

**INTRANSITIVE COMPETITION AND SPECIES COEXISTENCE**

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Intransitive competition is common across five major taxonomic groups and is driven by productivity, competitive rank and functional traits

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Abstract

1. Competition can be fully hierarchical or intransitive, and this degree of hierarchy is driven by multiple factors, including environmental conditions, the functional traits of the species involved or the topology of competition networks. Studies simultaneously analysing these drivers of competition hierarchy are rare. Additionally, organisms compete either directly or via interference competition for resources or space, within a local neighbourhood or across the habitat. Therefore, the drivers of competition could change accordingly and depend on the taxa studied.
2. We performed the first multi-taxon study on pairwise competition across major taxonomic groups, including experiments with vascular plants, mosses, saprobic fungi, aquatic protists and soil bacteria. We evaluated how general is competition intransitivity from the pairwise competition matrix including all species and also for each possible three-species combination (triplets). We then examined which species were likely to engage in competitive loops and the effects of environmental conditions, competitive rank and functional traits on intransitive competition.
3. We found some degree of competition intransitivity in all taxa studied, with 38% to 5% of triplets being intransitive. Variance in competitive rank between species and more fertile conditions strongly reduced intransitivity, with triplets composed of species differing widely in their competitive ranks much less likely to be intransitive.

4. Including functional traits of the species involved more than doubled the variation explained compared to models including competitive rank only. Both trait means and variance within triplets affected the odds of them being intransitive. However, the traits responsible and the direction of trait effects varied widely between taxa, suggesting that traits can have a wide variety of effects on competition.
5. *Synthesis.* We evaluated the drivers of competition across multiple taxa and showed that productivity and competitive rank are fundamental drivers of intransitivity. We also showed that not only the functional traits of each species, but also those of the accompanying species, determine competition intransitivity. Intransitive competition is common across multiple taxa but can dampen under fertile conditions or for those species with large variance in their competitive abilities. This provides a first step towards predicting the prevalence of intransitive competition in natural communities.

KEYWORDS

bacteria, bryophytes, competition hierarchy, functional traits, protists, rock-paper-scissors, saprobic fungi, vascular plants

1 | INTRODUCTION

The lack of competition hierarchy (intransitive competition) is the equivalent to the rock-paper-scissors game in that no single species out-competes all the others, and therefore local extinctions are avoided (Gilpin, 1975; Laird & Schamp, 2006; Rojas-Echenique & Allesina, 2011). Intransitive competition can occur if there are reciprocal competitive advantages. For example, a system could exhibit an intransitive loop if species A competes more effectively for nutrients than species B ($A > B$), B out-competes C ($B > C$), but C is able to prevent resource uptake, reproduction or growth by species A through interference competition, for example the production of allelochemicals ($C > A$; Aarsen, 1992; Gallien, 2017; Lankau & Strauss, 2007). Intransitive competition is gaining attention as a potential mechanism for species coexistence (Allesina & Levine, 2011; Laird & Schamp, 2006; Maynard, Bradford, et al., 2017; Soliveres et al., 2015) and could also affect other important community and ecosystem attributes such as spatial patterning, sensitivity to exotic invasions or diversity-function relationships (Henriksson, Wardle, Trygg, Diehl, & Englund, 2016; Maynard, Crowther, & Bradford, 2017; Vandermeer & Yitbarek, 2012).

In general, all taxa within a trophic level and with similar environmental preferences will compete against each other for key resources directly (e.g. nutrient uptake) or indirectly (e.g. allelopathic compounds), although the relative importance of resource or interference competition can vary substantially between organisms. For example, mosses, intertidal organisms or fungi might compete mostly for space and this competition can be dominated by interference mechanisms, which individuals use to prevent overgrowth by others (Buss, 1980; Maynard, Bradford, et al., 2017). Conversely, plants, protozoa or bacteria may compete more directly for resources although sessile organisms do so more locally than mobile organisms.

Intransitivity in competition networks may decline in well-mixed communities (Laird & Schamp, 2015; Reichenbach, Mobilia, & Frey, 2007; Yitbarek & Vandermeer, 2017) and therefore could be less common for mobile taxa. Despite intransitive competition has been described in many taxa (see reviews in Gallien, 2017; Soliveres & Allan, 2018), the wide range of ways in which different organisms can compete has been seldom considered. The lack of studies applying common methodologies across taxonomic groups, together with the different prevailing modes of competition within each taxon, limits our capacity to evaluate the extent of intransitive competition in nature, and to identify generalities in the factors driving it.

The degree of intransitivity observed in a community may also depend on environmental conditions such as productivity or heterogeneity (Allesina & Levine, 2011; Gilpin, 1975; Schreiber & Killingback, 2013). However, empirical evidence for these environmental effects remains rare (Bowker, Soliveres, & Maestre, 2010; Dormann, 2007; Soliveres et al., 2015; Ulrich, Kubota, Piernik, & Gotelli, 2018). Productivity might reduce intransitivity through two different mechanisms: (1) for sessile organisms, it might increase the asymmetry of competition by causing a shift to light competition at high productivity, which would allow a smaller number of species to monopolize limiting resources (e.g. DeMalach, Zaady, & Kadmon, 2017) or (2) if it reduces the number of resources species compete for (e.g. Harpole & Tilman, 2007). Heterogeneity, in turn, can increase intransitivity by the opposite mechanisms, reducing competitive hierarchies and allowing the species to compete for a larger variety of resources (Allesina & Levine, 2011; Schreiber & Killingback, 2013). However, a higher productivity could also increase the size of the species pool or the importance of competition for community assembly, potentially increasing the role of intransitive competition as driver of coexistence (Bowker, Soliveres, et al., 2010; Gilpin, 1975).

In addition to the environment, the functional traits of the species competing are important determinants of the outcome of pairwise competition (Herben & Goldberg, 2014; Kraft, Godoy, & Levine, 2015; Kunstler et al., 2012; Schamp, Chau, & Aarssen, 2007). According to the limiting similarity theory, species that differ in their functional traits should also differ in their niches and therefore should compete less strongly with each other (e.g. Herben & Goldberg, 2014). However, trait differences could also indicate strong differences in competitive ability (fitness differences) between species and, in this case, competition would be stronger between species with different trait values (De Bello et al., 2012; Mayfield & Levine, 2010). Strong intransitive competition arises from species reciprocally excluding each other and could therefore be promoted by large differences in traits linked to competitive ability for different resources. However, very heterogeneous competitive differences between species pairs (i.e. large trait differences) can also destabilize intransitive networks (Gallien, Zimmermann, Levine, & Adler, 2017), and thus, trait differences could also be expected to reduce intransitivity. Functional trait differences could therefore alter the degree of intransitivity in competition networks, although this effect is poorly understood (Gallien, 2017; Maynard, Bradford, et al., 2017). In addition to the effects of traits on intransitivity, the competitive rank of a species might affect its likelihood of participating in an intransitive loop, as it has been hypothesized that intransitive competition networks are nested, meaning that the dominant species form intransitive loops but that hierarchical competition occurs between dominant and sub-dominant species (Soliveres et al., 2015; see also Laird & Schamp, 2018). Despite the prominent role that functional traits could have in determining intransitivity in competition networks; their effect as drivers of competition intransitivity and whether this varies depending on environmental conditions or between different taxa is unknown.

Here, we explore the generality of intransitive competition in nature by combining re-analyses of published (Carrara, Giometto, Seymour, Rinaldo, & Altermatt, 2015a, 2015b; Delgado-Baquerizo et al., 2017; Maynard, Bradford, et al., 2017) and new pairwise competition experiments to explore the generality and nestedness of intransitive competition in nature. These experiments include 124 species across five different taxonomic groups: vascular plants, mosses, saprobic fungi, soil bacteria and aquatic protists. For mosses and bacteria, we also analysed how increasing productivity affected the degree of intransitivity in the competition network. Finally, we examined the effect of the functional traits of competing species as drivers of intransitive competition. Our hypotheses were: (1) intransitive competition is widespread across the taxa studied, but less pronounced in mobile taxa such as protists and bacteria, (2) intransitive competition is reduced (competition is more hierarchical) in more productive environments, (3) intransitive competition prevails between dominant species, but not between the dominants and the rest of species (i.e. intransitive competition networks are nested), (4) the functional traits of the competing species influence the degree of intransitivity in their competition, and (5) the functional traits driving intransitive

competition change under contrasting environmental conditions and with the focal taxa.

2 | MATERIALS AND METHODS

2.1 | Pairwise competition experiments

Experimental designs and species numbers differed depending on the taxa studied; however, all possible interspecific pairwise combinations and monocultures were included for all taxa.

2.1.1 | Vascular plants

Seeds of 20 species (see species identities and data in Soliveres et al., 2018) were bought from a commercial supplier (UFA Samen, Switzerland) and the seedlings were grown in every possible pairwise combination for 7 months (one replicate per combination). This was done in 2 L pots filled with a mix of commercial soil (Ricoter, Aarberg, Switzerland) and sand. After the 7 months, the above-ground biomass was harvested for each species in each pot.

2.1.2 | Mosses

Biomass samples were taken from 10 different species growing in grasslands of south-western Germany. Air-dried moss material (3 mg of each species) was used to start the competition experiments: all pairs of species were replicated three times and were grown in 5-cm Petri dishes filled with a commercial peat-based seedling substrate (Klasmann-Deilmann GmbH, Germany; 80% peat, 20% coconut fibres; N 90 mg/l, P₂O₅ 100 mg/l, K₂O 250 mg/l, buffered with CaCO₃ to pH 5.5). Petri dishes were watered every second day until 1 month after which mosses covered all the space in more than half of the Petri dishes (7 months in total). After this period, the cover of each moss species was estimated as a measure of its abundance.

2.1.3 | Saprobic fungi (EU)

All pairwise combinations of 31 species of saprobic fungi from Central Europe (hereafter EU fungi) were grown on potato dextrose agar in 9-cm Petri dishes. To inoculate the fungi, previously sterilized and subsequently colonized poppy seeds (two poppy seeds per plate) were used. After 4 weeks of growth at 22°C, the outcomes of each pairwise competition were scored as draw (if no species overgrew the other or if mutual intermingling without growth inhibition occurred), a win (if the target species overgrew its enemy) or a loss (if the target species was overgrown).

2.1.4 | Saprobic fungi (US)

Thirty-seven isolates from wood decay Basidiomycete fungi from North American populations (hereafter US fungi) were grown in 10-cm Petri dishes filled with 2% (w/v) malt extract agar. For each pairwise competition experiment, two competing species were

inoculated using three plugs placed at equal distances (see details in Maynard, Bradford, et al., 2017). After 8 weeks at 22°C, competition was inferred from whether one species overgrew the other or not.

2.1.5 | Protists

Every possible pairwise combination of a set of 10 protist and one rotifer species (hereafter “protists” for simplicity) were grown in microcosms with 10 ml sterilized culture medium and 0.45 g/L of protozoan pellets (Carolina Biological Supply, NC, USA; six replicates per combination; see Altermatt et al., 2015; Carrara et al., 2015a,b for further details). After 21 days at constant environmental conditions, the density of each protist species within each pairwise combination and monoculture was recorded to infer the outcome of competition.

2.1.6 | Bacteria

Strains from six terrestrial, dominant bacterial taxa were isolated from natural soil (see Delgado-Baquerizo et al., 2017 for details). Bacterial cultures were inoculated at equal abundances in 10 g of two different soils (gamma-sterilized) and were grown in hermetic containers for 8 weeks. Every pairwise combination was realized between these six bacterial cultures only once, resulting in a total of 15 microcosms. After 8 weeks, the relative abundance (number of gene copies per gram of soil) of each bacterial strain was quantified using qPCR. All data are available in the dryad repository (Soliveres et al., 2018).

2.2 | Measuring intransitivity

In all cases, individuals of each species were either grown with a neighbour of their own (intraspecific competition) or another (interspecific competition) species. This allows a comparison of the relative performance of each species in interspecific competition, after accounting for differences in intrinsic growth rates, by using relative yields (RY; Keddy & Shipley, 1989; Grace, Guntenspergen, & Keough, 1993; Dormann, 2007): $RY_i = \text{performance of species } i \text{ growing with species } j / \text{performance of species } i \text{ growing in monoculture}$. Our performance measures were above-ground biomass (vascular plants), percentage cover (fungi, mosses) or abundance (number of cells for protists, number of gene copies for bacteria) of each target species in each possible pairwise combination. By converting these to RY, we could generate a species by species competition coefficient matrix. Cover was not estimated for the US saprobic fungi, so instead of RYs, interspecific competition was inferred from the overgrowth data. For those pairwise competition experiments in which we had replicates (mosses, protists and bacteria), the average value of each species across those replicates was used to calculate RYs. The competition coefficients within the matrix were transformed to a binomial variable to obtain a single “winner” in each pairwise competition trial (1 if $RY_i > RY_j$; 0 otherwise; where i and j are the species in the row and the column of the matrix, respectively; see Supplementary Material S1 for a worked example). For the US fungi, draws could

also occur and these were scored as 0 for both sides of the matrix (i against j and j against i), so they did not influence our measure of (in)transitivity.

The transformation of RYs into a binomial variable allowed us to calculate the level of intransitivity as the number of competitive reversals that occurred. To do this, we first ordered the terms within the matrix by row and column totals, so that most wins were concentrated in the upper right corner of the matrix (see worked example in Supplementary Material S1). We then calculated the degree of intransitivity as the number of competitive reversals ($RY_i < RY_j$), which occurred (i.e. the number of 1s in the lower diagonal of the matrix Ulrich, Soliveres, Kryszewski, Maestre, & Gotelli, 2014; modified after Petraitis, 1979; Laird & Schamp, 2006). This metric therefore counts the number of times that the species in the column (j) displaces the species in the row (i). The number of reversals is likely to increase as more species (m) are considered (e.g. Grace et al., 1993). Thus, our metric is the normalized number of competition reversals after accounting for all potential pairwise combinations, so that: $I = (2 \cdot (RY_i < RY_j)) / (m \cdot (m - 1))$, where zero/one values indicate completely transitive/intransitive communities.

Converting the RYs to 1s and 0s removes any information on the strength of competitive reversals and even a small difference in competitive ability counts as a win for one of the species. This could lead to an overestimation of the degree of intransitivity if the competitive reversals that occur are mostly just random changes in competitive ability between similar species. This limitation is particularly important when pairwise competition experiments are conducted without replication (such as in our vascular plants and fungi). To address this issue, we calculated a new metric (*Inest*) based on the “nestedness” of the matrix, which allows us to use all the information from the RYs (see figure S2b in Ulrich et al., 2018). By using the RYs directly, we downweight competitive reversals that arise from small competitive advantages in our estimation of intransitivity (e.g. $RY_j = 0.53 > RY_i = 0.47$, would be weighted less than the case where $RY_j = 0.90 \gg RY_i = 0.10$). This metric also requires re-ordering the species \times species competition matrix by row and column sums to maximize the “wins” in the upper diagonal, but does not transform the RYs to 0s and 1s. Instead, *Inest* calculates the difference between the RYs in the upper diagonal and those in the lower diagonal (e.g. RY_{AB} vs. RY_{BA} in the worked example in Supplementary Material S1, see also Ulrich et al., 2018), weighting those differences by the distance of the position of a particular RY to the diagonal of the matrix. Both metrics of intransitivity (I and *Inest*) produced very similar results, although the strength of intransitivity was higher when using the *Inest* metric based on continuous measures of competitive advantage (Supplementary Material S2). We therefore focus on the use of I in the main text as it is more straightforward to understand, more comparable with previous approaches and in fact more conservative in our case.

It has been argued that RYs are not a good proxy of long-term competitive outcomes or fitness differences between two competing species (Levine, Bascompte, Adler, & Allesina, 2017). However, this important limitation seems only to occur in cases where the

intraspecific competition coefficient for one species in a pair is four or more times bigger than the other (i.e. $\alpha_{ij} > 4\alpha_{ji}$), which did not occur in our experiments and may be relatively uncommon in general (see full rationale and results in Supplementary Material S3). Relative yields based on biomass (or related measures) were used here in order to have comparable metrics for all of our taxa. However, it must be noted that, as with other metrics of biotic interactions (e.g. Holmgren, Scheffer, & Huston, 1997), results can strongly depend on the performance measure used and could be different if we had used survival, number of seeds or total extinctions as a measure of competition displacement (see e.g. Carrara et al., 2015a,b).

Our measure of intransitivity provides a single index for a community of any number of species. However, single measures of competition intransitivity may fail to fully describe these competitive networks (Alcántara, Pulgar, & Rey, 2017; Laird & Schamp, 2009). Therefore, to complement the community-level I metric, additional metrics based on three-species combinations (hereafter triplets) were calculated. To calculate the triplet-based measures, we scored each possible triplet as to whether it experienced competitive reversals (i.e. $A < B < C < A$; rather than $A < B < C$ and $A < C$), this was done for all possible combinations of three species within the community. There are only two possible states for each triplet and each one was scored as fully hierarchical if there were no reversals and as intransitive if there was a competitive reversal. The same approach was used to calculate competitive reversals as for the whole community measures: (1) RYs between the three species pairs in the triplet were converted to 1s and 0s, (2) the matrix was ordered by row and column totals, and (3) if after this re-ordering all the 1s were in the upper diagonal, then the triplet was transitive, if not, then it was intransitive. Considering intransitivity in each triplet allowed us to investigate the effects of the environment (i.e. productivity), the mean characteristics of the species (i.e. competitive rank, functional traits) and the variation in species characteristics (variance in competitive rank and functional traits) on intransitivity.

2.3 | Drivers of intransitivity

2.3.1 | Competitive rank

Intransitive competition has been hypothesized to be nested, that is to occur within guilds of competitively dominant or subordinate species, but not between these guilds (Soliveres et al., 2015). However, this hypothesis has not been tested experimentally. The nestedness of intransitive competition networks was evaluated by measuring how the variance in competitive rank of a triplet (which measures whether the triplet contains a mix of good and poor competitors) affected its probability of being intransitive. Competitive ranks were directly obtained from the pairwise competition matrix once it had been ordered by row and column totals. After ordering, the species at the top are the strongest competitors (the ones with more wins), whereas the species at the bottom of the matrix are the weaker competitors. Therefore, the row number occupied by each species in the pairwise competition matrix is a measure of its competitive

rank (the smaller the row number, the stronger the competitor). According to the nestedness hypothesis, species strongly differing in their competitive ranks should not form intransitive loops. Thus, we expected that a high variability in competitive ranks within a triplet would make it more likely to be transitive, while triplets consisting of species similar in their competitive ability would have a higher chance of being intransitive. The variability was measured as the non abundance-weighted mean pairwise distance (MPD) of competitive rank across the three species.

2.3.2 | Functional traits

Functional traits can be related to competitive ability, but can also offer additional information on how species differentiate in the ways they compete (e.g. reciprocal competitive advantages) and on how they respond to environmental changes. Thus, in addition to the effects of competitive rank, the functional traits related to growth rate, environmental tolerances or resource use were considered as potential drivers of intransitivity. The average of each trait across the three species in a triplet was used to test if particular types of species were more likely to participate in intransitive loops, and the MPD of each trait (non abundance-weighted) within the triplet was used to assess if intransitivity was more or less common between functionally different species.

Relative growth rate was available for all taxa and was calculated as the rate of biomass (or cover) accumulation over a given period of time. This was obtained from the monocultures for mosses, bacteria and protists, and from isolated individuals (growing without competition) for the rest of taxa. Since all the species started with exactly the same biomass (or cover), a single data point suffices to give an approximate measure of relative growth rate. Since this is likely to be an important trait related to competitive ability, it was included as a common predictor for all taxa. For vascular plants, height, specific leaf area, seed mass, leaf dry matter content and leaf N content (obtained from the TRY database; Kattge et al., 2011) were also included. These traits are linked to resource-use strategy and competitive ability in plants (Herben & Goldberg, 2014; Reich, 2014; Schamp et al., 2007). For mosses, colony type (three types depending on the degree of compaction: rough mat, smooth mat and weft; from maximum to minimum colony compaction) and mean shoot length (obtained from the Bryoatt database; Hill, Preston, Bosanquet, & Roy, 2007) were included in the analysis. Empirical links between moss functional traits and competition have rarely been established, although based on results for vascular plants and theory (Cornelissen, Lang, Soudzilovskaia, & During, 2007), the traits we selected should be important drivers of competition between mosses (Bowker, Maestre, & Escolar, 2010). For the US fungi, traits related to chemical aggressiveness (hydrolytic enzymatic activities), ability to overgrow other colonies (growth rate and density of the colony) and nutrient uptake (wood decomposition, enzymes related to C and P cycling) were obtained for published literature (Maynard, Bradford, et al., 2017; see details in Supplementary Table S1). For soil bacteria, enzymes related to their ability to capture P and degrade different

sources of C were considered in addition to growth rate (data from Delgado-Baquerizo et al., 2017). Functional traits for EU fungi were growth rate and phylum. For protists, invasibility (as estimated by Mächler & Altermatt, 2012) and functional group (small protists, large protists, mixotrophs; Carrara et al., 2015a) were available. These traits are related to feeding guild, environmental tolerances and growth rates.

2.3.3 | Environmental conditions

The role of environmental conditions was evaluated in two of the taxa (mosses and soil bacteria). For mosses, an N-fertilization treatment was added to our pairwise competition experiment, which aimed to increase productivity and therefore affect the degree of intransitivity (Bowker, Soliveres, et al., 2010; Gilpin, 1975). Similarly, soil bacteria were cultivated in two soils differing in their organic matter content and pH, which strongly affects the abundance of the bacteria (e.g. Lauber, Hamady, Knight, & Fierer, 2009; Maestre et al., 2015). The soils can therefore be seen as representing different levels of productivity. Our experimental results were compared with observational data from mosses growing in areas that differed in productivity (Supplementary Material S4).

2.4 | Statistical analyses

2.4.1 | Analysis at the community level

First, our six I metrics (one per group, with EU and US fungi analysed separately as they used slightly different approaches) were compared with 0 (values of $I = 0$ are related to perfect competition hierarchy as no competitive reversals are observed in the community) using a t test. To examine the role of mobility in affecting the degree of intransitivity, the difference in I between mobile (protists and bacteria) and sessile (vascular plants, mosses and fungi) taxa was analysed by means of a t test.

2.4.2 | Analysis including all three-species combinations (triplets)

Are intransitive competition networks nested?

To test for nestedness in the intransitive networks, we used the average competitive rank and its variance across the three species forming a triplet as predictors whether the triplet was intransitive. To analyse this, GLMs with the logit link function were fitted for each taxon separately. Variance was calculated as the presence/absence Rao's Q from the "FD" package in R (De Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016; Laliberté, Legendre, & Shipley, 2014).

Functional traits as drivers of intransitive competition

Functional traits are not only related to competitive ability, but also can offer additional information on how species differentiate in the ways they compete (e.g. reciprocal competitive advantages) and on

how they respond to environmental changes. Thus, in addition to the effects of competitive rank, the effects of functional traits related to growth rate, environmental tolerances or resource use on intransitive competition were also considered. We were interested in comparing the effect of mean traits with effects of the variability in such traits between the competing species. Thus, the averages and variance (Rao's Q) of the functional traits were analysed as predictors of the probability of a given triplet to be intransitive (using GLMs with the logit link function). All traits and their Rao's Q values were included in our models, together with the average and Rao's Q of competitive rank. In summary, we evaluated sequentially four sets of models to analyse the triplets:

1. Intransitivity of each triplet (binomial variable) as the response to competitive rank,
2. Intransitivity of each triplet (binomial variable) as the response to average and variance (Rao's Q) of competitive rank,
3. Intransitivity of each triplet as the response to competitive rank and average trait values across the three species, and
4. Intransitivity of each triplet as the response to competitive rank, average trait values across the three species and Rao's Q for competitive rank and functional traits.

We evaluated overall model fit by calculating Nagelkerke's pseudo- R^2 as implemented in the function "RsqGLM" of the modEvA package in R. This allowed us to assess the extra variation explained by the functional traits after considering competitive rank. In all cases, the triplets within a species pool are not totally independent, as they may share one or two species (e.g. ABC, ABD). To remove this pseudo-replication effect, p -values were calculated by permutation, using 1,000 permutations as implemented in the "PermTest" function of the pgrimess package in R. For bacteria, the low number of possible triplets and the low variance in the intransitivity levels of the triplets (only one was intransitive) prevented us from including more than one predictor each time. Thus, we evaluated each predictor separately, selecting the best (according to their pseudo- R^2 , see below) amongst the averages and amongst the coefficients of variance.

In addition to these analyses, we evaluated the effect of functional traits as predictors of competitive rank. This helped us to evaluate if the traits driving overall competitive ability are the same ones driving the way species compete (intransitively or hierarchically).

Do the functional traits driving intransitive competition change with productivity?

To test whether different traits drive intransitivity in productive environments, the changes in intransitivity in the triplets of moss species competing under fertile vs. control conditions were analysed using GLMs with a logit link function. In these models, fertilization and its interactions with competitive rank and with the functional traits were evaluated. Since no bacterial species were engaged in intransitive competition under fertile conditions, only the data on moss species could be analysed. All analyses were performed using R version 3.0.2 (R Development Core Team, 2013).

3 | RESULTS

3.1 | How widespread is intransitive competition?

All taxa studied, except the soil bacteria growing in rich soils, showed some degree of intransitivity (Figure 1). Our overall I metric, based on the proportion of competitive reversals in the pairwise competition matrix, was significantly higher than 0 (pure hierarchical competition): $t = 3.74$, $df = 5$, $p = .013$. Importantly, there was substantial variation in the levels of intransitivity found across taxa, with very low values in fungi (US) and bacteria, and much higher levels detected for mosses, vascular plants and protists (Figure 1). In general, high productivity reduced the degree of intransitivity in the communities, with declines detected in both mosses and bacteria when growing under more fertile conditions, consistent with field observations (Supplementary Material S4). These declines were consistent in both the community-level I metric (bacteria and mosses; Figure 1) and in the analyses focusing on the triplets (fertilization effect in the GLM for mosses: -5.91 ± 1.90 ; $p < .005$). We found no differences in the level of intransitivity between sessile and mobile organisms neither at the community level ($t = 0.29$, $df = 4$, $p = .78$). The proportion of intransitive triplets out of the total number of possible three-species combinations ranged from 38.1% (mosses) to 0% (bacteria in fertile soils; Figure 1), with higher proportions observed for mosses, vascular plants (18.8%) and protists (16.4%), consistent with the results found for the entire communities. These proportions are similar to those previously reported for annual vascular plants

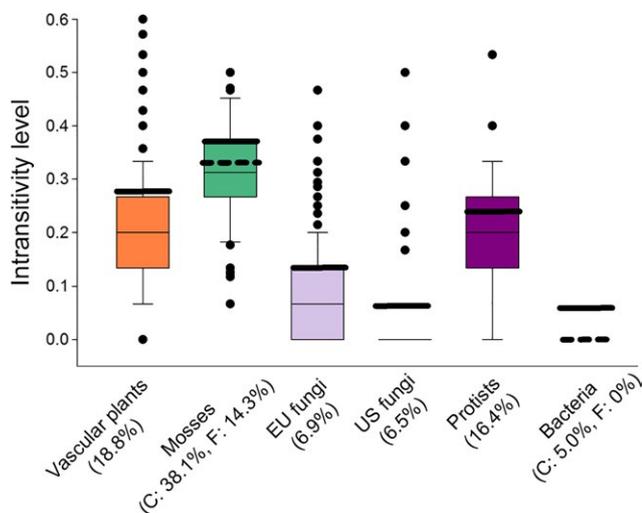


FIGURE 1 Intransitivity levels across the taxa studied. Thick black dashes show the intransitivity level as calculated using the pairwise experimental approach with all the species. Dashed lines indicate the fertilizer treatment and the fertile soil for mosses and bacteria, respectively. To allow comparison between taxa, the intransitivity level of all possible combinations of six species (the minimum species number in the experiments) are shown (box-plots) for all the taxa but soil bacteria. The percentage of all possible three-species combinations that were intransitive for each taxa are given in brackets (C = control, F = fertile conditions) [Colour figure can be viewed at wileyonlinelibrary.com]

(15%–19% in Godoy, Stouffer, Kraft, & Levine, 2017; 17%–39% in Matías, Godoy, Gómez-Aparicio, & Pérez-Ramos, 2018).

3.2 | Are intransitive competition networks nested?

We found strong evidence that intransitive competition networks are nested, as intransitivity was more frequent between species with similar competitive ranks. The coefficient of variance in competitive rank had a strong negative effect on competition intransitivity in vascular plants, fungi and protists, with a similar (non-significant) trend found in mosses and bacteria (Figure 2). The effects of mean competitive rank were less consistent: for the fungal groups intransitivity was more common amongst dominant species (Figure 2), whereas intransitivity was more common amongst competitively weak species (higher ranks) in mosses and was not affected by competitive rank in the rest of the taxa studied.

3.3 | Drivers of intransitive competition

Competitive ranks (average and variance [Rao's Q]) explained, on average, 12% of the variation in the probability of a triplet to be intransitive. This variation rose to 28% when including functional traits. The increasing explanatory power when including functional traits was due to both the average and the variance in the functional traits of the competing species (Figure 3, see also Supplementary Material S5). In general, species with trait values that indicate high competitive ability were less likely to be involved in intransitive competition, these were tall vascular plants with low leaf dry matter content and high leaf N, or fungi that grew faster (EU) or consumed more C (US; Figure 3). While variance in competitive ranks consistently decreased the probability of a given triplet to be intransitive, trait differences did not have consistent effects. Triplets with high trait variance tended to be less intransitive in vascular plants and protists, but not in fungi, mosses and bacteria (Figure 3, dashed columns).

Despite the strong effect of high productivity on intransitive competition, productivity levels did not alter which functional traits affected intransitivity in mosses, where this could be tested (no significant traits \times fertilization interactions were found). However, fertilization did influence how competitive rank affected intransitivity in mosses, with the relationship between moss average competitive rank and intransitivity shifting from negative in the control to positive in the fertilization treatment (fertilization \times average competitive rank: 0.91 ± 0.35 ; $p < .05$).

4 | DISCUSSION

4.1 | Intransitive competition is widespread across different taxa

Our results suggest that non-hierarchical competition is the norm, not the exception, in ecological communities. We found evidence

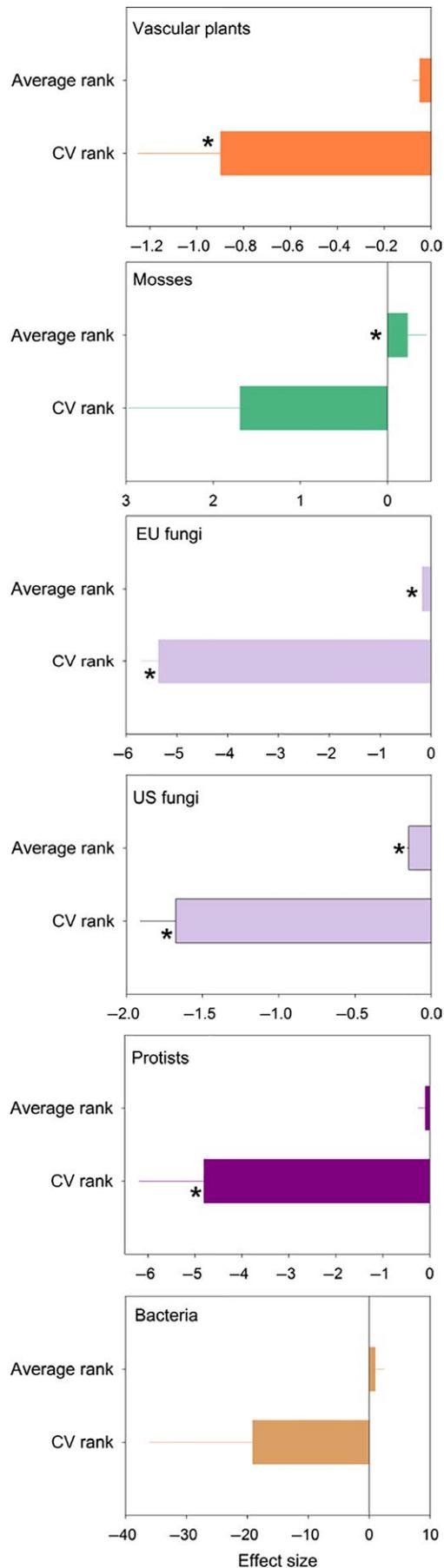


FIGURE 2 Effect of the average and the variance (CV) of the competitive ranks of the species involved in a triplet on the probability of such triplet to be intransitive. Asterisks indicate significant differences according to the permutation tests performed to control for pseudo-replication when obtaining the p -values. Predictors for intransitivity in bacteria were tested one at a time, as only one triplet was intransitive [Colour figure can be viewed at wileyonlinelibrary.com]

of non-hierarchical competition in all taxa studied, adding to the increasing evidence for intransitive competition between vascular plant species (Lankau & Strauss, 2007), marine intertidal organisms (Buss, 1980), biological soil crusts (Bowker, Soliveres, et al., 2010), plankton (Huisman & Weissing, 1999), bacteria (Kerr, Riley, Feldman, & Bohannan, 2002) and vertebrates (Sinervo & Lively, 1996). The apparent commonness of intransitive competition, across above- and below-ground, terrestrial and aquatic communities, suggests that a presumption of hierarchical competition in most current theories (e.g. Chesson, 2000; Tilman, 1982) may need to be revised.

Our results contrast with other studies that have found fully hierarchical competition (e.g. Grace et al., 1993 in vascular plants; Henriksson et al., 2016 in fishes; Friedman, Higgins, & Gore, 2017 in bacteria). The variety of methods used to measure competition may contribute to this lack of consensus. We used RYs, calculated from species abundances, to determine competitive outcomes. Relative yields could reflect reciprocal competitive advantages and affect relative abundances of species and the functioning of communities (e.g. Maynard, Crowther, et al., 2017), but caution should be taken in using them as measures of the long-term outcome of competition. Other methods for assessing competitive outcomes, based on long-term survival have shown lower levels of intransitivity in competition networks (e.g. Carrara et al., 2015a, 2015b for protists or Godoy et al., 2017; Matías et al., 2018 for vascular plants; but see Huisman & Weissing, 1999; Kerr et al., 2002). In addition, whereas some experiments have been performed under natural conditions, others keep environmental conditions constant, and this reduction in heterogeneity under more controlled conditions is likely to reduce niche differences and possibly intransitive competition. In general, the choice of the performance measure and the experimental approach can have important implications for how we perceive competition. Such issues are known in other areas where, for instance, dryland plants can compete during the growth phase but still facilitate each other's survival (Holmgren et al., 1997). This lack of agreement, and the knowledge gaps existing for many other organisms (e.g. insects, birds, mammals) where competition experiments are challenging, emphasizes the need to (1) better understand the conditions under which competition is intransitive, (2) how the degree of intransitivity in competition might change between life-history stages and (3) how this impacts coexistence between species but also their abundances and functioning. Multi-taxon studies using a consistent methodology to evaluate competition, such as the one presented here, are a first step towards addressing this important research gap.

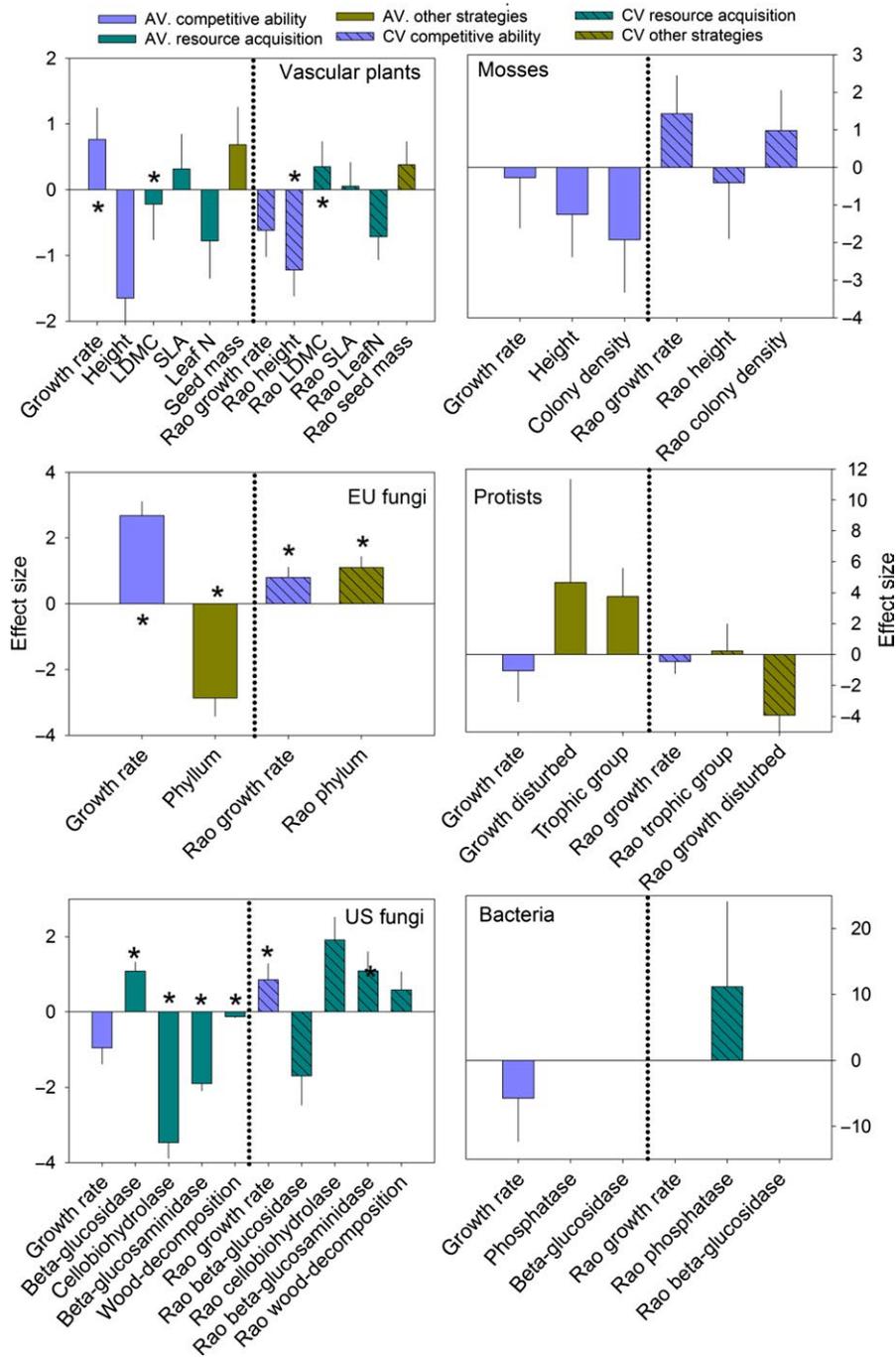


FIGURE 3 Effect of functional traits related to competitive ability (blue), resource acquisition (green) or other strategies (yellow; response to disturbances, trophic group) on the probability of each three-species combination to be intransitive. The effect (\pm SE) of both the average (AV, filled bars) and the variance (calculated as the presence/absence Rao's Q; dashed bars) is shown. Asterisks indicate significant differences according to the permutation tests performed to control for pseudo-replication when obtaining the p -values [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Intransitive competition is driven by species with similar competitive ranks

We found that intransitive loops are more likely to occur between species similar in competitive rank, which suggest that intransitive competition networks are nested (Soliveres et al., 2015). This was true for protists, EU fungi and vascular plants, for which a higher variability in the competitive rank of the species participating in a triplet negatively affected the odds of such triplet to be intransitive. The mean rank of species in the triplet had positive, neutral or negative effects on intransitivity depending on the group, meaning that intransitive competition could prevail either between only dominant

or only subordinate species, depending on the taxonomic group in question. We hypothesize that intransitivity in general is likely to be caused by trade-offs in competitive ability for different resources, or in resource vs. interference competition (e.g. C uptake vs. aggressiveness; see also Maynard, Crowther, et al., 2017). Assuming that functional traits were not only related only to competitive ranks, but also to the different ways by which different species compete for resources (Kraft et al., 2015; Kunstler et al., 2012; see also Ulrich et al., 2018, Supplementary Material S5), this could explain the positive effects of trait variation in the intransitivity level of triplets of fungi, mosses or bacteria (Figure 3) even when the variance in competitive ranks had a negative effect. However, when competing species are

too different in their ranks (i.e. between dominant and subdominant species), such reciprocal competitive advantages would not be sufficient to reverse very large competitive ability differences. Recent theoretical work has shown that where competitive ability differences are heterogeneous between pairs of species (e.g. species A and B are much better competitors than C but C is only slightly better competitor than A) the positive effects of intransitive competition on coexistence are reduced (Gallien et al., 2017). As it may be unlikely that very large pairwise competitive ability differences form intransitive loops, it may be more common for intransitive competitive reversals to stabilize coexistence between species similar in competitive ability.

4.3 | Intransitive competition is driven by the environment, the way species compete and the functional traits of the target and competing species

The conditions under which competition is more likely to be intransitive have only been explored in a handful of mathematical models (e.g. Allesina & Levine, 2011; Schreiber & Killingback, 2013) and in empirical studies focusing on a single taxon (e.g., Bowker, Soliveres, et al., 2010; Maynard, Bradford, et al., 2017; Soliveres et al., 2015). However, to our knowledge, no studies have simultaneously studied these different drivers of competition intransitivity and how they change according to the way different organisms compete.

We found that environmental conditions influenced the degree of intransitivity. Specifically, increased productivity reduced the number of competitive reversals in mosses and bacteria, which is consistent with results from field observations in vascular plants and mosses (Soliveres et al., 2015; Supplementary Material S4). More fertile and productive conditions could reduce the opportunities for intransitivity to emerge from reciprocal competitive advantages by two different mechanisms: (1) by reducing the number of resources species compete for (Harpole & Tilman, 2007), and therefore, the potential for trade-offs in competitive ability to lead to reversal, or (2) by increasing the asymmetry of competition, for instance by shifting competition from nutrients to light (DeMalach et al., 2017), which would also reduce intransitivity if large competitive ability differences are less likely to be reversed (as proposed by the nestedness hypothesis). Our study also shows that intransitive competition can shift from the dominant to the weak competitors under such productive conditions (fertilized vs. control mosses). This could be explained if dominant species compete mainly for a single resource which makes competition more hierarchical and less intransitive, whereas the remaining species need to fight for the leftovers using a variety of competition strategies and therefore continue to compete intransitively. The relationship between fertility and intransitive competition does not seem, however, to be monotonic. Field observations (Bowker, Soliveres, et al., 2010) and theory (Gilpin, 1975) suggest that an increase from very low to moderate productivity levels may enhance intransitive competition by increasing the species pool able to colonize a given site and the number of resources for which species compete, both factors which

should increase the chance that some species engage in intransitive competition. To identify under which fertility levels intransitive competition is maximized, and whether or not different taxa respond in the same way, is an exciting venue for future research.

Three-species experiments (Kerr et al., 2002) and mathematical models (Laird & Schamp, 2015; Reichenbach et al., 2007; Yitbarek & Vandermeer, 2017) suggest that intransitive competition is less frequent in mobile taxa that compete in “global” neighbourhoods as opposed to those that compete locally (sessile organisms). This is supported by the lack of intransitive competition found in other manipulative experiments with organisms growing in well-mixed environments, such as bacteria (Friedman et al., 2017), aquatic protists (Vandermeer, 1969), or necrophagous insects (Ulrich et al., 2014). Despite this, we found no strong evidence for a reduction in intransitivity in mobile taxa, mainly due to the high level observed in protists (but see Carrara et al., 2015a) and the moderate levels found in fungi. Mobility can, in theory, allow species to take up resources at different points in space, homogenizing resource distributions and preventing trade-offs in competitive ability for different resources. It might also allow competitive species to avoid the influence of allelopathic compounds, reducing the benefit–cost ratio of producing such toxins (Reichenbach et al., 2007). In addition, mobility can allow species to escape competition in well-mixed environments (Fronhofer, Klecka, Melian, & Altermatt, 2015) and can lead to greater opportunities for niche differentiation. All these mechanisms could reduce the opportunity for intransitive competition to stabilize coexistence, although we found little evidence to support this. Another explanation for the taxon-dependent changes in intransitivity we found is the relative size of the organism vs. the habitat in which it was grown. Soil bacteria were grown in a larger medium (relative to their size), and thus could more easily have avoided competition, perhaps explaining the low prevalence of intransitive competition in these communities. Exploring further the effect of mobility, local vs. global competition mechanisms and the spatial scales at which intransitivity emerges would allow a better understanding of its effects on coexistence.

Apart from mobility, size or competitive rank, we found some evidence that species with traits more related to competitive ability in productive environments (tall plants with high tissue nutrient levels and fast growing fungi) were less likely to engage in intransitive competition. This parallels what we discussed above regarding productivity and reciprocal competitive ability differences and suggests that species adapted to high productivity environments may also be less likely to form intransitive loops. If functional traits of species do affect their likelihood of engaging in intransitive competition then we might expect changes in intransitivity to also feed-back to affect trait distributions. Previous studies have shown an increase in functional trait diversity under intransitive competition (Maynard, Bradford, et al., 2017; Ulrich et al., 2018), but these changes are not always expected (Gallien, 2017). Our results suggest that, if intransitive competition is driven by reciprocal competitive advantages (as seems to be the cases for fungi, mosses and bacteria), then it should strongly relate to functionally

diverse communities. This is so because differences between species across contrasting trait or resource use strategies can enhance such reciprocal competition (Herben & Goldberg, 2014; Ulrich et al., 2018). However, in communities with strong fitness differences, or driven by other mechanisms of competition, large trait differences could relate to large fitness differences (e.g. De Bello et al., 2012; Kraft et al., 2015; Mayfield & Levine, 2010) which, taken together with our results, suggest in turn that high intransitivity will relate to low trait diversity. This is so because both simulations (Gallien, 2017) and our results suggest that too large fitness differences may dampen intransitivity, and if large fitness differences are associated to large trait differences, then intransitive competition will be linked to low trait diversity. In sum, the relationship between intransitive competition and functional trait patterns seems to depend on the importance of reciprocal competition vs. fitness differences as drivers of coexistence, and how the traits selected relate to these competitive ability differences.

It must also be noted that the functional traits driving intransitivity were highly taxon-dependent. Of course, this could be caused by the fact that we included different trait sets for each taxon, according to data availability. However, even where we could use similar traits across taxa, as in vascular plants, mosses and US fungi, the identity of the traits driving competition intransitivity differed substantially. Similarly, the single trait that we had for all our species (growth rate) had different effects depending on the organism. This lack of common trait effects should be considered when applying trait-based approaches to find general patterns across different groups of organism.

5 | CONCLUSIONS

Using a multi-taxon experiment, we found that fertility and competitive rank are generally good predictors of intransitive competition. Intransitivity is common in less productive environments, and between species that are similar in their competitive rank. We also showed the need to be cautious when drawing general conclusions about competition and coexistence from studies on single taxa. Finally, our results illustrate that not only the traits of the target species alone, but the structure of trait values of all competing species is an important driver of competition intransitivity. Our findings help to achieve a more predictive understanding of which organisms and species may depend more on intransitive competition for their coexistence, and also provide the first steps towards a more comprehensive theory on the linkage between the role of the topology of competitor networks and diversity patterns in real communities.

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AUTHORS' CONTRIBUTIONS

S.S. and E.A. designed the study; S.S. analysed the data and wrote the first draft. All authors contributed data and helped improving the text.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bh41r> (Soliveres et al., 2018).

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SUPPORTING INFORMATION

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