

1 **Everything you always wanted to know about intransitive competition but were**
2 **afraid to ask. Introduction to the special feature “Intransitive competition and**
3 **species coexistence”**

4

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13 **Summary**

- 14 • Over forty years after the introduction of the concept into ecology, intransitive
15 (i.e., non-hierarchical) competition remains overlooked by ecological theory,
16 despite theoretical work showing it could be a major driver of species
17 coexistence.
- 18 • This special feature presents six studies including models, reviews, experimental
19 studies and large-scale observational studies. Collectively, these studies help to:
20 i) link intransitive competition with short- and long-term coexistence and with
21 other ecological patterns, ii) evaluate the conditions under which intransitivity is
22 more common and iii) determine how best to quantify the degree of
23 intransitivity.
- 24 • The studies in this special feature show the generality of intransitive competition
25 in nature, explore interactions between intransitivity and other coexistence

26 mechanisms and illustrate the effect of environmental conditions (drought,
27 shade, fertility) on intransitivity and coexistence. They also show which metrics
28 best quantify intransitivity and highlight the importance of adopting a more
29 continuous view of competition as varying from strongly transitive to strongly
30 intransitive. The studies also examine relationships between intransitivity and
31 functional diversity and explore the evolution of intransitivity over time.

- 32 • *Synthesis:* The studies presented here advance the field by integrating
33 intransitive competition into species coexistence and general ecological theory.
34 We also highlight important research gaps that will hopefully inspire the next
35 generation of studies in this topic.

36

37 ***Keywords:*** cyclic competition, community assembly, coexistence theory, competition,
38 intransitivity, diversity, rock-paper-scissor dynamics

39

40

41 **What is intransitive competition?**

42 Competition networks are generally assumed to be hierarchical (transitive), with one
43 dominant species excluding all others, the second most dominant competitor excluding
44 all species but the first and so on. Coexistence between species, therefore, relies on: i)
45 mechanisms which reduce competitive ability (fitness) differences between species
46 (equalizing mechanisms), or ii) mechanisms that increase intra- relative to inter-specific
47 competition, thereby resulting in stabilising niche differences between species (Chesson
48 2000; Adler, Ellner & Levine 2007). However, competition can also be non-
49 hierarchical, or intransitive. Intransitive competition means that there is no single best
50 competitor and, just as in the game of rock-paper-scissors, all species can beat some
51 competitors while all lose to some others, i.e. there are "competitive reversals". This
52 could allow species to stably coexist even without niche differences (Huismann &
53 Weissing 1999; Wootton 2001, Laird & Schamp 2006). Intransitive competition was
54 first explored theoretically by May & Leonard (1975) and Gilpin (1975), and since then
55 a few studies have tested for the occurrence of intransitive competition and its effects on
56 coexistence, developing different indices to measure it (see reviews in Aarssen 1992;
57 Gallien 2016). However, the field has been dominated by modelling approaches or
58 small-scale, single site experiments, meaning we still know very little about how often
59 competition is intransitive or what conditions favour this type of competition.

60

61 **How common is intransitivity?**

62 Intransitive competition could be generated by a range of different ecological
63 mechanisms. One possibility is a trade-off between resource competition and the
64 production of species-specific allelopathic compounds: such as the one observed for
65 three *Escherichia coli* strains, which compete intransitively because strain S overgrows

66 strain R, R overgrows C, but C kills S by releasing colicin, to which R is resistant (Kerr
67 *et al.* 2002, see also Durrett & Levin 1997). Trade-offs in competitive abilities for
68 different resources could generate intransitive networks in similar way (summarized in
69 Aarssen 1992, see also Allesina & Levine 2011; Gallien 2016). Competitive reversals
70 from a strong hierarchy can also be caused by predators (LeBrun 2005), plant-soil
71 feedbacks (Lankau *et al.* 2011), or by the microclimatic changes produced by larger
72 species belonging to the same trophic level (e.g., nurse plants affecting competition
73 between understory species via shading and an increase in environmental
74 heterogeneity: Soliveres *et al.* 2011, Aschehoug & Callaway 2015). Finally, the
75 existence of spatial structures and competition-dispersal trade-offs (Edwards &
76 Schreiber 2010; Ulrich, Jabot & Gotelli 2017; Yitbarek & Vandermeer 2017) can also
77 enhance intransitive competition.

78 Many mechanisms are therefore able to drive intransitive competition, which
79 might imply that it is likely to occur in nature and, indeed, intransitive competition
80 networks have been observed among intertidal organisms (Buss 1980), plankton
81 (Huisman & Weissing 1999), lizards (Sinervo & Lively 1996), bacteria (Kerr *et al.*
82 2002), lichens and bryophytes (Dormann 2007; Bowker, Soliveres & Maestre 2010) and
83 vascular plants (Freckleton & Watkinson 2000; Soliveres *et al.* 2015; Godoy *et al.*
84 2017). However, despite the increasing body of evidence supporting the generality and
85 potential importance of intransitive competition in nature, it has long been treated
86 mostly as a curiosity rather than as a major mode of competition. Indeed, studies on
87 intransitive competition are uncommon, and most work on coexistence has ignored it
88 (Fig. 1). One factor that has slowed the incorporation of intransitive competition into
89 general ecological theory has been the difficulty of measuring intransitivity in the field.
90 Improved metrics of intransitivity are therefore important to allow us to determine the

91 circumstances under which intransitive competition is more likely to arise, and what its
92 consequences are for community-level patterns.

93

94 **What is this special feature about?**

95 Collectively the studies presented in this special feature aim to foster research on
96 intransitive competition by addressing the drivers and consequences of this type of
97 competition in natural communities, linking it with general coexistence theory and
98 evaluating how to best measure and study it. If the reader ever asked the questions: i)
99 how can we measure intransitivity? ii) how does intransitive competition affect
100 coexistence? iii) what are the consequences of intransitivity for community structure?
101 iv) what factors determine whether species compete intransitively or transitively? or v)
102 How do intransitive competition networks assemble? This special feature should
103 hopefully go some way towards answering them.

104

105 **A short story of a difficult task: how can we measure intransitivity?**

106 Quantifying the degree of intransitivity in multi-species competition networks is
107 challenging and there have been a large number of different approaches taken to
108 measure intransitivity and its effects on species coexistence (reviewed in Ulrich *et al.*
109 2014; Levine *et al.* 2017). Put simply, most of these metrics use pairwise competition
110 matrices to assess the number of competitive reversals (or cycles) occurring across the
111 whole network, or the proportion of n-species combinations that show competitive
112 reversals. In this feature, Laird & Schamp (2018) provide the first assessment of the
113 performance of these different metrics and conclude that those based on 3-species
114 combinations are best to assess short-term (transient) coexistence (i.e., time to the first
115 extinction). They also show that long-term (stable) coexistence is most strongly affected

116 by a very simple measure: the presence of an "unbeatable species" in the community.
117 Whether or not such unbeatable species are common in nature is an interesting research
118 gap to be addressed in the future. While nicely reviewing the existing metrics available
119 to measure intransitivity and their performance, Laird & Schamp (2018) also reveal a
120 crucial difference in the effects of intransitive competition on short- vs long-term
121 coexistence, which could be important in understanding relationships between
122 intransitivity and diversity in observational datasets. It is difficult to find generalities in
123 studies using very different approaches, as conflicting results are as likely to be driven
124 by different metrics of intransitivity as by differences in the way the target species
125 compete. Studies comparing different methodologies, such as the one by Laird &
126 Schamp (2018), are therefore essential if we are to draw generalities from existing
127 literature.

128 Most metrics of intransitivity consider competitive exclusion as a binary
129 process: a species either wins or loses in competition. However, two of the studies in
130 this special feature (Gallien *et al.* 2018; Ulrich *et al.* 2018) show the need to consider
131 more continuous measurements of competition (see also Gallien *et al.* 2017). If we take
132 a more continuous view, there are almost endless possibilities for how a simple 3-
133 species (A, B, C) competition network can organize, ranging from pure (or "strong")
134 hierarchy (A >> B >> C, A >> C) to strong intransitivity (A >> B >> C >> A) and
135 everything in between (e.g., A >> B > C = A, A >> B > C > A, A = B = C). Gallien *et*
136 *al.* (2018) provide metrics that quantify the degree of intransitive competition in n -
137 species combinations ($n \geq 3$) in a more continuous way, while, Ulrich *et al.* (2018)
138 provide a metric, based on the "nestedness" commonly used in matrix algebra to
139 measure intransitivity at the community scale.

140 In addition to the need for more continuous metrics, it has been recently argued
141 that single intransitivity metrics can fail to adequately reflect the topology of
142 intransitive competition networks or to capture the properties of those networks that
143 affect species coexistence. A range of factors such as the connectance of each species
144 with others (Alcántara *et al.* 2016), the number of species involved (Allesina & Levine
145 2011; Gallien *et al.* 2017), relationships between the competitive sub-networks existing
146 amongst the different species within a community (Cheng *et al.* 2014), or the
147 competitive ranking of each species (Laird & Schamp 2009; Soliveres *et al.* 2018) may
148 play a role in modulating how a given level of intransitivity affects species coexistence.
149 It is therefore important to use a range of metrics to quantify these different aspects of
150 intransitivity, or at least to consider the different ways in which intransitivity can affect
151 coexistence when interpreting a given metric. The methodological advancements in this
152 special feature will undoubtedly help future studies to properly quantify intransitive
153 competition and to address the circumstances under which it plays a role in the
154 maintenance of biodiversity. Importantly, studies on intransitivity extend to disciplines
155 other than ecology, with examples in law, economics and politics (Ziss 2007; Ludovic,
156 Musy & Saidi 2012; Klimenko 2015), to name but a few. The metrics offered in this
157 special feature will hopefully help to advance research within these fields too.

158

159 **How does intransitive competition affect coexistence?**

160 Early studies on intransitivity considered it a potentially important coexistence
161 mechanism; however, work on intransitive competition has largely taken place outside
162 the main body of coexistence theory (Fig. 1). "Modern coexistence theory" was
163 developed by Peter Chesson and others and contains the key insight that species can
164 coexist either by being similar in competitive ability (fitness) or by being different in

165 their niches (Chesson 2000). Coexistence theory typically assumes that competitive
166 ability or fitness differences are hierarchical, however they could also be intransitive
167 and coexistence models can be developed in which species fitness differences are
168 intransitive (Godoy *et al.* 2017; Matías *et al.* 2018; see also Gallien *et al.* 2017; Levine
169 *et al.* 2017; Saavedra *et al.* 2017).

170 The key question is then: *how important are intransitive fitness differences*
171 *relative to niche differences in promoting coexistence?* Strong intransitivity can drive
172 coexistence even without any niche differences between species, assuming that
173 competitive ability differences are perfectly balanced (Laird & Schamp 2006; Allesina
174 & Levine 2011), and most of the theoretical work on intransitivity has dealt with this
175 case, although such a scenario could be rather uncommon in nature. Only two studies
176 have so far looked at the interaction of weak intransitive fitness differences and niche
177 differences, both suggesting that intransitivity alone is unlikely to promote stable
178 coexistence (Gallien *et al.* 2017; Godoy *et al.* 2017). However, intransitivity could
179 enhance opportunities for species coexistence and allow two species to stably coexist
180 even in conditions where niche differences would otherwise be too small (Gallien *et al.*
181 2017; Godoy *et al.* 2017). Viewing competition in a more continuous way also shows
182 that the strength of competitive differences between species affects whether
183 intransitivity in these competitive differences can promote coexistence. Theoretical
184 studies suggest that, if fitness differences are too heterogeneous, i.e. if some species
185 pairs differ dramatically in fitness whereas others are similar, then intransitivity is less
186 effective at promoting coexistence (Gallien *et al.* 2017; see also Soliveres *et al.* 2018).
187 Future work therefore needs to more fully explore the roles of intransitivity, fitness
188 differences and niche differences in promoting coexistence.

189 A further factor that may be important to consider is the number of species
190 involved in an intransitive loop: a key result from theoretical studies is that intransitive
191 competition loops formed by an odd number of species will stabilize coexistence
192 whereas loops formed by even numbers of species will destabilize it (e.g., Gilpin 1975;
193 Allesina & Levine 2011; Gallien *et al.* 2017). However, to the best of our knowledge,
194 empirical support for this theory remains elusive. It also remains untested whether the
195 relative importance of fitness differences (including hierarchical and intransitive ones)
196 and niche differences, as drivers of coexistence, changes between communities with odd
197 vs even numbers of species.

198 Species coexistence is likely to be largely driven by environmental
199 heterogeneity, however very few studies have examined how environmental conditions
200 affect niche and fitness differences or the degree of intransitivity. Matías *et al.* (2018)
201 and Stouffer *et al.* (2018) are amongst the first studies to do so. Matías *et al.* (2018)
202 show more intransitive competition under experimental drought conditions, confirming
203 results from observational studies by Soliveres *et al.* (2015) and Ulrich *et al.* (2018).
204 However, Matías *et al.* (2018) also show that an increase in intransitivity under drought
205 is not sufficient to compensate for the reduction in niche differences that also occurs.
206 This means that fewer species could actually stably coexist under drier conditions,
207 nicely demonstrating that the drivers of intransitivity and of coexistence need not
208 always align. Stouffer *et al.* (2018) also reveal significant differences in competition
209 networks between sun and shade conditions, with shade providing unique coexistence
210 opportunities for some species pairs. These results also provide a mechanistic basis for
211 the observed influence of nurse plants on the competitive networks of their neighbours,
212 by showing how shading can alter competitive outcomes (e.g., Soliveres *et al.* 2011;
213 Aschehoug & Callaway 2015).

214 Another important extension for coexistence models is to consider temporal
215 variation in species abundances. Most coexistence models assume a fixed-point
216 equilibrium and calculate how many species can coexist at this equilibrium. The study
217 by Stouffer *et al.* (2018) shows that this may underestimate the number of species that
218 can coexist stably. These authors continue the work that Gilpin started back in 1975 and
219 show that cyclic intransitive competition dynamics may have a large impact on stable
220 species coexistence. Together, this study and the one by Ulrich *et al.* (2018) show that
221 ignoring spatial and temporal heterogeneity may underestimate the degree of
222 intransitivity present and the opportunities for coexistence. More studies determining
223 how coexistence mechanisms are affected by environmental factors are therefore
224 needed.

225 Research on species coexistence has mostly focused on single trophic levels but
226 intransitive competition could occur at multiple trophic levels. A few studies have
227 illustrated how higher trophic levels can disrupt competition hierarchies (i.e., by shifting
228 them from hierarchical to intransitive; LeBrun 2005; Cameron, White & Antonovics
229 2009) and have highlighted the importance of considering “mesoscopic” interactions
230 (i.e., interactions between competitive loops; Cheng *et al.* 2014) or multi-trophic stable
231 coexistence (Godoy *et al.* 2018). Determining the extent of coupling between
232 (in)transitive fitness differences across trophic levels is therefore emerging as a key new
233 topic that could help us to better understand the mechanisms of species coexistence in
234 complex communities.

235

236 **Beyond species coexistence: what are the consequences of intransitivity for**
237 **community structure?**

238 Research on the consequences of intransitive competition for community-level
239 attributes other than richness or species abundances is in its infancy. Changes in
240 competition hierarchy have been related to spatial, functional trait and phylogenetic
241 patterns (Gallien 2016; Maynard *et al.* 2017; Vandermeer & Yitbarek 2017). Reciprocal
242 competitive advantages, necessary to cause intransitivity, can arise from trade-offs in
243 competitive ability for different resources; and if functional traits are linked to
244 competition then more intransitive networks should have higher functional trait
245 diversity (Maynard *et al.* 2017; but see Gallien 2016). In this issue, Gallien *et al.* (2018)
246 suggest strong links between intransitive competition and the evolution of greater
247 functional trait divergences in a given clade, which is supported by the empirical,
248 bivariate relationships found by Ulrich *et al.* (2018) in salt-marsh plant communities.
249 Soliveres *et al.* (2018) also show that intransitivity is related to the functional traits not
250 only of the target species but also of those with which it is competing (see also Kunstler
251 *et al.* 2012). Interestingly, clear relationships between functional traits and competitive
252 dominance have been observed in a number of taxa when competition is hierarchical
253 (LeBrun 2005; Kunstler *et al.* 2016; Liouw *et al.* 2016; Miller *et al.* 2017), but a study
254 in this issue suggests that these relationships may dampen when competition is
255 intransitive (Soliveres *et al.* 2018). This opens the question of whether cases where
256 traits fail to predict competitive ability could be indicators of intransitive competition. If
257 intransitive competition is based upon contrasting competition hierarchies for different
258 resources, then traits related to the acquisition of only one of those resources should be
259 less predictive of the overall competitive rank of a species than if the competition
260 hierarchy is consistent for all resources.

261 If intransitive competition affects functional trait distributions, then it could also
262 affect other community/ecosystem properties. A couple of studies have shown effects

263 on invasion by exotic species (Henriksson *et al.* 2016; see also Gallien *et al.* 2018) and
264 diversity-function relationships (Maynard, Bradford & Crowther 2017). It has not been
265 until this decade that ecologists have started to investigate how the ways species
266 compete can affect the patterns that emerge at the community-level. The new methods
267 being developed to assess intransitive competition, and the slow but steady increase in
268 the number of studies in this topic, will certainly provide novel insights into the ways in
269 which intransitive competition affects community attributes and ecosystem functioning.

270

271 **What factors determine whether species compete transitively or intransitively?**

272 Despite the relatively low number of studies on the topic, and the variety of approaches
273 that such studies have undertaken, we are starting to gather some generalities on what
274 factors drive intransitive competition (Table 1). Amongst environmental factors, it has
275 been suggested that both productivity and heterogeneity should enhance the degree of
276 intransitivity in competition. Theoretical approaches suggest that intransitive
277 competition is more likely in heterogeneous environments (Allesina & Levine 2011;
278 Schreiber & Killingback 2013), where reciprocal competitive advantages (competitive
279 reversals) may disrupt competition hierarchies. A study within this special issue reports
280 the first empirical evidence for this (Ulrich *et al.* 2018). Gilpin (1975) also suggested
281 that intransitive competition should prevail in productive environments, especially in
282 the tropics; however, in this issue Matías *et al.* (2018) and Soliveres *et al.* (2018) refute
283 this hypothesis using a variety of approaches. These three studies show more
284 intransitivity under drier or unfertile conditions, meaning they find, in fact, that
285 competition tends to be more hierarchical under fertile and productive conditions (see
286 also Soliveres *et al.* 2015). This has important implications for understanding effects of
287 global change on biodiversity, as changes in productivity or heterogeneity following

288 land use or climate change could alter the nature of competition and therefore
289 opportunities for coexistence.

290 The characteristics of the competing species will also strongly determine
291 whether or not they engage in intransitive or hierarchical competition (see *Beyond*
292 *species coexistence: What are the consequences of intransitivity for community*
293 *structure?* above). Amongst these species-specific traits, mobile organisms seem less
294 likely to compete intransitively than sessile ones (Reichenbach *et al.* 2007). Evidence
295 for this idea is mostly indirect, with studies on mobile taxa including protists (Carrara *et*
296 *al.* 2015), ants (LeBrun 2005), flies (Ulrich *et al.* 2014), fish (Henriksson *et al.* 2016)
297 and birds (Miller *et al.* 2017) showing competition to be strongly hierarchical, whereas
298 studies on sessile organisms more often show intransitive competition (Buss 1980;
299 Dormann 2007; Bowker *et al.* 2010; Soliveres *et al.* 2015). However, it is easy to find
300 evidence against this apparently general pattern, as shown by the first multi-taxa
301 experiment testing this notion, published in this issue (Soliveres *et al.* 2018). In
302 addition, mobile organisms, such as lizards or plankton, are paradigmatic examples of
303 intransitive competition (Sinervo & Lively 1996; Huisman & Weissing 1999).
304 Whether or not the effect of mobility on competitive networks is modulated by other
305 traits, such as range size, the habitat where a species lives (spatially structured or not),
306 or the way it competes (i.e. whether competition for space is important, as in intertidal
307 organisms or lichens) remains to be studied.

308

309 **How do intransitive competition networks assemble?**

310 Environmental and species-specific factors may, therefore, modulate whether or not
311 species engage in hierarchical or intransitive competition. But how do intransitive
312 competition networks assemble in the first place? It has been argued that strong

313 intransitivity may not easily occur in nature as it requires the three species involved to
314 be present simultaneously (e.g., Gallien *et al.* 2017; but see Zhang & Lamb 2012;
315 Stouffer *et al.* 2018). In this special feature, Gallien *et al.* (2018) explore a potential
316 mechanism by which initially weak intransitive competition could strengthen through
317 time. The authors use theoretical models to explore how intransitivity could evolve in
318 sympatry, which is one of the first attempts to link intransitive competition to eco-
319 evolutionary dynamics (see also Vasseur *et al.* 2011; Lankau *et al.* 2011; Patel &
320 Schreiber 2015; Ehlers *et al.* 2016). The authors show that (weak) intransitivity emerges
321 in these models and tends to strengthen through time as species diversify, which
322 increase the resistance of the communities to invasion and slows further evolution.
323 Communities may also diversify during succession or community re-assembly, as
324 species shift abundances and phylogenetically or functionally distinct species come to
325 dominate communities (e.g., Allan *et al.* 2013) or as species evolve to differentiate in
326 their traits (Vasseur *et al.* 2011; Zupping-Dingley *et al.* 2014). The degree of
327 intransitivity might therefore also change as communities assemble, although this has
328 rarely been considered and theoretical predictions are lacking. One study showed that
329 intransitivity actually decreased during succession (Ulrich *et al.* 2016) but there is as yet
330 no consensus on how intransitivity might change over time, as communities assemble
331 and evolve.

332

333 **Conclusions and research gaps**

334 The papers in this special feature, and a growing body of evidence, show that
335 intransitive competition may be much more common than previously thought and
336 should therefore be incorporated into general ecological theory. Progress in the field has
337 been hampered by large inconsistencies in how we assess pairwise competitive abilities,

338 how we measure competitive reversals and intransitivity, and how we infer coexistence.
339 This clearly limits our ability to extract general conclusions from the existing literature,
340 and calls for further research aimed at reconciling results derived from these different
341 approaches. The studies presented here use a range of approaches to quantify
342 intransitivity and one of the key conclusions from them is that we need to broaden our
343 view of what constitutes intransitivity beyond only "strong" intransitivity (full
344 competitive reversals) to consider also more partial or "weak" intransitivity. This
345 expanded view allows us to ask how competition varies continuously from transitive to
346 intransitive along environmental gradients (or with global change) and through time.
347 Studies within this special feature suggest that intransitive competition will be more
348 likely under heterogeneous and unproductive conditions, and for those species relatively
349 similar in their competitive abilities: future work is needed to determine how general
350 this is. Comparisons of the various metrics also suggest that those based on 3-species
351 combinations can be more informative than whole community metrics. Linking
352 intransitive competition to coexistence is a major aim of this special feature and the
353 studies here show that weak intransitive competition can enhance short-term
354 coexistence, and that effects on stable coexistence can depend on interactions between
355 intransitivity and niche and fitness differences. They also show that coexistence studies
356 need to expand their focus to consider environmental variation and temporal variation in
357 population sizes, i.e. multiple-point equilibria, as these will have large effects on
358 intransitivity-coexistence relationships.

359 What are the main open questions? As highlighted above, we definitely need
360 more empirical work evaluating: how general intransitive competition is in a range of
361 systems, which factors drive it, how it combines with niche and fitness differences to
362 drive coexistence and what consequences it has for community-level attributes and

363 ecosystem functioning. This is especially true for complex and realistic communities,
364 including multiple trophic groups: research on multitrophic coexistence, let alone
365 intransitive competition at multiple trophic levels, has hardly been done. Long-term
366 studies, evaluating changes in competition over time, remain rare (see Ulrich *et al.*
367 2016; Gallien *et al.* 2018) and theory incorporating temporal change is also uncommon.
368 A key frontier in intransitivity research is therefore to evaluate changes in intransitivity
369 over time to ask how it develops as communities assemble and how intransitive
370 competition interacts with evolutionary processes. It is our hope that the papers in this
371 special feature will help to inspire the next generation of studies aimed at linking
372 intransitive competition with other coexistence mechanisms, assessing its generality and
373 the factors driving it, and evaluating the consequences of intransitivity for the structure
374 and functioning of natural ecosystems.

375

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389

390 **Data accessibility**

391 This manuscript does not use data.

392

393 **Author's contribution**

394 SS and EA contributed equally to this work.

395

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571 **Table 1.** Summary of the research gaps and generalities that can be drawn from the
572 contributions in this special issue and those of previous literature on intransitive
573 competition.

Increasingly well-supported evidence

-Intransitive competition has been observed in too many organisms to keep ignoring it.

-Methods based on triplets (3-species combinations, or cycles) seem to work best to measure intransitivity.

-We need to adopt a more continuous view of competitive interactions and see purely transitive or intransitive competition as extremes at the end of a gradient.

-Only strong intransitivity can allow coexistence in the absence of any other stabilising mechanisms but weak intransitivity can increase the range of conditions under which species can stably coexist.

- Competition tends to be more hierarchical under fertile than unfertile conditions.

- Intransitive competition is more likely in heterogeneous environments.

- Intransitive competition is more likely (or more likely to enhance coexistence at least) in communities with an odd number of species. Although, empirical support for this theory is lacking.

-The effects of intransitive competition on ecosystems may extend beyond species coexistence, with possible effects on spatial and functional trait patterns, resistance to disturbances, or evolutionary rates.

Research gaps

-How important are intransitive competitive ability differences compared to other stabilizing or equalizing mechanisms in promoting coexistence? Does this vary in a predictable way depending on species number (even vs odd number of species) or environmental conditions?

-Where along the continuum from strongly transitive to strongly intransitive do most natural communities lie? And how often are unbeatable species found in nature?

-Do the same ecological processes promote niche differentiation and intransitivity?

-How do intransitive competition networks emerge over the long term: do they frequently evolve in sympatry?

-What are the consequences of intransitive competition for functional trait distributions?

-Does the relationship between functional traits and competitive ability tell us anything about how hierarchical competition is?

-Is transient or short-term coexistence (time to first extinction, current diversity patterns) important and does intransitivity affect transient and/or stable coexistence?

-How does intransitive competition and the mechanisms promoting coexistence within a single trophic level extend to species from other trophic levels?

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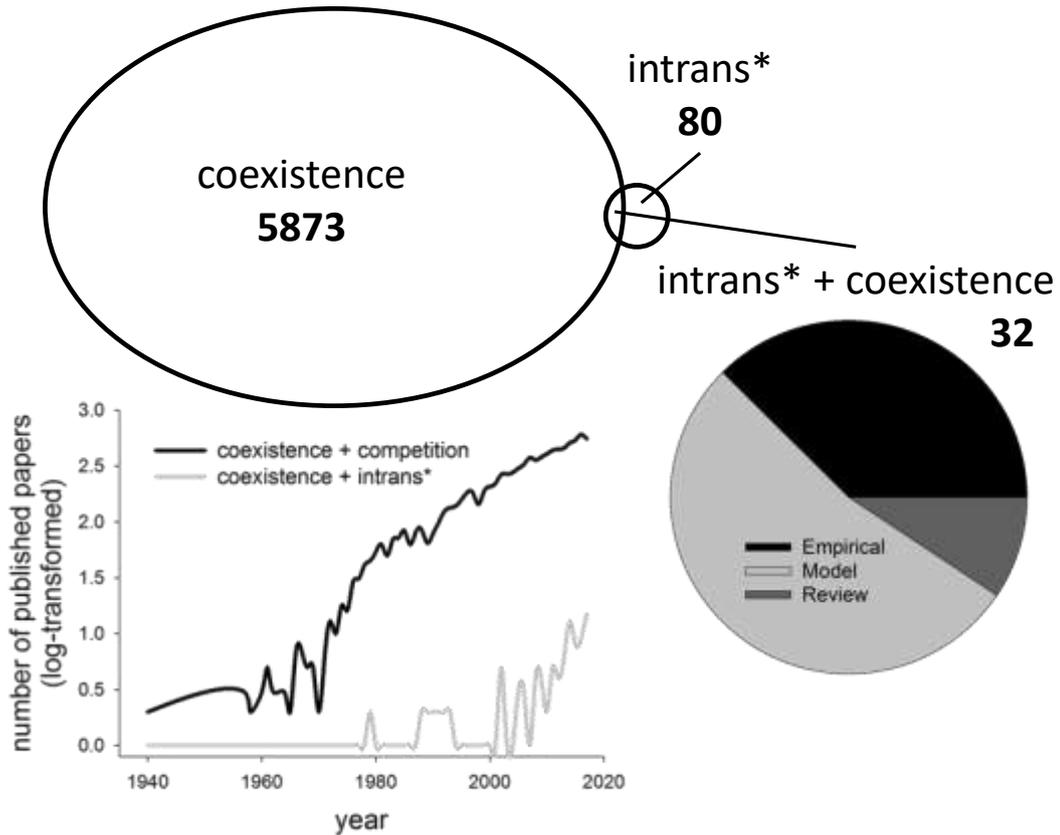
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597 **Figure 1.** Bibliographic analysis showing the number of hits ($\log(x+1)$ transformed) for
598 a search including “coexistence” (5873), “intrans*” (80), and both terms together (32) in
599 the Web of Knowledge (accessed January 2018). The pie chart shows the dominance of
600 theoretical (model approaches and reviews) studies linking intransitive competition to
601 coexistence. The lines show the much larger number of papers published under the
602 terms “competition” and “coexistence” (black) than those using the terms “intrans*”
603 and “coexistence” (grey), which have experienced a sustained growth only since the
604 year 2000 onwards.