

**SUPPORTING INFORMATION: *Intransitive competition is widespread in plant communities and maintains their species richness***

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

As the dryland dataset had greater intra-site replication ( $n = 80$  quadrats sampled per site), we could evaluate the consequences of using different numbers of dominant species to calculate our intransitivity metric. In the main text we consider only the five dominant species for two reasons: i) to standardize comparison with results from the grasslands dataset and also with previously published studies, which were performed with a relatively low number of species (e.g., Aarsen 1989; Grace *et al.* 1993; Engel & Wetzin 2008), and ii) because  $I$  values are more robustly estimated when using the dominant species than when all the species within the community are considered as it is harder to properly estimate competition coefficients for rare species due to the lack of data. 79% of the  $I$  values calculated using only the five dominant species exceeded  $R^2$  of 0.6 for the best fitting matrices (Law *et al.* 1997 used the same threshold when estimating competition from observational data) vs. 38% of those obtained using all the species; Fig. A1). Only those sites (drylands) or clusters (grasslands) whose best-fitting matrices showed  $R^2 \geq 0.6$  were retained for any of the analyses presented here. Results obtained by using only those matrices showing goodness of fit with different thresholds ( $R^2 \geq 0.7$ ) gave very similar results (data not shown).

It must be noted that the goodness of fit of the best fitting matrices obtained with our Markov chain approach can vary substantially between communities, depending on the importance of competition in the assembly of the target community, relative to other mechanisms such as environmental filtering or dispersal limitation. These mechanisms can reduce matrix fit where they are operating (Ulrich *et al.* 2014a), which is itself a

measure of which part of the observed variability in species abundance can be explained by competition.

When calculating  $I$  with an increasing number of dominant species (5, 10, 15, 20 and all species in the community), we found an exponential decay in  $I$  values as more subordinate species were considered. Indeed, the average  $I$  values detected when considering either 10+ species or all the species within the community was significantly below 0.05, and less than 5% of the studied communities lay above the threshold of  $I > 0.05$  (Fig. A1). These results suggest that no important departure from full transitivity in plant communities was found when considering all the species of the community, which sharply contrasts with the results found for the five dominant species. These results are very unlikely to be a mathematical artifact of the statistical approach used (see Ulrich *et al.* 2014 for robustness of the methodology across different richness levels).

What is the reason for these contrasting results? We argue that, as happens with the co-occurrence metrics often used in ecology (Stone & Roberts 1992; Ulrich & Gotelli 2007), strong nestedness in intransitive networks could lead to the underestimation of the degree of intransitivity when considering all the species in the community. This nestedness would reflect a high degree of intransitivity among species with similar abundances (see shaded submatrices in Fig. A2) but a low level of intransitivity among all the species together (Fig. A2). This suggests greater opportunity for intransitivity between ecologically similar species but a strong competition hierarchy between species with contrasted dominances in the field (i.e., rare vs. dominant species). To test this idea we simulated a matrix with a highly nested structure in their competitive outcomes (i.e., highly intransitive among dominant species, and among rare species, but no intransitivities between dominant and rare species; Fig. A3). Our results support the idea that the degree of intransitivity in the community would be

very low ( $I = 0.06$ ), even if intransitivity within particular clusters of species in the community (e.g., within dominant or within rare) is relatively high ( $I > 0.16$ ). This simulation demonstrates the possibility that nestedness in competition networks might lead to underestimations of the degree of intransitivity (up to three-fold in our example).

An alternative explanation for the decrease in intransitivity levels when including more species could also be that rarer species have fewer occurrences and, therefore, there is less statistical power to define changes in their abundance. Although we cannot completely rule out this explanation, one would expect this lack of statistical power to increase the error in estimations of  $I$ , when an increasing number of species are considered. However, we found that the error in estimates of  $I$  remained similar regardless of the numbers of species considered. It must be noted that, although  $I$  values decreased as more species were considered, the effect of  $I$  on species richness (i.e. increases in species richness with higher  $I$  values) were similar when  $I$  was estimated with all species within the community (Fig. A4).

Our results were robust after including an increasing number of species included in our calculations (this Appendix), accounting for spatial heterogeneity across sites (Appendix S2), and controlling for changes in the species pool considered (Appendix S3). However, it must be noted that the relationship between intransitivity and species richness became non-significant when considering a “sixth species” in our calculations adding up the cover of the species in the community other than the five dominants. This “sixth species” approach, however, is not free from caveats as: i) it assumes that all the rarer species respond to, and have the same effect on, the dominant species, which is a highly unrealistic assumption. There could be substantial turnover in the rarer species between communities, which would be entirely overlooked by aggregating them into one "species", ii) around 17% of the community (1 out of 6 species) is composed of the

artificial aggregated "species" and 33% of the pairwise interactions, which our metric relies upon (15 pairwise combinations in a  $6 \times 6$  species matrix vs. 10 in a  $5 \times 5$  species matrix), involve the artificial species. It therefore has a large influence on metrics of intransitivity, and iii) if there are many "non-dominant" species, the sum of their respective cover values is higher than the cover of some, if not all, of the dominant species themselves. Considering this sum as a single species when analyzing the data, could, therefore, artificially inflate the degree of dominance (and hence transitivity). Despite these potential problems, the intransitivity metrics used in the main text were reasonably correlated to the ones considering this "sixth species" (drylands:  $\rho = 0.44$ ,  $P < 0.0001$ ,  $n = 188$ ; grasslands:  $\rho = 0.24$ ,  $P < 0.05$ ,  $n = 85$ ). The intransitivity levels recorded with the "sixth species" approach greatly exceeded the threshold of 0.05, as in the results presented in the main text. Drylands:  $I = 0.20 \pm 0.02$  (mean  $\pm$  SE); t-test = 6.4;  $P < 0.0001$ , 47.6% of sites with  $R^2 > 0.6$ . Grasslands:  $I = 0.26 \pm 0.01$  (mean  $\pm$  SE); t-test = 14.5;  $P < 0.0001$ , 95.4% of sites with  $R^2 > 0.6$ .

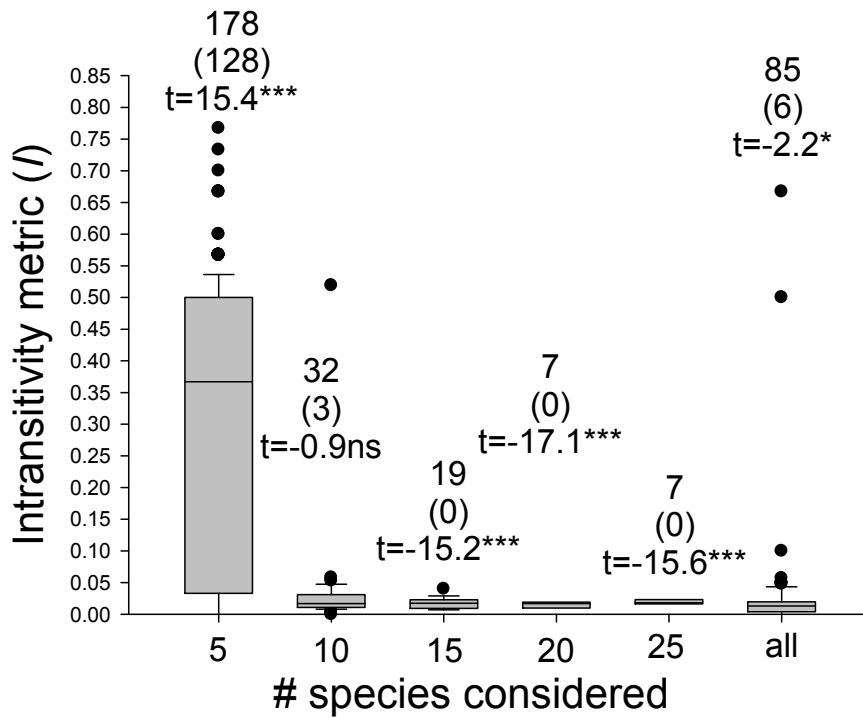
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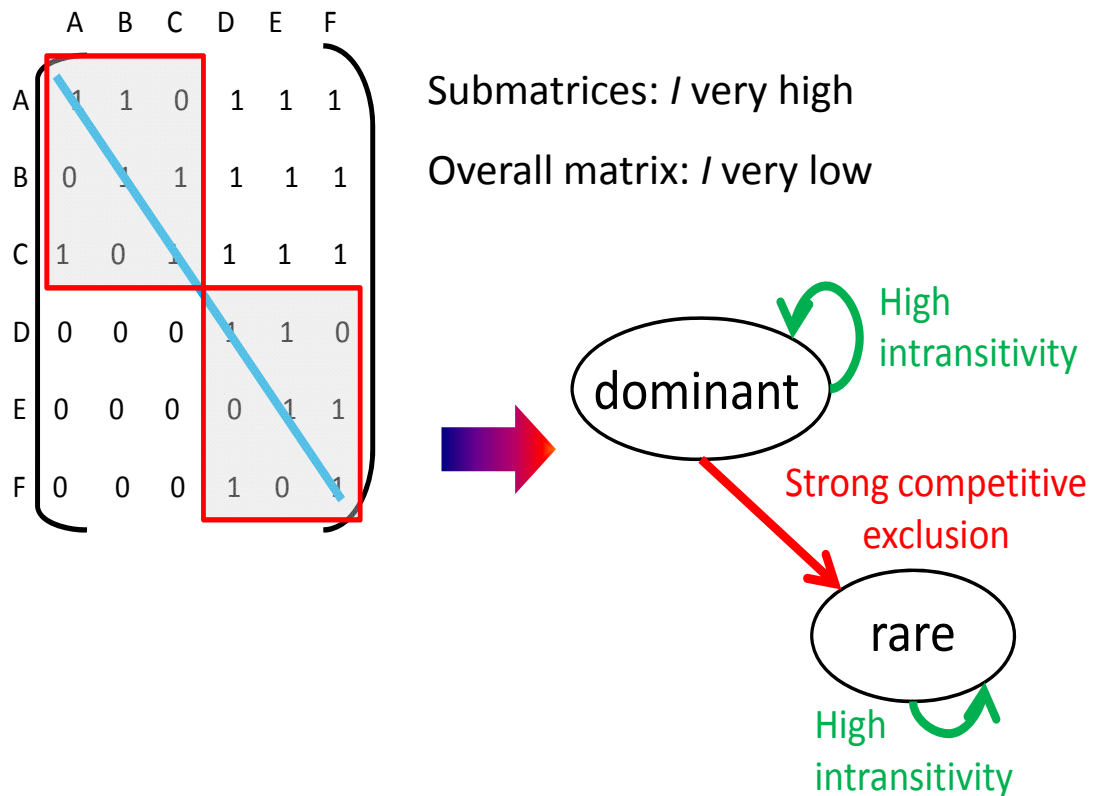
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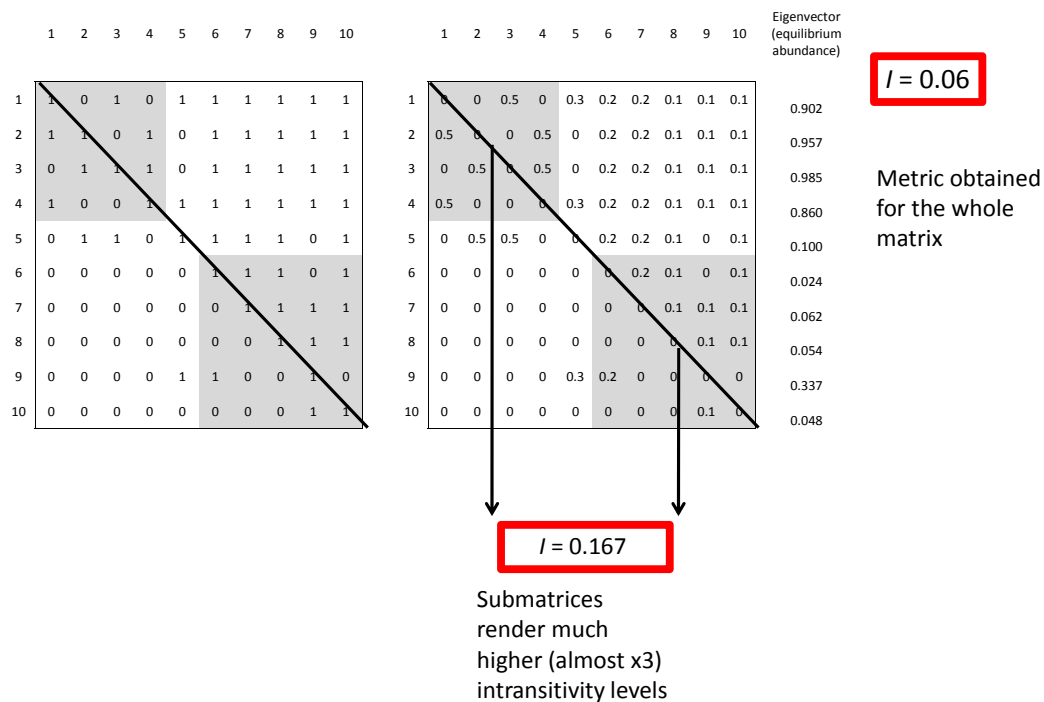


**Figure A1.** Box-plot for the intransitivity metric obtained from considering different numbers of species within the community in the drylands dataset. Numbers above bars are, from top to bottom, the number of plots with  $R^2 > 0.6$  for the best fitting matrices, the number of plots with  $I > 0.05$  (in parentheses), and the t-test (difference between the metrics and 0.05) for each subset.  $^{***} = P < 0.001$ ;  $^* = P < 0.05$ ; and ns = no statistically significant difference from 0.05.

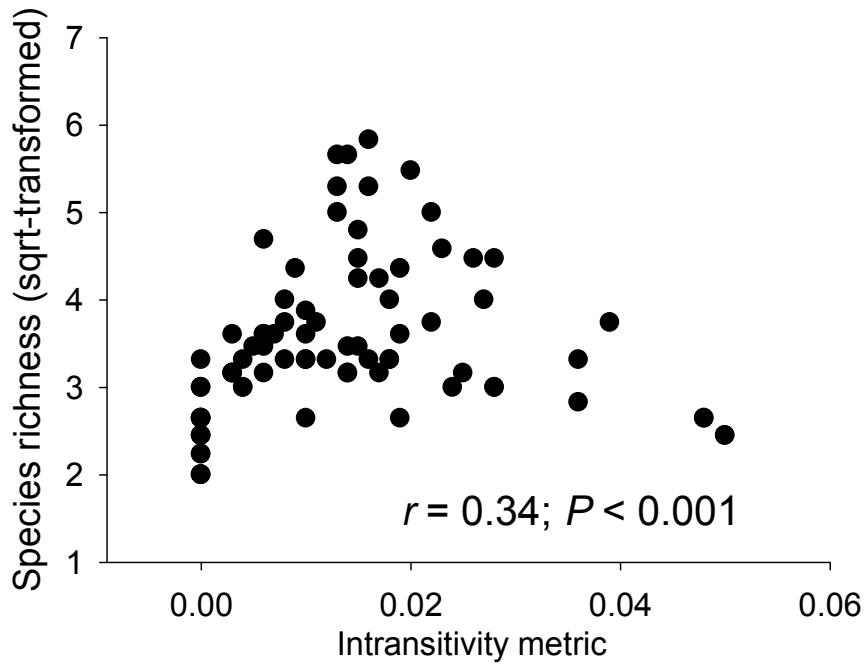


**Figure A2.** Conceptual model showing a high level of nestedness in intransitive competition networks in the simplest scenario (three dominant species [A to C] and three rare species [D to F]). The figure shows a high degree of intransitivity within the dominant species ( $A > B > C > A$ ) and within rare species ( $D > E > F > D$ ). However, the high degree of intransitivity within the different groups (shaded areas) translates to a very low level of intransitivity when considering the entire matrix.





**Figure A3.** Worked example with 10 species (1 to 10) to show the effects of nestedness in intransitive networks. Two matrices are presented: pairwise competition matrix (left; win [1], lose [0]), and a patch transition matrix (right; fraction of a patch previously occupied by a species that is now occupied by other species, range between 0 and 1). Shaded areas show high levels of intransitivity within dominant and within rare species (see equilibrium abundances in the right side of the matrix). However, rare species are generally competitively excluded by dominant species (shown as a general nested structure in the full matrix). Although the degree of intransitivity is relatively high when analyzing the shaded areas, the metric drastically decreases when analyzing the overall pattern.



**Figure A4.** Relationship between the intransitivity metric ( $I$ ) obtained when considering all the species and species richness in drylands. Spearman's correlation results are shown ( $n = 80$ ).

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

The methodology used assumes that the sampled sites within a given cluster (grasslands) or sampling quadrats within a site (drylands) are environmentally homogeneous, as competition ranks are more difficult to establish from observational datasets when environmental variation across sites plays an important role in defining the observed abundances (Ovaskainen *et al.* 2010; Ulrich *et al.* 2014a). We therefore performed sensitivity analyses to evaluate the robustness of our results to environmental heterogeneity.

To test for the effect of across-site heterogeneity we applied the "spatial and environmental data" algorithm in the *Transitivity* program, which accounts for environmental variation across sites (grasslands). The variables introduced were related to nutrient availability (pH, soil organic C and N, sand content, soil depth and a topographic wetness index including inclination and position within the slope, [Gessler *et al.* 1995; Sørensen *et al.* 2006; Manning *et al.* in prep.]). We also included elevation as a surrogate of temperature. In short, the method uses the residuals of a multiple regression between species abundances (response) and the environmental data (predictor) to calculate the intransitivity metric, instead of using the raw abundance data (see Ulrich *et al.* 2014a for full methodological details). Overall, our results were qualitatively the same, although weaker, when including these environmental variables, as they accounted for much of the variation in abundance across sites. The percentage of site clusters with match levels above our threshold ( $R^2 = 0.6$ ), and therefore reliable metrics of intransitivity, diminished drastically, and only 14% of them were above this threshold in comparison with the 92% when not including environmental data.

However, when competition was important it was nearly always intransitive, with 96%

of the sites with  $I > 0.05$ . Due to the low sample size ( $<60$ , as recommended; Legendre 2008), we could not fit the overall richness-intransitivity relationship using type II regression; instead, we used Spearman's correlations to do this. The overall relationship between intransitivity and species richness was not significant (Spearman's correlation ( $\rho$ ) = 0.09,  $P = 0.7$ ,  $n = 26$ ), probably due to the much lower sample size and to region-dependent relationships. Consistent with our previous results, however, the relationship between intransitivity and richness varied depending on the region, with a strong negative relationship ( $\rho = -0.72$ ,  $P = 0.1$ ,  $n = 6$ ) in the Northeastern region, and positive relationships in the rest (Fig B1; Central:  $\rho = 0.28$ ,  $P = 0.1$ ,  $n = 7$ ; Southwest:  $\rho = 0.45$ ,  $P = 0.1$ ,  $n = 13$ ).

Robustness of results from the dryland database could not be tested as we did not have environmental data for each quadrat. However, climatic data are expected to be consistent across quadrats within a  $30\text{ m} \times 30\text{ m}$  site. Furthermore, soil properties are more likely to be modified by the presence of perennial plants, which form islands of fertility (Niering *et al.* 1963) rather than *a priori* soil characteristics are to affect plant abundances. A recent study supports the latter statement, as soil characteristics did not differ between shrub seedlings and open interspaces, but the latter showed sharp differences when compared with soil beneath adult shrubs (Sortibrán *et al.* 2014). This recent study shows that, at least in the dryland studied by these authors, it is the plant that modifies soil properties and not otherwise. Thus, although we cannot rule out this potentially confounding effect, realized abundances of perennial plants within a given site in the dryland database are more likely to be driven by interactions between species than by spatial environmental heterogeneity across sampling quadrats.

Another assumption of the method is that the communities studied are at equilibrium. This is a necessary assumption to apply a Markov chain approach and

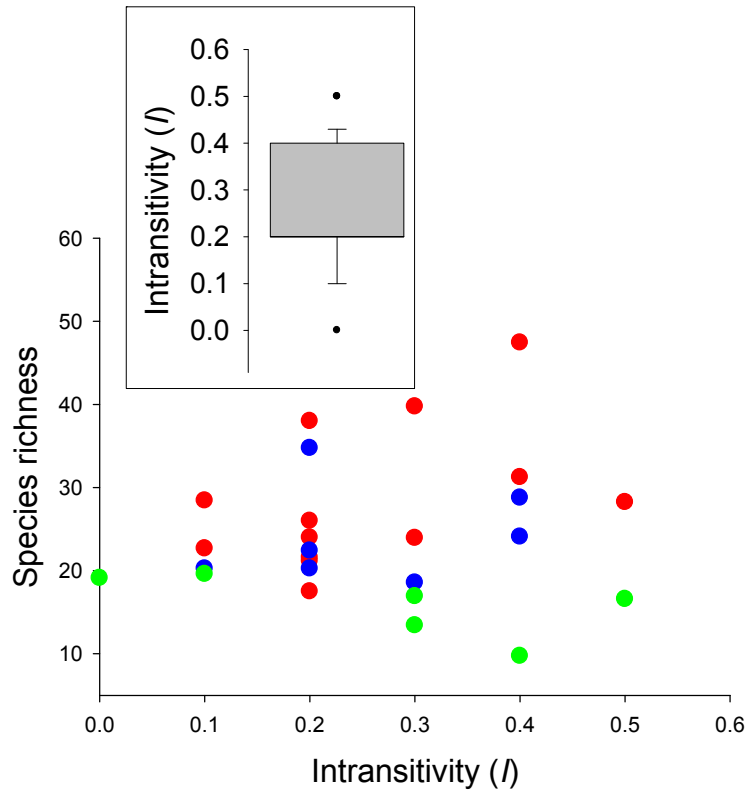
evaluate the degree of intransitivity of plant communities from observational studies. Violations of such assumption, however, are unlikely to have had a major influence on our results because the match between predicted and observed data indicates that competition matrices were able to predict a large part (70%) of the observed abundance distributions (see main text).

To test whether transient dynamics might have biased the results in these grasslands we compared the  $R^2$  values between intensively and non-intensively used grasslands, assuming that intensively used (and therefore most disturbed) plots would experience a higher risk of transient dynamics and departures from equilibrium abundances. Intensively and non-intensively used grasslands did not differ in their match between observed and simulated abundances ( $R^2 = 0.70$  vs.  $0.74$  for fertilized vs. unfertilized plots;  $R^2 = 0.70, 0.74, 0.76$  and  $0.73$  for 0 to 3 annual cuts;  $R^2 = 0.72$  vs.  $0.78$  for permanent vs. rotational grazing), and neither did drylands and grasslands ( $R^2 = 0.70$  and  $0.75$ , respectively). Thus, we feel confident in assuming that our results are largely unaffected by transient dynamics.

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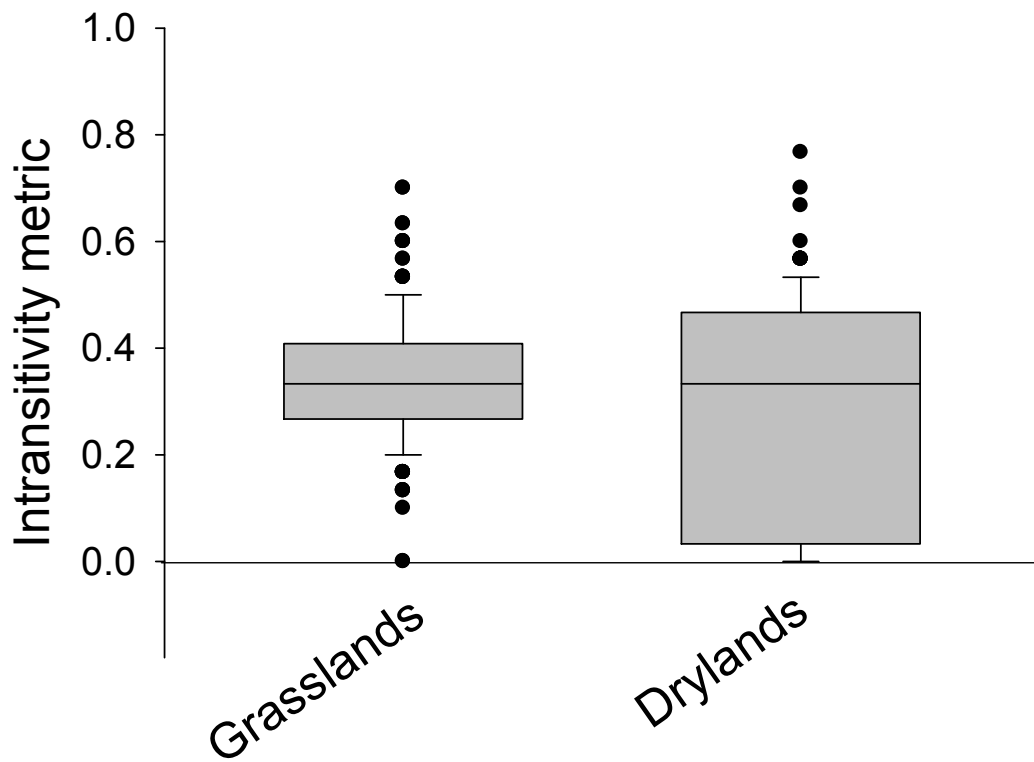


**Figure B1.** Relationship between intransitivity ( $I$ ), calculated with the "environment + abundance" algorithm and species richness. The different colors in the upper panel show the three different study regions: Southwest (red,  $n = 13$ ), Central (blue,  $n = 7$ ) and Northeast (green,  $n = 6$ ). A box plot with the median and 25% and 75% quartiles for the  $I$  metric is also shown.

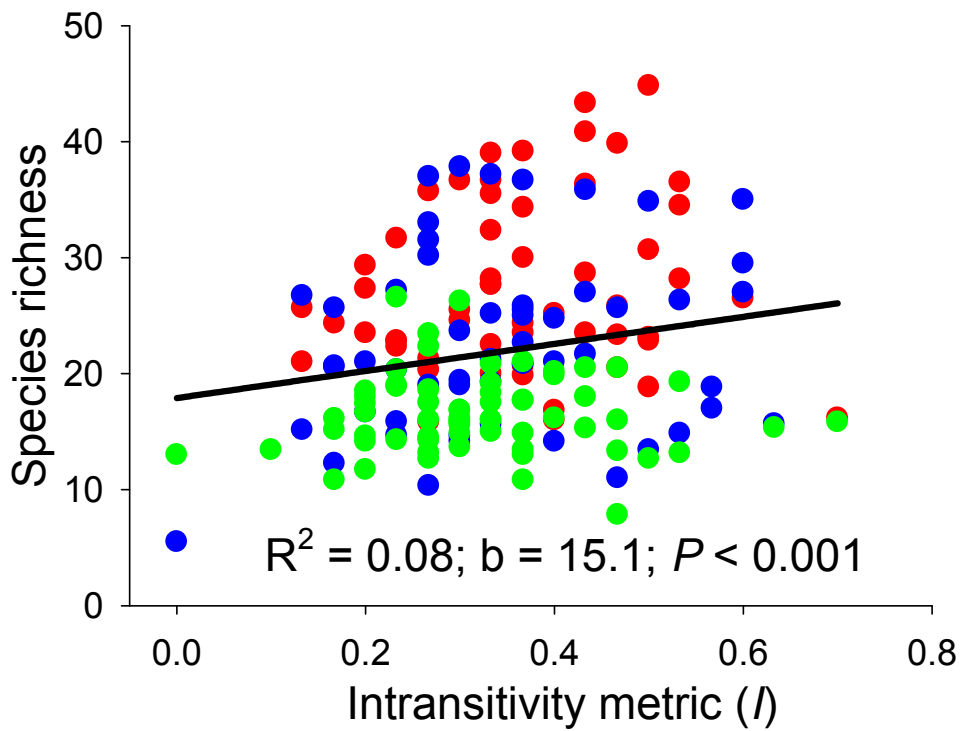
### **Appendix S3. Results using the five dominant species within each region instead of cluster in the grassland database.**

In addition to the analyses of the grasslands dataset presented in the main text (using the five dominant species per cluster), we also conducted the analyses per region, i.e. using the same five dominant species for every cluster within a region. The latter approach ensures that differences in the intransitivity metric ( $I$ ) between clusters are not driven by differences in the species used to calculate  $I$ . It has the disadvantage that the species used to calculate  $I$  may not be the dominants within that particular cluster. The two approaches qualitatively gave the same results: 1)  $I$  significantly differed from 0.05, indicating that the studied communities had some degree of intransitivity (Wilcoxon's test:  $z = -11.0$ ,  $P < 0.001$ ,  $n = 182$ ; Fig. C1), 2) a large percentage (99%) of these communities showed some degree of intransitivity, and 3) a positive and significant (although weaker) relationship between  $I$  and species richness were found (Fig. C2). The conclusions gathered from the SEMs at both general and regional scales were also very similar and led to the same conclusions as those presented in the main text (Fig. C3). These are: 1) variable (although weaker) effects of land use on intransitivity (positive: water drainage and grazing, negative: mowing and fertilization), and 2) strong variation in results between study regions.

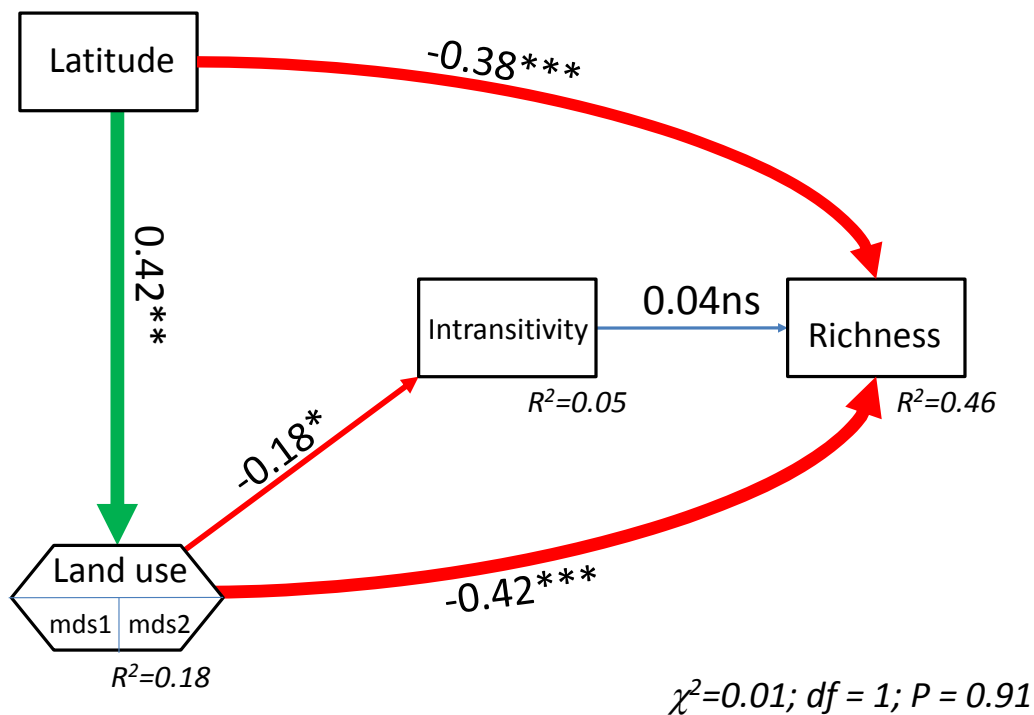




**Figure C1.** Box plots showing the median, 25% and 75% quartiles of degree of intransitivity ( $I$ ) observed in temperate grasslands ( $n = 175$ ) and drylands ( $n = 151$ ). The difference between this figure and Fig. 1 in the main text is that the degree of intransitivity for the grasslands was calculated for the five dominant species within each cluster instead of within each region.



**Figure C2.** Relationship between the intransitivity metric ( $I$ ) and species richness in the grasslands. Model II regression results are shown. The different colors in the upper panel show the three different study regions: Southwest (red,  $n = 50$ ), Central (blue,  $n = 54$ ) and Northeast (green,  $n = 71$ ). The difference between this figure and Fig. 2 in the main text is that the degree of intransitivity for the grasslands was calculated for the five dominant species within each cluster instead of within each region.



**Figure C3.** Structural equation models for the grassland dataset using dominant species for each cluster instead of for each region. The model depicts the effects of region, land use and soil characteristics on intransitivity and species richness. The composite variable is shown with the variables forming it in small quadrats. The width of arrows is proportional to the standardized path coefficient, with green and red lines for positive and negative relationships, respectively. Grey paths are those showing the same trends than in the main text, but rendering non-significant results. The overall goodness-of-fit test and the  $R^2$  for each variable introduced are given.  $P$ -values are: \*\*\* =  $P < 0.001$ ; \*\* =  $P < 0.01$ ; \* =  $P < 0.05$ ; ns = non-significant. mds= non-metric multi-dimensional ordination axes performed with the different land-use variables.

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

We used the rationale developed by Soliveres *et al.* (2011) to separate intransitive competition networks from other coexistence mechanisms that lead to a reduction in competition between co-occurring species, when using observational datasets such as ours. The main characteristic distinguishing these mechanisms is that intransitivity relies on strong competition to maintain diversity, while other coexistence mechanisms should reduce competition between plant species, thus reducing competitive exclusion. To assess the level of competitive exclusion, we calculated the degree of co-occurrence at spatial scales small enough to detect plant-plant interactions (interaction neighbourhood; 1.5 m × 1.5 m quadrats in the dryland dataset). If niche segregation is important, species should be able to co-occur at this spatial scale (they just compete for different resources), whereas if there is strong competition species should not be able to co-occur in the same quadrat (Soliveres *et al.* 2011).

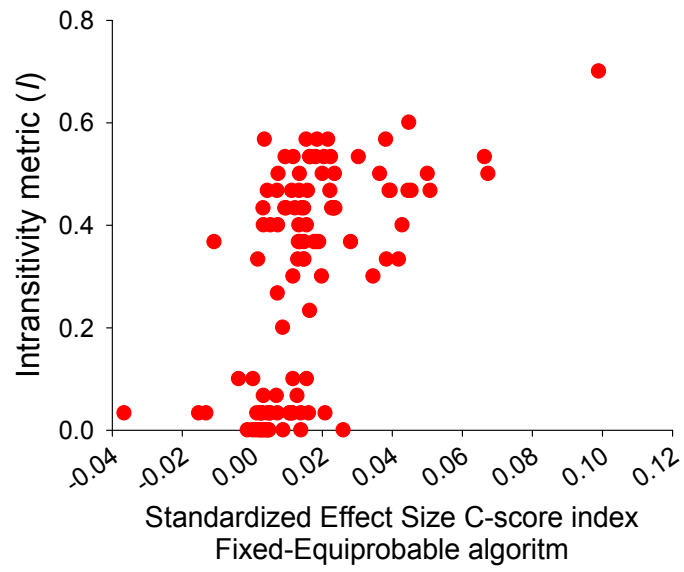
We estimated species co-occurrence with the abundance-data version for the widely used C-score index (Gotelli 2000, Ulrich & Gotelli 2010). In our case, we used cover of each species within each quadrat as surrogate of their abundance. This index is a measure of species segregation (i.e., competitive exclusion), and we estimated it from abundance data by using the *CoOccurrence* software (Ulrich 2006; [www.keib.umk.pl](http://www.keib.umk.pl)). To determine the strength of co-occurrence in a sample, the observed C-score value is compared against a set of null models which serve as a baseline for what a community unstructured by species interactions would look like (Connor & Simberloff 1979; Gotelli & Graves 1996).

The values of the C-score are dependent on the number of species and co-occurrences observed within each plot; thus, we obtained a standardized effect size (SES) as  $(I_{\text{obs}} - I_{\text{sim}})/S_{\text{sim}}$ , where  $I_{\text{obs}}$  is the observed value of the C-score, and  $I_{\text{sim}}$  and  $S_{\text{sim}}$  are the mean and standard deviation, respectively, of this index obtained from the simulations performed. Higher values of this index mean higher species segregation. To calculate the simulated matrices (and therefore the SES), we used ‘fixed rows–equiprobable columns’ algorithm (“ia” in *CoOccurrence*) and 500 iterations (Gotelli 2000). With this approach, we conserve the abundance of each species within each site, whereas each quadrat was assumed to have the same probability of being colonized by the same number of species. We also used the “fixed rows-fixed columns” algorithm to assess the robustness of our results. The latter algorithm conserves both the abundance of each species, and the number of species within each quadrat, and provides a more conservative test than the ‘fixed rows–equiprobable columns’ algorithm.

Our metric of intransitivity was highly correlated with the standardized C-score index (Spearman’s  $\rho = 0.59$  for the fixed-equiprobable algorithm [Fig. D1] and 0.45 for the fixed-fixed one [data not shown];  $P < 0.0001$  in both cases). This shows that higher levels of intransitivity are associated with higher species segregation, and thus higher competitive exclusion within the local interaction neighbourhood, as expected when strong competition occurs (Soliveres *et al.* 2011). These results are unlikely to be attributable to the fact that the C-score and  $I$  are derived from the same dataset, since these metrics used different information. C-score uses the degree of co-occurrence of the species within quadrats, regardless of their total abundances (which are constrained in the null model). Our intransitivity metric, instead, uses solely the realized abundances for each species.

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**Figure D1.** Relationship between our metric of intransitivity and the abundance-weighted C-score (higher values indicate spatial segregation).

## Appendix S5. Methodological details of the SEM analyses conducted

The different land-use categories (grazing and livestock types, number of cuts per year, fertilization or water management) were simplified with a non-metric multidimensional ordination (NMDS), which can handle categorical and continuous variables (McCune & Grace 2002). These ordinations can be two (2D) or three (3D) dimensional, with stress values  $< 0.2$  generally reflecting a satisfactory ordination of the data (McCune & Grace 2002; Anderson *et al.* 2008). The 2D ordination had stress values well below 0.2 and therefore we used it for further analyses. The first axis of this ordination was related to water drainage (Spearman's  $\rho = 0.76$ ), rotational grazing (Spearman's  $\rho = -0.65$ ) and grazing by sheep (Spearman's  $\rho = 0.62$ ), while the second axis was related with grazing by livestock other than sheep (Spearman's  $\rho = -0.88$ ), number of cuts (Spearman's  $\rho = -0.77$ ), and rotational grazing (Spearman's  $\rho = 0.64$ ). As the latter axis was inversely related to land-use intensity (rotational instead of permanent grazing, and mowing), it was multiplied by -1 to ease interpretation. Overall, higher values of these axes mean more intensive land uses. The usage of NMDS ordinations allowed us to obtain continuous variables from these binomial land-use categories and to account for all of them with just two variables within the model. High values of both axes indicate high land-use intensity and our land use gradient ranges from extensively managed grasslands, rotationally grazed by sheep, to intensively managed grasslands, which are either frequently mown or grazed heavily by cattle. Note that we have no sites that are both ungrazed and unmown (climatically determined grasslands are almost absent from western and central Europe). We conducted NMDS ordinations on previously normalized data (equivalent to Z-score transformation; Anderson *et al.* 2008) with the PRIMER v6 statistical package for Windows (PRIMER-E Ltd., Plymouth Marine



Laboratory, UK), using the Euclidean distance for the resemblance matrix and 25 re-starts to calculate stress values.

To simplify model interpretation, we collapsed the effect of multiple related variables into composite variables (Grace & Bollen 2008), which do not alter the underlying model but allow the user to assess the cumulative effect of multiple conceptually related variables as a single path (something similar to a multiple regression; Grace 2006; see details in Table E1). We used composite variables to collapse the spatial component (latitude and longitude) in drylands and land use (non-metric multidimensional axes 1 and 2) in grasslands. We also used composite variables to collapse the effect of the different grazing indicators in the grassland database for the regional-level SEMs; see Table E2)

SEMs estimate path coefficients (i.e., causal relationships among variables), with their associated *P* values, from the field data. The path coefficient is analogous to a partial correlation coefficient, and describes the strength and sign of the relationships between the introduced variables (Grace 2006). Significance of path coefficients in the SEMs performed were estimated with bootstrapping because some of our data were not normally distributed and this technique is preferred to maximum likelihood estimation in these cases. Results were confirmed using the Bayesian approach, which is not sensitive to error distribution.

Apart from estimating single path coefficients, SEMs test the overall goodness-of-fit of the model against the dataset, that is, whether or not the *a priori* model structure is a plausible causal scenario which could account for the correlations among the variables in the model. To test the overall goodness-of-fit of the model against the dataset, the traditional  $\chi^2$  test, the RMSEA index and the Bollen-Stine bootstrap test were used. It must be noted that when using these indices high *P*-values indicate that the

covariance structure of the proposed model is similar to that of the data and that it is therefore a plausible causal scenario. Since all the indices rendered very similar results, only the  $\chi^2$  tests are reported. Also, a satisfactory fit does not indicate that a given model structure is the best possible model, or the only plausible model.

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**Table E1.** Loadings of the different predictors introduced to build the composite variables in the general models (those in Fig 2 in the main text). Columns are the response variable towards each composite was directed and rows are the predictors introduced in a given composite. Abbreviations are as follow: PCA = component of the PCA ordination performed with soil variables, CV = coefficient of variation, Axis = dimension of the non-metric multidimensional ordination performed with the land-use measurements.

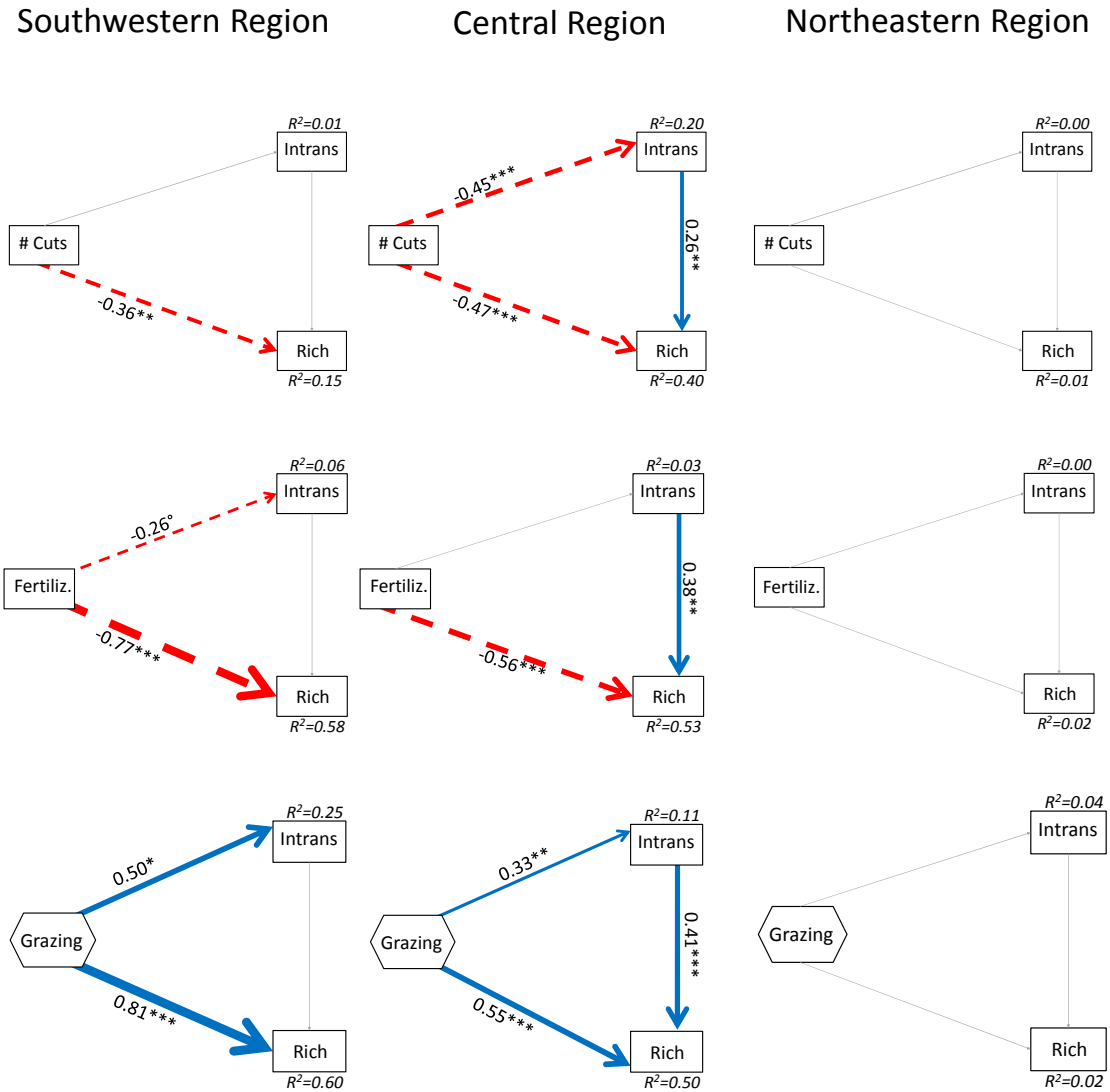
			Intransitivity	Richness
Drylands	Spatial	Latitude	0.85	0.04
		Longitude	0.04	1.00
Grasslands	Land use	Land-use Axis 1	0.88	0.99
		Land-use Axis 2	-0.45	0.09

**Table E2.** Loadings of the different predictors introduced to build the “grazing” composite variables in the regional models for the grasslands dataset (those in Supplementary Information, *Results of the interrelationships between land use, intransitivity and richness for the grassland dataset divided by each region*). Columns are the response variable towards each composite was directed and rows are the predictors introduced in a given composite. Abbreviations are as follow: *I* = intransitivity, SR = species richness.

	SW region		Central region		NE region	
	<i>I</i>	SR	<i>I</i>	SR	<i>I</i>	SR
Permanent grazing	-0.87	-0.19	1.00	0.96	-0.75	1.11
Grazing by sheep	0.49	0.98	-0.06	0.25	1.06	-0.39

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

Fertilization, grazing and mowing exerted the effects reported in the main text regarding intransitivity (see Table 1) in the central region. Grazing also increased both intransitivity and richness in the SW region, and in this same region fertilization also decreased both intransitivity and richness. However, these factors did not affect intransitivity in the rest of the cases (mowing in the SW and any of the factors in the NE; Fig. F1). In the NE region, however, water drainage (which had a negligible effect in the other regions) was the most important management practice for both species richness and intransitivity (results presented in Table 1 in the main text). Water drainage significantly reduced plant richness but increased intransitivity and therefore had an indirect positive effect on richness.



**Figure F1.** Regional structural equation models for the temperate grasslands using each major land use (number of cuts [# cuts]: upper panels; fertilization [fertiliz]: middle panels; grazing: lower panels) as a separate predictor. For the details of the composite variables (those represented as hexagons) see Table D2. The width of arrows is proportional to the standardized path coefficient, with blue and red lines for positive and negative relationships, respectively. Non-significant paths are shown in grey. The R<sup>2</sup> for each variable introduced are given. *P*-values are: \*\*\* = *P* < 0.001; \*\* = *P* < 0.01; \* = *P* < 0.05; ° = *P* < 0.1.