

**INTRANITIVE COMPETITION AND
SPECIES COEXISTENCE**

Functional traits and environmental characteristics drive the degree of competitive intransitivity in European saltmarsh plant communities

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Abstract

1. Competitive intransitivity, the existence of loops in competitive hierarchies, is one mechanism that can promote the local coexistence of competitors and maintain high local species diversity, although its prevalence and importance remain largely unknown. A full understanding of local community assembly needs knowledge of how transitive and intransitive competitive interactions are linked to species functional traits and the strength of biotic and abiotic filters.
2. We apply a recently developed statistical tool to quantitative data on central European inland saltmarsh plant communities to infer causal relationships between soil characteristics, species occurrences and functional traits, and we estimated coefficients of competition.
3. We found a predominance of intransitive competitive hierarchies. The proportion of such hierarchies was positively correlated with local species richness and compositional variability. Average soil characteristics were not correlated with competitive intransitivity, whereas high soil pH and the high variability in local pH and soil salinity decreased the overall impact of competition on community composition. In pairwise comparisons of species, dissimilarity in morphology, resource demand and reproductive phenology was significantly negatively correlated with differences in competitive performance, while higher environmental dissimilarity was particularly linked to intermediate degrees of competitive superiority.
4. Our results suggest that habitat filtering for similar traits might intensify competitive interactions, but might also give rise to intransitive competitive loops that subsequently promote species coexistence and permit species' functional equivalence. Intransitive competition appears to increase local diversity and small scale-species turnover. The observed local differences in competitive structures suggest frequent competitive plasticity and context-dependent competitive interactions. Finally, our results support the view that local abundance distributions can be used to infer the strength and outcome of competitive interactions.
5. *Synthesis.* Our results confirm that intransitive competitive interactions might be a strong force structuring local plant communities. Intransitivity needs to be

considered when studying plant community assembly and species co-existence.

KEY WORDS

competitive hierarchy, halophytes, matrix methods, meta-communities, species co-occurrence

1 | INTRODUCTION

The hypothesis of competitive intransitivity (Gilpin, 1975) has regained attention among ecologists as new empirical approaches (Soliveres et al., 2011; Zhang & Lamb, 2012) and analytical tools (Rojas-Echenique & Allesina, 2011; Ulrich, Soliveres, Kryszewski, Maestre, & Gotelli, 2014) have revealed complex competitive interactions in multi-species ecological communities (Allesina & Levine, 2011; Engel & Wetzin, 2008; Gallien, 2017). Here, intransitivity refers to loops in the hierarchy of competitive interactions in which species A is superior to species B, B is superior to C and C is superior to A. Thus, intransitive competition networks (ICN) involve a minimum of three players, although they can occur in two-species communities if the competitive hierarchy is temporally unstable (Zhang & Lamb, 2012).

Theoretical analyses by Rojas-Echenique and Allesina (2011) and simulation studies by Ulrich, Jabot, and Gotelli (2017) have shown that competitive intransitivity can promote the coexistence of competitors and is, thus, a candidate mechanism for the maintenance of high local (α -)diversity (Laird & Schamp, 2006). For example, in global drylands (Maestre et al., 2012) and temperate grassland communities (Soliveres et al., 2015), the degree of intransitivity is positively correlated with species richness. Far less known is the potential impact of intransitivity on the variability in species composition among local communities, that is, on the degree of species turnover (β -diversity). Recent analyses of ecological drift models (Ulrich et al., 2017) have shown that intransitive competition might either decrease (in dispersal limited communities) or increase (high dispersal) species turnover compared with a simple neutral model. The only published empirical study (Ulrich et al., 2016) reported a positive correlation of spatial species turnover and competitive intransitivity in early plant succession.

Based on the methodological framework of Ulrich et al. (2014), Soliveres et al. (2015) and Ulrich et al. (2016) demonstrated that ICNs of vascular plant communities are more common than previously reported (Gallien, 2017; Grace, Guntenspergen, & Keough, 1993; Keddy & Shipley, 1989) and confirmed a positive correlation between species richness and the frequency of ICNs. This work and prior studies by Freckleton, Watkinson, Dowling, and Ley (2000), Huisman, Johansson, Folmer, and Weissing (2001) and Allesina and Levine (2011) also indicated that the structure of ICNs in local plant communities might vary with changing environmental characteristics. For instance, Soliveres et al. (2015) found that anthropogenic pressure influenced relative competitive strength, Ulrich et al. (2016) reported changes in competitive network structure along

successional gradients, and Huisman et al. (2001) suggested that environmental heterogeneity is an important factor maintaining competitive intransitivity.

Nevertheless, the precise mechanisms that generate and/or maintain ICNs remain largely unknown (Maynard et al., 2015). Of course, the proximate cause for the existence of an ICN is the specific species composition of a focal community. Because species have different functional and life-history traits, it is the particular mix of traits that ultimately maintains ICNs or simple competitive hierarchies (cf. Aschehoug, Brooker, Atwater, Maron, & Callaway, 2016). For example, functional traits of coexisting species are often over-dispersed in plant communities (e.g. Westoby, Falster, Moles, Vesk, & Wright, 2002; Paine, Baraloto, Chave, & Herault, 2011; but see Kusumoto et al., 2016 and Gallien, 2017), and this separation of species in trait space may generate sufficient niche differentiation to permit species coexistence (Adler, Fajardo, Kleinpellink, & Kraft, 2013). However, a different although not mutually exclusive explanation for the observed degree of coexistence is that the mix of competitively counteracting traits, such as root and shoot competition (Zhang & Lamb, 2012), or complementary resource use (Yachi & Loreau, 2007), generates a dynamic balance of competitive strength through ICNs, which allows for species coexistence in spite of high niche overlap. Thus, we interpret ICNs as a cause, not an effect, of high species richness.

The composition of species and their functional traits in a local assemblage is closely linked to the strength of habitat filters through which species have to pass (reviewed in Kraft et al., 2015). As a consequence, environmental conditions determine trait structure and niche overlap, which determines competitive interactions. Trait similarity might also have an indirect effect on species fitness if species of comparable competitive strength have similar niches and reproductive output (Mayfield & Levine, 2010). Further, the stress gradient hypothesis (SGH, Bertness & Callaway, 1994) predicts increased competition at high levels of productivity and increased facilitation at low levels of productivity. Empirical evidence (Callaway, 2007) and theoretical refinements (Maestre, Callaway, Valladares, & Lortie, 2009) have linked increased competition to hierarchical (transitive) competitive structures (pecking orders) and reduced species richness. In this scenario, low productivity might favour “flatter” competitive hierarchies (Snow & Vince, 1984) possibly turning transitive competitive hierarchies into intransitive networks.

Extending the SGH to make explicit predictions about intransitivity, we reason that transitive competitive hierarchies should be found in sites of high productivity and low species richness, whereas ICNs should be found in sites with low productivity and high species

richness. Consistent with that prediction, Soliveres et al. (2015) found ICNs were more common in arid, low productivity sites with high species richness. In addition, increased competition in plants might be linked to limitation of several important resources, including water, light and critical stoichiometric ratios (e.g. N/P or C/N). This resource limitation might favour otherwise competitively inferior species, which tolerate low-resource availability. Thus, species-specific stress tolerance might balance competitive interactions, leading to trade-offs between competitive ability and stress tolerance. Such balanced competitive interactions are another candidate mechanism for competitive intransitivity.

Here, we use an extraordinarily well-documented dataset on European inland saltmarsh communities (Piernik, 2012) to link the structure of the observed competitive hierarchies to the expression and variability of associated plant functional traits and respective environmental characteristics. We first estimated the strength of competitive interactions and the degree of competitive intransitivity by the “reverse engineering” methodology developed by Ulrich et al. (2014), which is to simulate a large set of random species interaction matrices, and retain that matrix that most accurately generates observed relative abundance distributions. We then searched for correlations between soil conditions in each site and the structure of competitive relationships as depicted in the best-fitting species interaction matrices.

Based on theoretical work indicating that environmental heterogeneity should reduce the importance of competition on local community structure (Loreau & de Mazancourt, 2013), we predicted a negative correlation between average competitive strength and variability in soil characteristics (environmental hypothesis 1). We also predict an increase in average competitive strength and an associated increase in transitivity associated with decreasing environmental stress (environmental hypothesis 2) and with decreasing resource availability (environmental hypothesis 3). Respective analyses revealed which particular soil variables were most strongly correlated with competitive hierarchies and ICNs. In addition to testing these predictions, we explored the links between traits, community structure and competitive strength.

Because our data included measures of functional traits of each species, we were able to explore the links between traits, community structure and competitive strength. For this task, we calculated the average overlap in niche space (the functional diversity) and predicted a negative correlation between competitive strength and niche overlap (trait hypothesis 1). We also hypothesized that niche overlap should influence the degree of competitive intransitivity. According to limiting similarity theory (MacArthur & Levins, 1967), competitive interactions and consequently the degree of transitivity should be more pronounced at high niche overlap (trait hypothesis 2).

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

In Europe, inland saltmarshes are spatially and environmentally well-defined (Waisel, 1972) and occur either on fossil salt deposits or

around salty springs (Brandes, 1999) or are of anthropogenic origin (Piernik, Kaźmierczak, & Rutkowski, 1996). Due to the extreme environmental conditions of high ionic concentrations and low nutrient availability, local communities are relatively static and are not dominated by colonization–extinction dynamics. They largely depend on seed bank composition and are relatively stable in species composition (Ungar, 2001). In these assemblages, community structure and relative abundance distributions primarily reflect initial habitat filtering and subsequent species interactions (Alvarez Rogel, Alcaraz Ariva, & Ortiz Silla, 2000). Besides of salinity, local soil and micro-climatic conditions might vary considerably leading to zonal or micro-mosaic vegetation structures (Piernik, Hulisz, & Rokicka, 2015). These features make halophyte communities an ideal object to study the links between competitive relationships, functional traits and local environmental conditions.

To study the relationships between observed species dominances, functional trait and environmental characteristics, and predicted competitive hierarchy, we used quantitative phytosociological survey data from 60 Polish and 24 German inland saltmarshes in Central Europe (Supplementary Material S1a,b; complete dataset in Piernik, 2012). These data include measures of species relative abundance using the nine-step scale of van der Maarel (1979) from a total 188 Polish and 97 German plots, each covering an area of 10 m². This plot size should encompass the local interaction neighbourhoods of most species and is appropriate to assess competitive interactions (McNickle et al., 2017). Nomenclature of vascular plants followed Mirek, Piękoś-Mirkowa, Zająć, and Zająć (2002). In total, we found 154 species and *Taraxacum officinale* was included as a collective taxon (Supplementary Material S1b).

From the Leda database (Kleyer et al., 2008; Supplementary Material S1c), we obtained species-level measures of one reproductive trait (seed mass, SM) and three morphological traits (specific leaf area, SLA; leaf dry matter content, LDMC; canopy height, CH). We also used five soil properties measured in each plot that were previously shown (Piernik, 2005) to have a strong influence on saltmarsh vegetation: soil moisture (H), organic carbon content (C_{org}), total nitrogen content (N_{tot}), dissolved salt ratio (DSR = Ca²⁺/Na⁺) and salinity, expressed as electrical conductivity of the saturated extract (EC_e; Supplementary Material S1d). Within each of the 84 saltmarshes, we estimated variability in soil characteristics among the plots from their respective coefficients of variation (CV). In addition, we compiled species-level data on their environmental requirements, as obtained from the Ellenberg values for humidity, pH, nitrogen and salt (Ellenberg et al., 1992). These traits are closely related to the habitat demands of a focal species. Missing data at the plot level (<10% of all observations) were replaced by plot medians.

2.2 | Data analysis

To assess species competitive strength, we used the “reverse engineering” approach of Ulrich et al. (2014). This approach simulates a large number (here 100× matrix size) of trial $m \times m$ competitive interactions matrices \mathbf{C} (m species) to find the one that best predicts

equilibrium species dominance order. Species completely missing at a site were always excluded from the simulations for that site. Ulrich et al. (2014) provided extensive tests of this approach and demonstrated that it identifies sets of matrices that capture the structure of underlying competitive interactions if such interactions were the major process for generating species abundances.

Ulrich et al. (2014) showed that a competition matrix \mathbf{C} can be unequivocally translated into an associated transition matrix \mathbf{P} . In a Markov chain process, the dominant eigenvector (EV) \mathbf{U} of \mathbf{P} is an estimate of the equilibrium species relative abundance. Following Ulrich et al. (2014) and Soliveres et al. (2015), we identified the best \mathbf{C} matrix from the average Spearman rank order correlation r_s of \mathbf{U} and the observed relative abundance per plot (cf. Supplementary Material S2a for a flow diagram of the method). Thus, r_s is a metric of whether and how close observed abundance distributions can be generated by competitive interactions alone. High environmental heterogeneity generally limits the impact of competition on observed species abundances (Dufour, Dagallah, Wagnr, Guisan, & Buttler, 2006) and consequently might reduce r_s values. r_s might, therefore, also be cautiously interpreted as a measure of the relative importance of competitive and other (often environmental) forces on species abundances.

Competition matrices allow for the quantification of the degree of competitive intransitivity, that is, the degree to which linear competitive hierarchies ($A > B > C > D$) are punctuated by competitive reversals (e.g. $A > B < C > D$). Because the impact of each reversal on species abundances depends on its position in the competitive chain, we used the nestedness concept to weight each reversal by its position, giving highest weight to position in the upper right corner of \mathbf{C} after sorting the \mathbf{C} matrix according to the row and column degree distributions. We used the temperature metric of nestedness as advocated by Laird and Schamp (2006) (further explained in Supplementary Material S2b) for quantifying the degree of transitivity τ_N .

Following Atmar and Patterson (1993), the nestedness degree of transitivity is the unity complement of the average squared distance (d) of a competition value <0.5 (a hole) from the upper right matrix triangle of the ordered occupancy matrix divided by the total squared length (L) of respective diagonal line to the matrix border. The competition matrix has to be sorted by marginal totals prior to analysis to ensure a maximum number of competition values >0.5 in the upper right triangle. Ulrich et al. (2014) used a simpler metric (τ_C) for competitive transitivity, which is the count of all transitive relationships in the competitive strength matrix normalized by the number of species pairs (Soliveres et al., 2015; Ulrich et al., 2014). Both approaches gave qualitatively similar results but τ_C appeared to be of lower discrimination power. Therefore, we show the results only for τ_N and provide results for the count metric τ_C in Supplementary Material S3. We note that the theoretical derivation in Ulrich et al. (2014) assumes environmental homogeneity. As mentioned above, heterogeneity within each site might decrease r_s and the uncertainty in the estimates of competitive strength might increase. Therefore, we calculated r_s , τ_N and τ_C for each plot and used the respective average values per site in subsequent calculations. As low r_s values

indicate that competitive effects are of minor importance, we considered only that 40 sites with $r_s > 0.6$ (cf. Soliveres et al., 2015). We note that the results remained qualitatively unchanged using all 84 sites. Including the 44 sites where competition was of minor impact did mainly increase the noise in the data.

For each pair of species present at each site (16,638 species pairs), we calculated the Euclidean distances in functional trait and environmental (soil) space. Prior to analysis trait and environmental variables were normalized by the common Z-transformation ($Z = \frac{x - \mu}{\sigma}$), where μ and σ are the mean and standard deviation of the vector x . With respect to the environmental distances, we used only plots in which the focal species was present. In the case of species traits, we calculated for each species pair separate distances for soil demands (Ellenberg scores of pH, nitrogen, salt and humidity demands), morphology (specific leaf area, leaf dry matter content and CH) and reproduction. To compare pairwise distances in trait and environmental space with the respective competitive coefficients, we grouped the competitive coefficients of the competitively stronger species into nine classes (0.5–0.6, 0.65–0.7, ..., 0.95–1.0) and calculated for each group average trait and environmental distances. Values less than 0.6 indicate that the two species differed by $\tau_N < 0.2$. This was interpreted as no effective competitive difference. Because environmental distances and competitive coefficients tend to be noisy at low sample sizes, we show only the results for sites with at least five plots ($N = 8,517$ species pairs). To confirm that our results are independent of this arbitrary cut-off, we present in the Supplementary Material S3 respective results for three-site ($N = 11,490$) and eight-site ($N = 4,936$) cut-offs. In addition, we used Mantel correlations to relate the competitive strength matrices to the associated functional trait Euclidean distance matrices. Because this analysis was based on competitive coefficients between pairs of species, a positive correlation indicates that competitive superiority is linked to low niche overlap. We assessed the average dissimilarity in trait space per plot by the mean functional attribute diversity (MAD), which is calculated from the sum of the pairwise Euclidean distances (FAD, Walker, Kinzig, & Langridge, 1999) divided by the number of these pairs. This dissimilarity measure has been shown to be least dependent on species richness compared with other measures of trait space (Petchey & Gaston, 2006). Accordingly we calculated the mean environmental diversity (MED) as the sum of Euclidean distances in soil characteristics averaged over all pairs of species.

We linked the competitive strength matrices as quantified by r_s and τ_N of each study site, local species richness and turnover (α - and β -diversity, respectively), and the respective matrices of functional traits and soil conditions. We quantified β -diversity from the degree of proportional species turnover $\beta = 1 - \frac{\alpha}{\gamma}$ (Tuomisto, 2010), where α is the average number of species per local plot and γ is the total local species richness. For testing the trait hypotheses, we fitted general linear models to characterize the relationship between functional attribute diversity (MAD) and r_s and τ . As the data came from geographically clustered sites in Central Europe, the spatial structure might influence significance levels (spatial autocorrelation). Thus, we included the dominant EV of the geographical Euclidean distance matrix of the

TABLE 1 General linear modelling linking average soil parameters (natural logarithm of total dissolved salt ratio, ln DSR; natural logarithm of conductivity, ln EC_e; soil pH and moisture) to α - and β -diversity ($N = 77$), potential impact of competition (r_s) and transitivity (τ_N) (both $N = 40$). Given are beta values and effect sizes (partial η^2). Total abundance (N_{total}) and the dominant eigenvector (EV1) of the geographical distance matrix of sites served as covariate. Parametric significances: * $p(F) < .05$; ** $p < .01$; *** $p < .001$

Effect	α -diversity		β -diversity		r_s		τ_N	
	Beta	Partial η^2	Beta	Partial η^2	Beta	Partial η^2	Beta	Partial η^2
N_{total}	0.38	0.09*	0.19	0.01	-0.17	0.03	-0.31	0.05
ln DSR	-0.15	0.03	0.04	<0.01	0.03	<0.01	0.29	0.07
ln EC _e	-0.27	0.07*	0.07	<0.01	-0.31	0.07	0.1	0.01
pH	0.04	<0.01	0.06	<0.01	-0.41	0.07	0.42	0.10*
Moisture	-0.21	0.03	-0.17	<0.01	0.06	0.07	0.04	<0.01
τ_N	-0.22	0.08*	0.09	<0.01	-0.31	0.1	–	–
EV1	-0.35	0.12**	0.13	0.01	-0.21	0.03	-0.3	0.09
r^2 (model)	.45***		.05		.12		.28*	

TABLE 2 General linear modelling linking the variability of soil parameters (natural logarithm of total dissolved salt ratio, ln DSR; natural logarithm of conductivity, ln EC_e; soil pH and moisture) (quantified by the coefficient of variation CV) to α - and β -diversity ($N = 77$), potential impact of competition (r_s) and transitivity (τ_N) (both $N = 40$). Given are beta values and effect sizes (partial η^2). Total abundance (N_{total}) and the dominant eigenvector (EV1) of the geographical distance matrix of sites served as covariate. Parametric significances: * $p(F) < .05$; ** $p < .01$; *** $p < .001$

Effect	α -diversity		β -diversity		r_s		τ_N	
	Beta	Partial η^2	Beta	Partial η^2	Beta	Partial η^2	Beta	Partial η^2
CV N_{total}	-0.02	<0.01	0.08	0.01	-0.12	0.01	<0.01	<0.01
CV DSR	-0.09	0.01	0.12	0.02	-0.16	0.04	0.12	0.01
CV EC _e	0.04	0.01	0.35	0.14***	-0.11	0.04	-0.17	0.01
CV pH	0.03	<0.01	0.30	0.13***	-0.18	0.01	-0.04	<0.01
CV moisture	0.14	<0.01	0.11	<0.01	-0.38	0.11*	0.19	0.02
τ_N	-0.29	0.10**	0.06	0.01	0.08	0.01	–	–
EV1	-0.43	0.20***	0.24	0.12**	-0.26	0.12*	-0.16	0.02
r^2 (model)	.30***		.57***		.53***		.06	

study sites as covariate in these analyses (Dray, Legendre, & Peres-Neto, 2006). This EV covers information on the broad geographical structure of the study sites and explains 94% of variance. We tested the environmental hypotheses with a similar approach and used average values of C_{org}, N_{total}, DSR, EC_e and pH, as well as the respective CV as predictors of species richness and competitive structure in general linear modelling, and again EV as covariates. DSR and EC_e entered the model as log-transforms to avoid non-linearity. As a complement to these analyses, we used structural equation modelling (covariance based SEM with maximum likelihood parameter estimation as implemented in Statistica 12.0) to explore the relative strength of different cause-and-effect relationships among these variables.

3 | RESULTS

High soil organic carbon (C_{org}) and nitrogen (N_{total}) content and low salinity (EC_e) were positively associated with higher plot α -diversity,

but not higher β -diversity (Figure S3a). After spatial autocorrelation was accounted for, nitrogen and salinity remained significantly linked to α -diversity (Table 1, Table S3a). In turn, variability in soil characteristics among plots (Figure S3b), particularly in salinity and pH (Table 2, Table S3b), was consistently positively correlated with higher β -diversity but was not correlated with α -diversity (Table 2, Figure S3a). α - and β -diversity were marginally negatively correlated ($r = -0.08$, $p > .1$).

Only 40 of the 84 sites ranged above the cut-off level of $r_s > 0.6$, indicating that competitive interactions might have structured these communities. r_s was independent of α -diversity (Figure 1a) and decreased with local species turnover (Figure 1b). Soil characteristics did not markedly influence the competitive structure at the plot scale (Figure S3d, Table 1, Table S3a). Environmental variability, particularly with respect to conductivity and pH, was negatively correlated with r_s (Table 2, Table S3b, Figure S3) and influenced competitive hierarchy. Perfect transitivity occurred only at low variability in salinity (one-way ANOVA $p(F_{1,82}) < .001$) and pH ($p(F_{1,82}) < .01$).

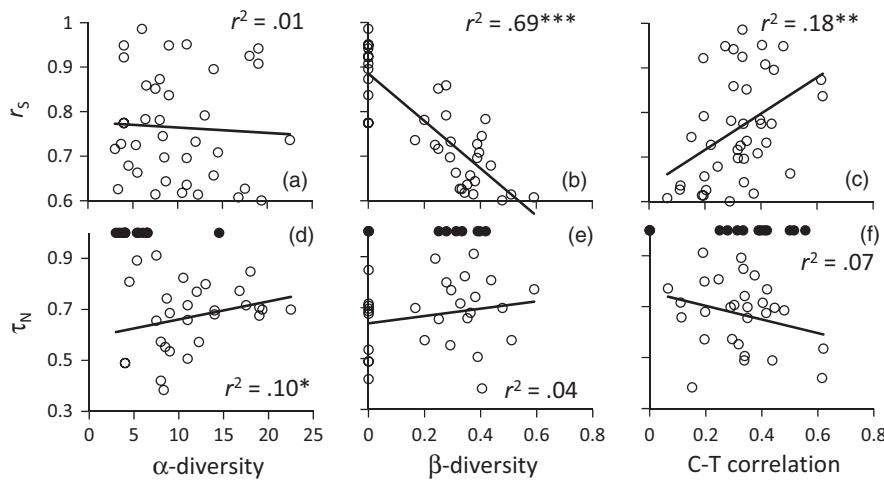


FIGURE 1 In saltmarsh communities, the possible impact of competition (quantified by r_s) was independent of α - (a) and decreased with β -diversity (b). The degree of transitivity τ_N increased with α - (d) and β -diversity (e). The correlation between pairwise morphological trait dissimilarity and competitive strength (C-T correlation) increased with r_s (c) and decreased with τ_N (f). Parametric significances: $^*p < .05$; $^{**}p < .01$; $^{***}p < .001$

We found only 15 communities (17.9%) with a perfect competitive hierarchy, most of them having low α - and β -diversity (Figure 1a,b, Table 1). However, in intransitive communities, τ_N significantly increased with increasing average plot α - and site β -diversity (Figure 1d,e, Table 1), while τ_C was uncorrelated with α - and site β -diversity (Table S3a,b, Figure S3c). Average soil characteristics were not related to τ_N (Tables 1 and 2) and τ_C (Table S3a,b).

Mean functional attribute diversity, but not MED, was significantly negatively correlated with α -diversity (Figure S3f). This means that additional species do not contribute proportionally to trait diversity because they introduce traits already present in the community. MAD based on Ellenberg scores and morphological traits were positively correlated with r_s (Figure 2b,c) and negatively with τ_N (Figure 2f,g), even after accounting for species richness effects and the geographical distribution of study sites (Table 3). In turn,

τ_C was not significantly related to environmental and trait diversity (Figure S3g).

In a pairwise approach, we compared Mantel correlations between the competitive strength and morphological trait distance matrices, which captures the relationship between competitive superiority and niche overlap with r_s (Figure 1c) and τ_N (Figure 1f). All but one pairwise correlation (98.9%) were positive, indicating that high morphological segregation was associated with strong competitive hierarchies. Strong associations were also shown for resource demand traits (100% of pairs) and reproductive traits (80.6% of pairs; data not shown). When comparing among all study sites, the higher the potential impact of competition, the higher the correlation (Figure 1c). Similarly, competitive transitivity was negatively related to the correlations between pairwise competitive strength and trait distance (Figure 1f).

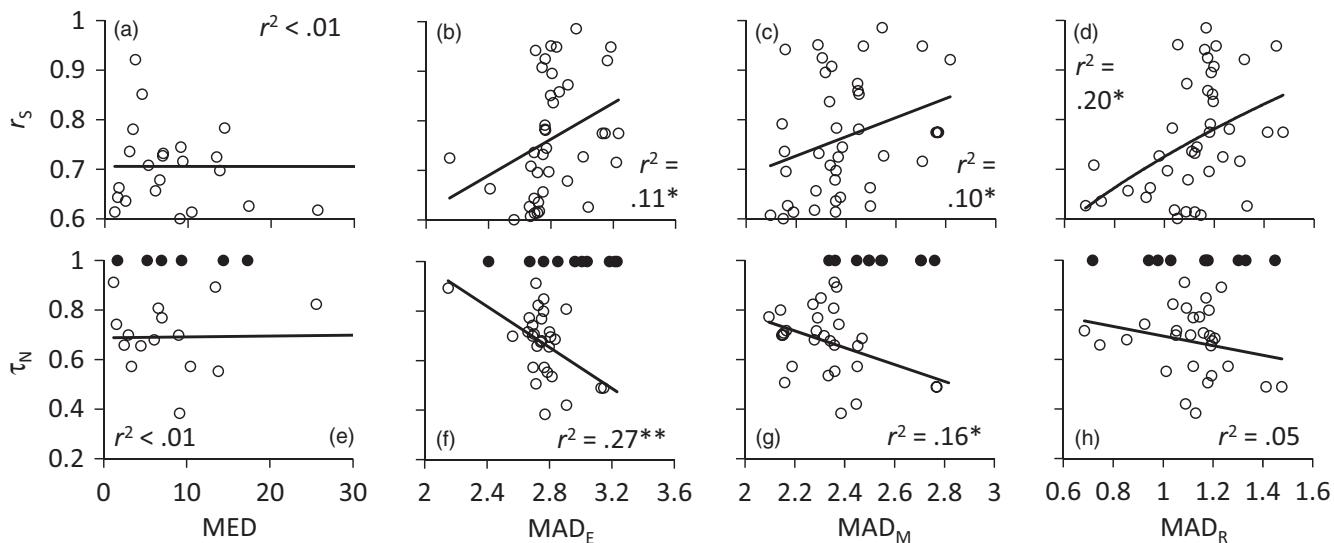


FIGURE 2 In saltmarsh communities, the possible impact of competition (quantified by r_s) and the degree of transitivity (τ_N) was independent of local environmental diversity (a, d) while r_s increased (b-d) and τ_N decreased with trait diversity (f-h). Parametric significances: $^*p < .05$; $^{**}p < .01$. MED: the environmental diversity calculated from the average of Euclidean distances in soil characteristics. MAD: mean functional attribute diversity calculated from Ellenberg indicator values (MAD_E), morphological (specific leaf area, leaf dry matter content and canopy height: MAD_M) and reproductive (seed mass: MAD_R) traits

TABLE 3 General linear modelling identified morphological functional attribute diversity (MAD_M) but not mean environmental diversity (MED) as influencing τ_N and r_s . Given are beta values and effect sizes (partial η^2). The dominant eigenvector (EV1) of the geographical distance matrix of sites and α -diversity served as covariate. $N = 40$. * $p < .05$, ** $p < .01$

Effect	r_s		τ_N	
	Beta	Partial η^2	Beta	Partial η^2
MAD_M	0.93	0.27**	0.58	0.11
MED	0.01	0.13	0.20	0.04
α -diversity	0.29	0.04	-0.03	0.01
EV1	-0.04	0.01	-0.10	0.01
r^2 (model)	.37**		.29*	

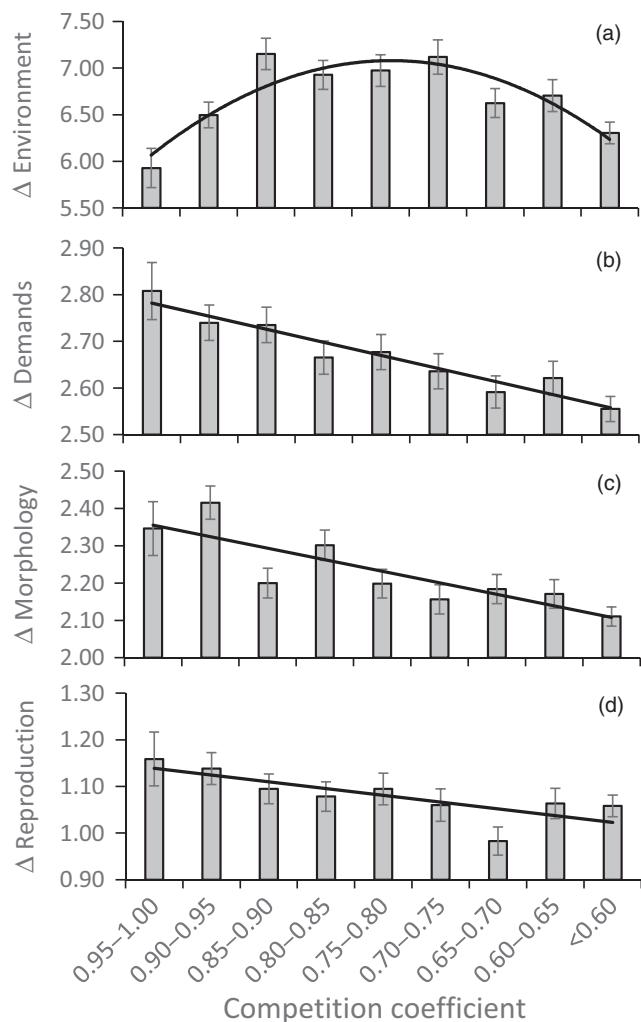


FIGURE 3 Euclidean distances in environmental space (a), habitat demands (b), morphology (c) and seed mass (d) decreased with competitive dominance in pairwise species comparisons in all studied inland saltmarshes with at least five plots ($N = 8,517$). Second-order OLS regression in a: $r^2 = .81$, $p(F) < .001$; first-order OLS regression in b: $r^2 = .92$, $p(F) < .001$; in c: $r^2 = .71$, $p(F) < .01$; in d: $r^2 = .61$, $p(F) < .05$. Error bars denote one standard error (SE)

We further compared the estimated competition coefficients with associated pairwise dissimilarities in functional trait and environmental niche space (Figure 3). Environmental niches differed most at an intermediate degree of competitive superiority (Figure 3, Figure S3h). High competitive superiority, but also similar competitive strength, was, on average, associated with relatively high environmental similarity (Figure 3a, Figure S3h). In turn, differences in resource demands tended to be highest for species pairs with marked differences in competitive strength (Figure 3b, Figure S3h). Species pairs with equal competitive strength were, on average, also similar in resource demand. These results were independent of differences in local occurrence: a general linear model that included the numbers of occurrences of both species as covariates also returned a highly significant effect for competitive strength ($F_{8,8506} = 4.4$, $p < .0001$, data not shown).

Pairwise dissimilarity in morphological and reproductive trait space was negatively correlated with the difference in competitive strength (Figure 3c,d, Figure S3h). Irrespective of trait type (morphology and reproduction), high competitive superiority was associated with dissimilarity in trait space. With respect to morphology, but not to SM, this result was again independent of species occurrences (morphology: $F_{8,8506} = 5.9$, $p < .0001$, SM: $F_{8,8506} = 1.8$, $p > .05$, data not shown).

4 | DISCUSSION

4.1 | Environmental triggers of competitive intransitivity

Our initial hypothesis predicted that variability in soil characteristics should decrease average competitive strength, which implies that highly variable or disturbed habitats should harbour plant communities less structured by competitive interactions and governed by intransitive competitive loops. Therefore, we linked specific habitat filter regimes with subsequent competitive structures as predicted by the hierarchical concept of filtering for species functional traits (de Bello et al., 2013; Grime, 2006). Indeed, a recent study of alpine plant community assembly (Takahashi & Tanaka, 2016) found particularly plant height and specific leaf area to be filtered for and to decrease with increasing elevation and pH. Our study is in line with these predictions (Table 3), and our analyses revealed that dissimilarity in these traits was positively correlated with competitive transitivity in pairwise comparisons (Table 3, Figure 3).

These results suggest that filtering effects may not only shape community composition but may also influence the competitive structure of these communities. Filtering for similar traits might intensify competitive interactions, but might also give rise to intransitive competitive loops that subsequently allow species coexistence. This latter scenario suggests that competitive intransitivity mediated by environmental filtering might increase species' functional equivalence, possibly leading to comparable species fitness and to increased probability of species coexistence. This mechanism might explain the random assortment of functional traits in

subtropical forest communities in spite of strong environmental filtering (Kusumoto et al., 2016).

We found the predicted negative correlations between competitive strength and variability in soil characteristics, particularly in pH and conductivity, the latter reflecting soil cation exchange capability and salinity (Table 2, Figure S3e). Respective effects on the degree of transitivity were mediated by local diversity (Figure 1a,b). Soil conductivity is the major determinant of species composition and richness in other saltmarsh plant communities (e.g. Cantero, Cisneros, Zobel, & Cantero, 1998). Because earlier theoretical (Ulrich et al., 2017) and empirical (Soliveres et al., 2015) studies linked competitive intransitivity to increased total species richness, we also expected to see a positive correlation between soil variability and the variability in species composition among local plots (β -diversity). This was indeed the case (Table 2). Our findings, thus, indicate that at least in these communities high variability in soil salt content and pH favours communities without strong competitive hierarchies and increased local diversity. In this respect, the SGH (Bertness & Callaway, 1994) predicts an increase in mutualistic and a decrease in competitive interactions in severe environments. Our results indicate that environmental variability and stress might have similar ecological consequences. Stress and variability might not only moderate the impact of competition (Table 2) but also support intransitive competitive hierarchies (Figure S3e).

Our second hypothesis predicted a decrease in competitive transitivity with decreasing environmental stress. Again this relationship was mediated by environmentally determined community composition (Figure 1). Major stressors in saltmarsh communities were high salinity and high pH that induce strong environmental filters and reduced species richness and recruitment (Reimold & Queen, 1974). We expected to see these stressors affect community composition in a way that favours pronounced competitive hierarchies. Indeed, we found a strong link of increased salinity with low plot species richness (Figure S3a). However, we did not

find evidence for a direct effect of salinity and pH on the degree of competitive transitivity (Table 1, Figure S3d). Interestingly, Matias, Godoy, Gomez-Aparicio, and Pérez-Ramos (2018) reported increased levels of competitive reversals (intransitivity) at higher levels of environmental stress in pairwise plant sowing experiments. These and our results strongly point to a complex pathway of competitive structure but not to direct impacts of environmental states on the competitive network.

Our third hypothesis predicted increasing resource availability to favour competitive intransitivity. This was not the case (Table 1). Soil organic carbon and soil nitrogen content and their respective variability did not significantly influence competitive structure (Table 1, Figure S3d) and the potential impact of competition (Table 2). In this respect, Soliveres et al. (2018) reported intransitive competition to be less likely under fertile habitat conditions. Nonetheless, nitrogen and carbon were positively linked to α - and β -diversity (Figure S3a,b). These results again point to a complex pathway of indirect effects of soil variables on species interactions (Figure 1).

Complex relationships between ecological variables are not readily disentangled by a conventional statistical framework such as general linear modelling. In the present case, the species diversity mediated pathways to competitive structure that might be the result of statistical non-independencies and loops of influence between the variables. For example, trait expression (Table 3, Figure 2) and average habitat conditions (Table 1, Figure S3a,b) influenced local species richness and directly or indirectly possible competitive relationships. In addition, variability in habitat conditions (Table 2) might directly affect competitive structures or indirectly influence on the degree of spatial or temporal species turnover. Finally, the spatial structure of the study sites and, therefore, autocorrelative effects might mask important ecological relationships. To unravel these pathways and to develop additional hypotheses for the determinants of local competitive structures, we first constructed

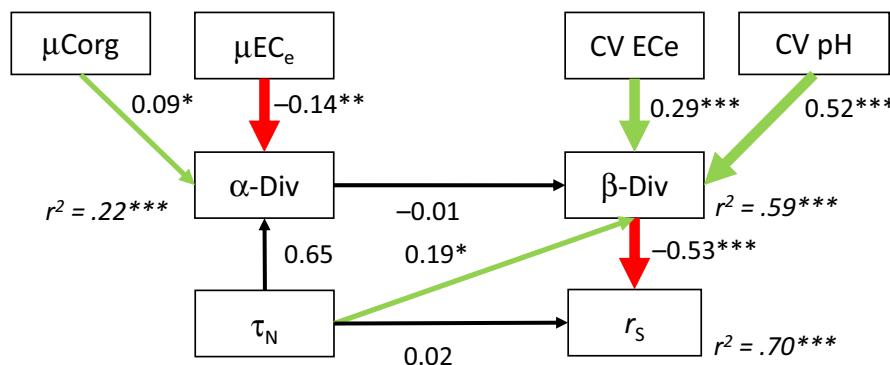


FIGURE 4 Structural equation modelling including α - and β -diversity, average soil parameters (μ) and respective coefficients of variation (CV) of soil organic carbon (C_{org}), soil salinity (EC_e) and pH, as well as the degree of transitivity τ_N , and the potential impact of competition r_s pointed to major pathways influencing the degree of α - and β -diversity. Parametric statistical support: * $p < .05$; ** $p < .01$; *** $p < .001$. r^2 values for each target variable are given in italics. Thickness of arrows is approximately proportional to statistical support of positive (green) and negative (red) influences. Whole model $\chi^2 = 21.2$, $p > .30$ ($df = 19$). Root mean square error = 0.09 (90% confidence limits: 0.00–0.10) [Colour figure can be viewed at wileyonlinelibrary.com]

a complex path analytical model that reflected the pairwise relationships indicated by our results (Tables 1–3, Figures 1 and 2, Figure S3a–e). The best model (Figure 4) with regard to predictive power (χ^2/df ratio = 1.11) corroborated our basic findings, revealing significant positive effects of salinity, pH and organic carbon content on local richness but no significant direct effect on the degree of transitivity (Figure S3d,e).

Importantly, the model predicted high transitivity to increase β -diversity, whereas the reverse path was statistically not supported. This result may be interpreted as an indication that competitive hierarchy and environmental clues jointly determine local richness and also species composition. The model did not return a significant positive influence of transitivity on local richness. However, we note that more than 90% of our communities were identified as containing intransitive loops. Perfect competitive transitivity occurred only in comparably species poor local communities. Thus, our results corroborate the findings of Ulrich et al. (2017), who found a similar cause–effect relationship in competitively structured ecological drift models. Our analysis also supports the findings of Soliveres et al. (2015), who reported a similar positive relationship between transitivity and species richness in temperate grassland and dryland plant communities.

The path analytical model is also consistent with our findings regarding habitat variability (Table 2) and demonstrated a significant positive relationship between variability and β -diversity (Figure 4). However, the path model did not point to a direct influence of habitat variability on transitivity. Instead, environmental variability determined the turnover of species among local plots and, therefore, the degree of spatial segregation. Together with the finding of a direct influence of competitive structure on the spatial patterning of species, our results suggest that strong competitive hierarchy in combination with local filter effects might cause increased species turnover and consequently a spatial segregation of species as predicted by community assembly theory (Diamond, 1975). Indeed, recent theoretical work also predicts strong interspecific competition to affect the spatial pattern of species co-occurrences, although the specific way may depend on landscape structure and dispersal ability (Ulrich et al., 2017). Specifically, the model in Ulrich et al. (2017) pointed to an increased degree of β -diversity among communities in case of transitive competitive hierarchies and low dispersal while high dispersal rates caused the opposite effects. Given that the halophyte species of our study are comparably weak dispersers, the findings corroborate the model of Ulrich et al. (2017). In turn, indication of increased faunal homogenization (reduced β -diversity) under strong competitive regimes has from recent observations on dispersive Australian farmland bird communities (Robertson, McAlpine, House, & Maron, 2013). In halophytic communities, compositional homogenization has been linked to stress adaptation (Flowers & Colmer, 2015). For instance, at highest salinity, only few species are able to survive. Clearly, the links between compositional homogenization and types of competitive interactions need further study.

4.2 | Species functional traits and competitive intransitivity

Our trait hypotheses predicted a negative correlation between the competitive impact on community composition (estimated by r_S) and niche overlap. Saltmarsh plant species sharing similar functional traits should have similar competitive performance. This was indeed the case (Figure 2, Table 3). In pairwise comparisons, morphological, resource demand and reproductive traits but not environmental dissimilarity was significantly negatively correlated with difference in competitive performance (Figure 3). This result implies that niche differences indeed tell something about the strength and the outcome of species interactions. Our results are also in line with limiting similarity theory (MacArthur & Levins, 1967), which predicts that species with similar functional traits linked to possible niche overlap should compete more intensely (have similar τ_C coefficients) than functionally dissimilar species.

A next step in this route of analysis should be to compare the spatial distribution of functional traits in relation to competitive and niche dissimilarity. The competitive exclusion principle (Gause, 1934) predicts species of high performance to exclude competitors leading to low local diversity in trait space and marked differences in reproductive success (fitness). Although there is evidence for a spatial patterning of plant genetic structures in dependence of the presence of competitors (Matesanz, Gimeno, de la Cruz, Escudero, & Valladares, 2011) and of non-random assortment of functional traits possibly reflecting competition (Gallien, 2017), we are not aware of any study that compared the geometry of traits with the pattern of competitive performance and of plant fitness. Thus, the impact of competitive intransitivity on the fitness landscape of a community remains unclear. The effects of niche and competitive differentiation on the spatial distribution of traits need also further study.

4.3 | Performance of the Markov chain approach to competitive intransitivity

Our method to estimate competitive impact and coefficients of competitive strength uses observed abundance distribution as the standard (Ulrich et al. 2014). This raises the question whether these coefficients reflect real species interactions or whether they are merely transforms of abundance differences. Here, we took the opportunity to compare the estimated coefficients with species functional traits. If these coefficients reflect interactions, they should be related to those traits linked to competition. Previously, SM (Turnbull, Coomes, Hector, & Rees, 2004), leaf area and dry matter (Wilson, Thompson, & Hodgson, 1999), and soil nutrients (Zhu, Riley, Tang, & Koven, 2016) have been shown to determine competitive interactions. Consequently, we expected to see significant relationships between traits and estimated competitive strength coefficients. This was indeed the case (Table 3, Figures 1c,f, 2 and 3). Empirical species traits were generally significantly correlated to the associated competitive coefficients. Even more, the observed positive correlations between pairwise trait dissimilarity

and competitive superiority (Table 3, Figure 1f) are in line with the expectation that species similar in morphology or other functional traits should also be similar in competitive performance (MacArthur & Levins, 1967). We interpret these results as a corroboration of the method used in Ulrich et al. (2014), Ulrich et al. (2017) and Soliveres et al. (2015).

Interestingly, the two metrics designed to quantify competitive transitivity, τ_N and τ_C , partly behaved differently. This contrasting performance is best seen by the positive and negative correlations of τ_N and τ_C , respectively, with α - and β -diversity (Figure 1, Figure S3c) although both transitivity metrics were significantly positively correlated ($r = .44$, $p(F_{1,82}) < .0001$) and thus capture a similar pattern. Prior work on the positive effect of competitive intransitivity on species richness used the count metric τ_C that provides the proportion of intransitive loops within the competitive hierarchy. Our results confirmed that high intransitivity was associated with increased local richness (Figure S3c). However, the richness effect may be context dependent. When focusing on the strength of each loop and its possible total effect on the competitive dynamics, a different picture appears. Again perfect transitivity occurred only in small communities (Figure 1). However, in intransitive communities, the strength of intransitivity increased with community size (Figure 1). These contrasting results warn against premature conclusions about the impact of intransitivity. On the other side, the use of two metrics might provide a better insight into the mechanisms of competitive dynamics.

4.4 | Outlook

Competitive relationships and whole networks are not static. They are context dependent and vary with environmental conditions (Chamberlain, Bronstein, & Rudgers, 2014), indicating a respective competitive plasticity. For instance, Turcotte and Levine (2016) reported that plant species are able to directly adjust their competitive performance to local environmental conditions. Our study was not targeted to reveal this plasticity. However, the finding that saltmarsh competitive networks clearly varied with environmental conditions despite of the limited number of associated species strongly suggests local adaptations of competitive relationships. Future work has to reveal the species-specific variability in competitive performance. Our methods of estimating competitive strength provide a tool for this task.

We currently lack a quantitative theory that foresees the degree of competitive intransitivity from the set of functional traits. Given that the specific expression of traits determines competitive performance, we wish to predict the outcome of competition (and possibly other forms of species interactions) from these traits. Limiting similarity (MacArthur & Levins, 1967) aimed at this goal but remained largely qualitative and mainly restricted to the two-species case (Abrams, 1983). Early quantitative extensions to multi-species communities (Roughgarden, 1979) did not converge to a unified theoretical approach. We hope that the present special edition of *Journal of Ecology* on intransitive competitive networks inspires the development of such a quantitative theory.

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AUTHORS' CONTRIBUTIONS

W.U. conceived the study, analysed the data and wrote the first draft; A.P. contributed the raw data; A.P. and Y.K. provide plant ecological and N.J.G. theoretical input. All authors contributed to the final version.

DATA ACCESSIBILITY

Data used in this study have been archived in Figshare: <https://doi.org/10.6084/m9.figshare.5777532.v1> (Ulrich & Piernik, 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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