanism. Our results also suggest that incorporating multi-species (rather than multiple pairwise) competition dynamics and nested competition networks, which have been largely neglected before, can contribute explaining species coexistence. More studies are needed to confirm whether the patterns we find are consistent across ecosystem types and different groups of organisms; our results and the methodology employed (Ulrich *et al.* 2014a) pave the way for such future research.

Effects of global change drivers on intransitivity and diversity

Could an increase in intransitivity offset the negative effects of GCDs on diversity? This would require three conditions: (1) GCDs (here, aridity or land-use intensity) directly decrease richness, (2) intransitivity increases richness and (3) GCDs increase intransitivity. While (1) and (2) were supported by our results, we found that (3) was largely dependent on the GCD studied (Table 1).

We speculate that the contrasting effects of aridity and land-use intensity on intransitivity are related to their different effects on temporal heterogeneity. We minimised the role of spatial heterogeneity on our intransitivity metric. Thus, although spatial heterogeneity across local interaction neighbourhoods would normally be an important driver of intransitivity and plant coexistence (Huisman *et al.* 2001; Sears & Chesson 2007; Allesina & Levine 2011), it should not affect intransitivity here. However, temporal heterogeneity is still expected to increase opportunities for intransitivity. Temporal heterogeneity could enhance intransitivity in competition networks through temporal storage effects (Chesson 1983) as a given species will experience higher intra- than inter-specific competition during favourable time periods and this may hinder its ability to compete with others, enhancing the chances to form intransitive

competition loops. It may also provide more opportunities for niche differentiation, where slightly different environmental conditions across time can generate different competition hierarchies and therefore enhance community-level intransitivity and allow coexistence (Allesina & Levine 2011). In this regard, aridity is known to increase temporal heterogeneity in water availability (e.g. Whitford 2002) which might explain the more pronounced effects of intransitivity in drylands. Land-use intensification (grazing and fertilisation) instead, reduces temporal heterogeneity in biomass (Osem *et al.* 2002; Grman *et al.* 2010) and also asynchrony of species fluctuations in diverse communities (Hautier *et al.* 2014). Additionally, both grazing and mowing can compromise potential trade-offs between competition abilities (e.g. those between resource uptake and pollinator attraction) and reduce the chances for intransitive competition (Aarssen 1992). Overall, more intensive land uses can reduce temporal niche dimensionality (analogous to the reduction in spatial niche dimensionality; Harpole & Tilman 2007) and therefore shifts in competition hierarchy across time, preventing intransitive competition. This may explain why increasing temporal heterogeneity in land use has been shown to increase diversity (Allan *et al.* 2014) as it might also increase intransitivity and other coexistence mechanisms. Overall, our results point to another means by which GCDs alter competition between plants (see Tilman & Lehman 2001 for a review) and suggest that the effects of such GCDs depend on how they impact upon the temporal heterogeneity of resources. The unique nature of our data also allowed us to shed some light on other drivers of intransitivity within natural communities, which have been largely overlooked by previous studies and also are likely to be linked to changes in temporal heterogeneity. For example, the strong latitudinal gradient in intransitivity found in the drylands could be due to rainfall variability, which decreases from north to south in the studied sites (Ulrich *et al.* 2014b).

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

CONCLUSIONS

We found that intransitive competition networks are widespread in natural plant communities and explained 4–9% of

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

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AUTHORSHIP

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

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