Towards the integration of niche and network theories

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Abstract

The quest for understanding how species interactions modulate diversity has progressed by theoretical and empirical advances following niche and network theories. Yet, niche studies have been limited to describe coexistence within tropic levels despite incorporating information about multi-trophic interactions. Network approaches could address this limitation, but they have ignored the structure of species interactions within trophic levels. Here we call for the integration of niche and network theories to reach new frontiers of knowledge exploring how interactions within and across trophic levels promote species coexistence. This integration is possible due to the strong parallelisms in the historical development, ecological concepts, and associated mathematical tools of both theories. We provide a guideline to integrate this framework with observational and experimental studies.

Niche theory meets network theory

One central aim in ecology is understanding how species interactions modulate biodiversity. At the origin of this interest is Darwin's legacy, who reasoned that species coexistence is less likely among closely related species as they tend to compete for similar resources for surviving and reproducing [1]. Giving this reasoning, ecologists built the concept of the *niche* (see Glossary) to assess the degree of resource overlap among species [2, 3], and early work explored the consequences of competition for a single-resource niche dimension [4, 5]. However, researchers soon recognized that a species' niche is composed of multiple dimensions [6, 7]. For instance, plants compete directly and indirectly for abiotic resources such as water, nutrients, and light [8-10], as well as for biotic resources in the form of mutualistic interactions (e.g., pollinators, disperses, and mycorrhizae) [11-14]. In addition to resource competition, parallel work has shown that antagonist interactions within a trophic level (i.e., intraguild predation) [15] as well as those coming from other trophic levels (e.g., predation, herbivory, and parasitism) are also part of a species' niche [16-19]. Moreover, positive interactions such as facilitation can be as important as competitive interactions for structuring ecological communities [20, 21]. This body of knowledge has revealed that species coexistence is a much more complex process than originally thought.

Parallel to describing the multi-dimensional nature of species' niche, ecologists have obtained critical progress by revealing general principles of the consequences of multiple species interactions for species coexistence. For example, the concept of *apparent competition* [22, 23] has been particularly key to understand the role of indirect multi-trophic interactions in coexistence by describing how competition within a guild of species is modulated by shared enemies (e.g., predators and pathogens). This concept set the path to recently recognize that competition for resources and predation can be of equal importance for limiting or promoting diversity within a guild of primary producers or

68   consumers (e.g., plants or herbivores) [24, 25]. However, these advances together with

69   niche studies are limited in their approach as their goal is to understand the role of species

70   interactions in shaping species coexistence within one single trophic level [26]. The rest of

71   species within a community that does not belong to the focal trophic level is considered to

72   be always present and static. This critical limitation of niche studies clashes with the

73   increasing interest of ecologists in disentangling the mechanisms maintaining species

74   coexistence in more than one trophic level (see Figure 1 for a schematic representation).

75   Indeed, part of this motivation is due to having multi-trophic information readily available

76   [27, 28], but the fundamental question is how to extend niche theory to study the effects of

77   species interactions on determining diversity across multiple trophic levels simultaneously.

78

79   To address this limitation, here we call for the integration of niche theory with network

80   theory. Network theory has already partially addressed the challenge of how to consider the

81   role of species interactions in shaping species coexistence across several trophic levels [29,

82   30], but it has missed the information of within trophic levels that niche theory

83   incorporates. In particular, network studies have focused on the association of the structure

84   of species interactions with community dynamics in mutualistic (e.g., plant-pollinator and

85   plant-disperser) [31-35] and antagonistic systems (e.g., host-parasite, prey-predator, and

86   plant-herbivore) [34, 36-38] Yet, because network studies emphasize species interactions

87   between trophic levels, they consider that species within the same trophic level do not

88   directly interact or they all interact with the same strength [33, 35].

89

90   Because niche studies lack the ability to describe species coexistence for more than one

91   trophic level, and network studies ignore the structure of species interactions within trophic

92   levels (Fig. 1), it is surprising that both theories have not spoken fluently to each other

93   despite their complementarities can provide new research avenues and understanding of

94   how species diversity is maintained. Our aim here is to show a direct integration of both

95   theories as they share strong similitudes in their theoretical motivations, ecological

96   concepts, and mathematical tools. This path of mutual understanding paves the road to

97   combine theoretical concepts and associated toolboxes from both theories into a common

98   methodological framework. We believe the emerging framework is particularly useful for

99   investigating species coexistence in multi-trophic networks, which include competitive,

100   mutualistic, and antagonistic interactions simultaneously. Additionally, we provide a road

101   map that accommodates this new framework to experimental and observational studies.

102

103   **Conceptual parallelisms between niche and network theories**

104   Obtaining a common theoretical framework from the integration of both niche and network

105   theories is straightforward as these studies have started from similar conceptual constructs,

106   and after decades of research have independently converged on equivalent conclusions

107   about the conditions leading to species coexistence. To reach the maximum audience, we

108   verbally detail this historical convergence and explain here why both theories speak the

109   same language despite using different technical terms. We also aim to present a rigorous

110   mathematical explanation of this conceptual parallelism. This is possible because both

111   theories use similar population dynamics models to build ecological theory rooted in the

112   Lotka-Volterra form [4, 24, 25, 35, 38-41] (Box 1). We are aware that the direct application

113   of Lotka-Volterra models to describe natural systems might be limited because assume

114   species linear responses, and do not take into account meta-community dynamics. Part of

115   these limitations will be solved later when we will present more mechanistic models that

116   capture additional nonlinear species responses in order to explain how to apply this

117   emerging framework to experimental and observational approximations [42, 43].

118

119   As we previously mentioned, the *niche* concept was a fundamental construct to understand

patterns of species distribution and co-occurrence within a trophic level based on how species

interact with the habitat they experience (Grinnellian niche), how they modify the habitat

(Eltonian niche) and how interact with other species in the community (Hutchinsonian niche)

[44]. Under classic niche theory, the only condition modulating species coexistence was the

amount of niche overlap between species [4, 45], which ecologists assumed to arise for instance

from differences in phenology, bill size, shade tolerance, or feeding preferences. The rationale

was that the smaller the niche overlap, the larger the chances of species coexistence [7, 46,

47].

However, subsequent work [25, 41, 48] showed that niche differences alone are not

enough to determine species coexistence. Under recent advances of niche theory (also known

as "modern coexistence theory"), niche differences are only a stabilizing mechanism that tends

to promote coexistence when species limit themselves more than they limit others [48]. Modern

coexistence theory has provided techniques to directly measure niche differences as the relative

ratio between intra and interspecific competition [25], and consider that neutral dynamics occur

when species do not differ in their niches but have equivalent fitness [49]. The estimation of

niche differences using coexistence theory techniques remains phenomenological (i.e., the

source of variation is unknown), and recent studies are for instance mapping how species

functional trait differences relate to niche differences [50].

Conversely, species can also differ in their fitness. Fitness differences are related to

species' ability to capture and transform resources into offspring, which is generally a

combination of demographic parameters (e.g., fecundity, survival, and recruitment) and the

species' sensitivity to reduce these demographic parameters in the presence of neighbors

[25, 43, 49]. Fitness differences in essence determine the superior competitor within a

species pair in the absence of niche differences. It has been well recognized that

146   coexistence is the result of a balance between the relative strength of niche versus fitness

147   differences. That is, two species will stably coexist when their niche differences overcome

148   their fitness differences [48, 49] (see Table 1 for examples of both species differences

149   across a wide range of organisms). This condition has also been reinterpreted as the larger

150   the niche difference between two species, the larger the combination of their fitness

151   differences compatible with their coexistence [49, 51] (Box 1). This reinterpretation is

152   critical as it provides the main bridge of common understanding between niche and

153   network theories explaining how species coexistence is possible.

154

155   Network research on species coexistence started by studying the stabilizing mechanisms

156   for entire communities [5], rather than focusing on pairwise interactions. This stability was

157   defined in a dynamical rather than a static way. Dynamical stability is the property of a

158   system to return to an original equilibrium point (if it exists) after a pulse perturbation

159   (e.g., a change in species abundances) coming from demographic stochasticity, which

160   includes migration and random changes in birth and death processes. Early network

161   studies showed that this dynamical stability depends on species interactions (analogous to

162   niche differences) within and between trophic level compartments (contained in β matrix,

163   Box 1). Importantly, a number of interesting questions emerged from these concepts, such

164   as whether the observed structure of large multi-trophic systems necessarily leads to more

165   dynamically stable communities [5]. However, extensive research showed that dynamical

166   stability alone (as niche differences alone) is not enough to guarantee stable coexistence of

167   all species in a community. This means that it can be possible to have a dynamically stable

168   community where the equilibrium point will always lead to one or more species with zero

169   abundance (N_i^*=0), even if reintroduced into the community [35, 52, 53]. In other words,

170   the system is dynamically stable but contains only a subset of species from the original

171   pool.

172

173   As it has happened with the historical development of niche theory, subsequent work on

174   network theory have shown that it is also necessary to account for the species' fitness in

175   order to evaluate the condition of whether species can attain positive abundances at

176   equilibrium [54]. Network studies called this condition feasibility, which also depends on

177   the species interactions contained in the matrix (β) and the species' demographic

178   parameters (r) [35, 52, 55] (Box 1). Importantly, these recent advances have shown that the

179   structure of species interactions between trophic levels can modulate the range of

180   combinations of demographic parameters leading to feasible systems [35, 55]. Therefore,

181   in line with niche theory, network studies also found that species coexistence within

182   communities depends on how the demography of species match the constraints imposed by

183   species interactions.

184

185   This historical convergence shows the existence of a common theoretical framework for

186   understanding how species interactions modulate diversity, which has two key ingredients:

187   1) species' demography and 2) the structure of species interactions. This structure is

188   contained in the β matrix described in Box 1. The take-home message of this framework is

189   that a community of species can coexist when both ingredients are combined in the

190   following way: species interactions define the coexistence space (i.e. the feasibility region)

191   and species coexist when the combination of their demographic parameters (i.e. fitness)

192   falls within this space (Box 2, Fig. 2). One crucial advantage of this framework is that it is

193   not limited to any particular type of multi-trophic interactions, and can be therefore

194   accommodated to both mutualistic and antagonistic interactions such as a plant-pollinator

195   or a predator-prey community. Another key important advantage is that this framework is

196   not either limited to two trophic levels. It can be extended to multi-trophic structures,

197   where three or more trophic levels are considered simultaneously. Indeed, these multi-

198   trophic structures are simply the combination of competitive/facilitative interactions within

199   trophic levels as well as antagonistic and mutualistic interactions between trophic levels

200   [56] (Box 2).

201

Coupling the integration of niche and network theories with experimental and observational work

204   We acknowledge that one critical step to consider in full this integrative framework

205   depends on how easily researchers can adapt it to their particular systems. The basic task is

206   to obtain information of demographic parameters as well as species interaction coefficients

207   within and between trophic levels. However, it is not so obvious how this information can

208   be obtained and related to theory. We can start learning from the ability of recent advances

209   in niche theory to couple theory with field and lab experiments [42, 57-60].

210

211   These studies suggest that the most rigorous way to proceed would be to conduct

212   experiments in order to parameterize and validate a system of equations containing a

213   model of population dynamics for each trophic level. Technically, this parameterization is

214   easier to obtain when the life-span between organisms is similar. In particular, population

215   models describing species dynamics with an annual life cycle seem among the best

216   approximations to choose for several reasons. They define the network structure and

217   species fitness in the exact same way as the original definition using the Lotka-Volterra

218   framework [25, 43], yet they are complex enough to include nonlinear mechanisms of

219   species coexistence such as the storage effect, and saturating functional responses to

220   competitive, mutualistic and antagonistic interactions (Box 3). They can also take into

221   account the effect of environmental variation in space and time on modifying diversity

222   maintenance due to changes in intransitive competition [59], intraspecific trait variation

223   [61] or phenotypic plasticity [62]. Moreover, annual species are relatively easy to

224 manipulate, models describing population dynamics have been successfully used for plants

225 [43, 57], and can be extended to other annual organisms including pollinators (e.g., wild

226 bees), herbivores (e.g., snails, grasshoppers), or pathogens (e.g., fungal seed pathogens).

227

228 An alternative to experiments is the use of observational data (e.g., [63, 64]).

229 Observational approaches are justified when organisms differ in their life-span, or when

230 their manipulation is not feasible for technical or conservation issues. The traditional

231 limitation of observational studies is that the structure of species interactions between

232 trophic levels is often easier to describe, at least at the species level, than the structure of

233 species interactions within trophic levels. This limitation can be solved by using

234 mathematical models fed with spatially explicit and/or temporal series data. These

235 methodologies allow inferring species demographic parameters and species interactions

236 from changes in species fitness due to both natural variations in the community density and

237 species relative abundances [65, 66]. For example, recent work [64] combined statistical

238 models for survival, growth, and recruitment with individual-based models to describe

239 temporal pattern is plant species co-occurrences. These model-generated population

240 abundances were then integrated into projection models to estimate the structure of

241 competitive interactions within plant species.

242

243 Regardless of the approach selected, we stress the urgency of linking theory and empirical

244 work. We are at the dawn of understanding whether species characteristic, commonly

245 reported in the niche and network literature, are more strongly related to differences in

246 species demography or to the strength and sign of species interactions [50, 67, 68].

247 Moreover, we are not aware of a single study that has attempted to empirically estimate in a

248 quantitative way the matrix of species interactions within and between trophic levels

249 simultaneously. We believe that taking such approach is crucial for answering an

250   outstanding research question that emerges with the integration of both theories, namely,

251   how species interactions between trophic levels drive niche and fitness regions within

252   trophic levels and vice-versa. Therefore, this is the topic of our next section.

253

254   **How do species interactions between trophic levels drive niche and**

255   **fitness differences within trophic levels?**

256   By coupling recent conceptual advances of niche and network theory, we are ready to

257   understand how the species differences that determine coexistence within trophic levels

258   (niche and fitness differences) feedback with the structure of species interactions that

259   determine coexistence between trophic levels and vice-versa. To illustrate these ideas, let

260   us consider a mutualistic plant-pollinator system (see graphical example in Fig. 2). What

261   we have learned from prior work is that differences in feeding behavior, body mass, or

262   insect phenology can contribute to the niche differences that tend to stabilize coexistence

263   between plants (see Table 1) [69, 70]. However, pollinators also contribute to the fitness

264   differences promoting plant competitive dominance. For instance, changes in the

265   abundance of pollinators can, in turn, modify the competitive hierarchy of a plant guild by

266   increasing the number and the quality of seeds produced by pollinator-dependent plants.

267   Differentiating between these alternatives is crucial because if pollinators primarily drive

268   niche differences over fitness differences between plant competitors, then we can expect a

269   more diverse plant community (e.g. [11, 70]). A completely different outcome would occur

270   if pollinators primarily drive fitness differences among plants. In that case, a dominant

271   plant species favored by pollinators can dominate the community.

272

273   Similarly, considering pollinators beyond being a resource for plants implies that we have

274   to assess simultaneously their population dynamics. For instance, plant characteristics such

275   as floral morphology or plant phenological timing can contribute to the different pollinator

276   requirements (i.e., niche differences) that stabilize their coexistence. But some plant

277   species can also contribute to the dominance of a few pollinators (i.e., fitness differences)

278   if those can particularly benefit from them as occur with pollinator specialists. All in all,

279   this could lead us to rethink if mutualistic interactions between trophic levels always

280   increase the likelihood of species coexistence. Traditionally, mutualisms have been

281   considered a positive interaction that enhance coexistence because the individuals involved

282   obtain a certain benefit that can be translated to their population growth rates (but see [16]

283   in a general context). However, to what extent these beneficial effects between particular

284   species across trophic levels can reduce the likelihood of species coexistence in the entire

285   system (i.e., within and among trophic levels) is not known yet (Fig. 2).

286

287   Note that we need to use a geometrical rather than an algebraic approach to study fitness

288   and niche differences for more than two species (see Fig. i in Box 2). This approach

289   informs us whether species coexistence is possible when the fitness differences between

290   species falls within the feasibility domain (Fig 2). Moreover, this approach allows us to

291   quantify how environmental variation modulates the extent of the feasibility domain and

292   the differences in fitness between species. Estimating these environmental-dependent

293   relationships is important as they determine how strongly can be an ecological community

294   perturbed without pushing species towards extinction. As a rule of thumb, the closest the

295   fitness differences to the edge of the feasibility domain, the lowest the ability of the

296   community to face perturbations (Fig. 2) [71]. It is also important to note that this

297   approach can be applied to other network types, such as food webs, parasitoid webs [24,

298   72], and multi-trophic networks combining antagonistic and mutualistic interactions [56,

299   73].

300

301   Answering this question using empirical approaches involves three steps (Box 3). First, we

302   need a framework for describing species population dynamics as function of species

303   demographic parameters and species interactions within and between trophic levels. For

304   example, for a plant-pollinator system, this framework can be a system of two annual

305   population models (one for each trophic level) that can include a storage effect component

306   if desired (Box 3). Second, in order to parameterize the models, we need information on

307   species demography. For species demographic parameters, such as per capita growth rate in

308   the absence of competition, germination rate, or larval survival, can be inferred relatively

309   easy from experimental or observational data [43, 57, 64, 66]. Third, we need to estimate

310   the matrix β that summarizes species interactions across trophic levels.

311

312   This third step is by far the most challenging aspect as the number of parameters that need

313   to be estimated grows exponentially with the number of species in the community. In

314   principle, these estimates can be obtained from statistical models fitting empirical or

315   observational data [27, 59, 74]. For intra and interspecific competitive coefficients within

316   plants and within pollinators, these parameters can be obtained by describing how species

317   per capita growth rates depends on each competitor's relative abundance [50, 59] (Fig. ii

318   in Box 3). For the case of mutualistic effects of plants on pollinators and vice versa, the

319   procedure is similar to the one previously described, but this time per capita growth rates

320   should be described as a function of the relative abundance of each mutualistic species. In

321   the likely case that this option is not feasible, one possibility is to group species by

322   functional groups, and estimate interaction coefficients (at that resolution) via changes in

323   population size of both trophic levels through time [75]. While the functional-group

324   approach assumes uniformity of responses within functional groups, it might be a

325   requirement when scaling up to higher dimensions. Another possibility is to use novel

326   techniques that combine ecological, phylogenetic, and geographic information to predict

327   forbidden links and define a realized rather than a potential matrix of species interactions

328 for large communities [76]. This latter possibility infers the strength of species interaction

329 (e.g., competition, mutualism, etc.) without the necessity of measuring fitness directly. In

330 sum, obtaining information for estimating the matrix β is challenging, but there are

331 techniques available to solve that limitation [75-77].

332

333 This three-step approach can also be combined with variation in species functional traits,

334 phylogenetic relatedness, or intra-specific variation to test a myriad of ecological questions

335 regarding the functional and phylogenetic assembly of communities (e.g. limiting

336 similarity hypothesis, Darwin's naturalization hypothesis) [4, 78]. Moreover, measuring

337 emergent properties of the community such as biomass or food production would allow

338 linking the mechanisms of biodiversity maintenance to ecosystem functioning (e.g.

339 biodiversity insurance hypothesis, biodiversity-complementarity hypothesis) [79, 80]. For

340 instance, experimental assemblages varying plant and flower morphology and pollinators'

341 body size can allow testing the role of species traits in providing higher food production

342 yields [81] by the effects of plant and animal traits on niche and fitness differences (see

343 Ref. [82] for details).

344

345 **Concluding remarks**

346 The integration of niche and network theories provides a natural pathway to obtain a

347 deeper understanding of the role of species interactions in modulating species coexistence.

348 Here, we show that this integration is straightforward thanks to the strong parallelism of

349 ecological concepts, complementary approaches, and associated mathematical tools found

350 across these two research areas. The emergent property of this integration is the

351 consideration that diversity within ecological communities is maintained when species

352 interactions creates a coexistence space that accommodates the differences in fitness

353 between species. Importantly, we have provided a methodological framework readily

available to investigate how the strength of mutualistic, antagonistic, and competitive

interactions across trophic levels promote species coexistence in multi-trophic networks

and variable environments. The key limitation we face now is the empirical

parameterization of the interaction matrix, which summarizes the structure of species

interactions across trophic levels. It should be no surprise that applying the integration of

niche and network theory to experimental and observational approaches can be

challenging, but we have provided a guideline to accomplish this aim. While this is not an

easy task, the benefits can be unlimited.

Author contributions

All authors contribute equally to the paper.

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577

578   Table 1: Examples of niche and fitness differences for different organisms and trophic levels. Some examples explicitly separate the study of

579   the species' niche from the species' fitness while in other examples researchers have only studied one component or both niche and fitness

580   differences have been considered together. Note that for many trophic levels, information of niche and fitness differences is asymmetric,

581   these differences are better known for one trophic level than for the other (e.g. plants-fungi or insects-vertebrate).

582

Trophic level	Evidences of niche and fitness differences	References
plant - plant	Niche: Spatial segregation, phenology, or plant morphology differences reduce niche overlap. Fitness: Species ability to draw down common limiting resources determines species fitness.	[4, 8, 48]
plant-insect	Niche: Fragmented evidences suggest that differences in pollinators can stabilize plant coexistence. Fitness: Herbivorous insects and their network of hyperparasitoids can significantly affect plant fitness.	[11, 70, 83]
plant-vertebrate	Niche and fitness: Interactive effects between abiotic stress, tolerance to herbivory and herbivore body size determine plant abundances and richness.	[84, 85]
plant - fungi	Niche: Fungal pathogens mediate coexistence through trade-offs between competitive ability and resistance to pathogens and through pathogen specialization. Fitness: Low specificity of fungal pathogens determines local abundance of plant species in tropical forest.	[19, 86]
insect - insect	Niche: Plant species, stem size and location within stem determine niche differences within a guild of herbivorous insects. Time partitioning for predating acorns determine niche differences within a guild of	[87, 88]

phytophagous insects.

Fitness: Searching ability, female fecundity, and resource degradation and preemption determine fitness

differences among parasitoids, phytophagous insects and arachnids.

insect - plant	Niche: Wild bees specialize in their floral reward including nectar, pollen, pollen resins, volatiles, lipids, and waxes. Fitness: Foraging rates and food storage determine fitness differences (i.e. drone production, winter survival) among genetically diverse honey-bees colonies.	[11, 89]
insect - vertebrate	Tick habitat differs greatly among species from rodent burrows, caves to bird nest. Fitness: The timing and duration of aquatic insect emergence is regulated by temporal variation in salmon density.	[90, 91]
vertebrate – vertebrate	Niche: Differences in bill shape and body size stabilize coexistence between birds by the use of different resources. Fitness: Intraguild predation of large carnivores on African wild dogs reduces its population size	[92, 93]
plant - vertebrate	Niche: Strong overlap of dietary requirements between wild and domestic herbivores.	[94, 95]
insect - vertebrate	Niche: Vertebrates differ in the number and specificity of their parasitic insects. Fitness: Ticks reduce offspring and increase mortality in a wide variety of animal including birds, lizards and mammals.	[90, 96]

trematode - mollusk	Niche: Spatial heterogeneity stabilizes coexistence of a guild of salt marshes trematodes.	[72]
	Fitness: Competition-colonization trade-offs determines trematodes fitness.	
alga – alga	Niche and fitness: Phylogeny relatedness does not predict competitive outcomes between fresh water algae.	[58]
bacteria – vertebra	Niche: Specific immunity of Streptococcus pneumoniae serotypes stabilizes coexistence.	[97]
	Fitness: Acquired immunity to non-capsular antigens determines serotypes fitness.	
protist - bacteria	Niche and fitness: Differences in mouth size of bacterivorous protist species reduces competitive exclusion.	[46]

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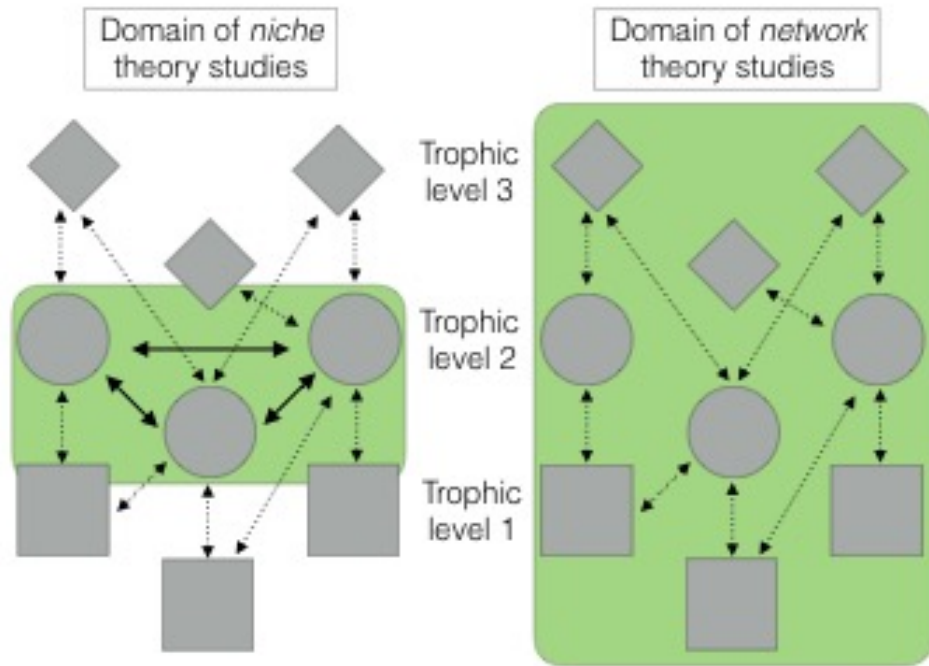
Figure 1: Research domains of niche and network theories. Niche theory (left side) has been successful in incorporating the effect of direct and indirect interactions within and between trophic levels (denote by arrows in black) on determining species coexistence within a single trophic level (light green rectangle) [7, 16, 22, 24]. However, niche studies have not addressed how these direct and indirect trophic interactions modulate coexistence across trophic levels. In contrast, this task has been addressed by network research (right side). While the area of study is bigger (green rectangle), network studies have not considered the structure of interactions within trophic levels (no solid lines present). By integrating niche and network theories we can start considering explicitly and simultaneously species interactions across trophic levels and their role (feed-backs) in modulating species coexistence. Note that arrows are double headed indicating the existence of such feedbacks. Solid and dashed arrows indicate whether the interaction is within or between trophic levels, respectively.
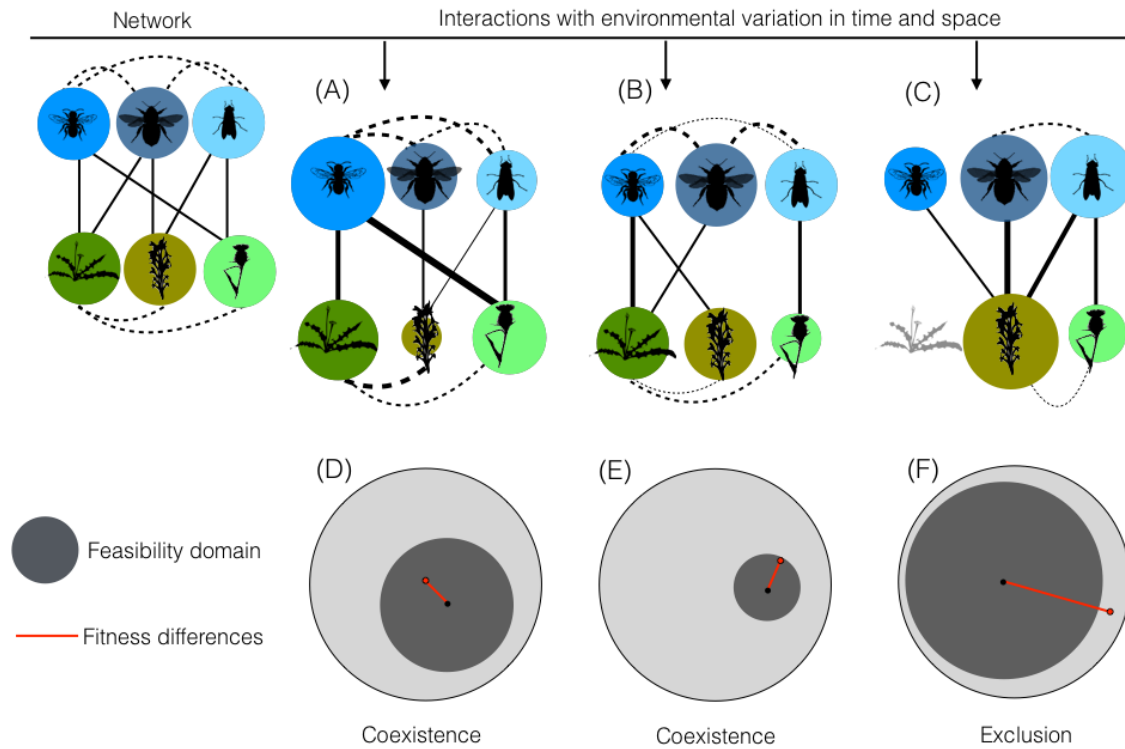
597
598 **Figure 2:** Effects of species' intrinsic properties and network structure on species

599 coexistence. Species traits such as body size, phenological timing, or feeding preferences

600 interact with environmental variations in space and time to determine 1) network structure

601 and 2) species' fitness. Dashed lines represent the strength of species interactions within

602 trophic levels and solid lines represent the same across trophic levels. Obtaining

603 information on how such trait-environment interactions modified these two elements in

604 ecological communities remains fundamental to predict the consequences of species

605 interactions for the maintenance of diversity [98]. Consider a hypothetical case of a plant-

606 pollinator system in which environmental variation modifies these two elements in three

607 different ways (Panels A, B, and C). The size of the circles denotes the realized species'

608 fitness, which arises as a combination of species interactions and their demographic

609 parameters (plants in green and insects in blue). Additionally, we have learned from the

610 integration of niche and network theories that the structure of species interactions within

611 and between trophic levels renders the feasibility domain (Here represented in two

612   dimensions for simplicity; dark gray area in Panels D, E, and F). Note that each network

613   structure gives a different size of feasibility domain. In principle, the larger the feasibility

614   domain, the more likely species coexist as it allows for a larger combination of fitness

615   differences (see F feasibility domain compare to D and E cases). However, it is paramount

616   to point out that even with a large feasibility domain, species may not coexist if the

617   position of the vector containing species' fitness (red line) falls outside the feasibility

618   domain (i.e., falls within the light gray area) [71]. This is the case of F where one plant

619   species is excluded. Conversely, the system can be maintained despite showing a smaller

620   feasibility region if the vector of species' fitness falls within the feasibility domain (cases

621   D and E). Therefore, the take-home message is that coexistence occurs when species

622   interactions creates a feasibility domain compatible with the observed fitness differences.

623   Recall that fitness differences are measured as the distance between the center of the

624   feasibility domain and the position of the vector containing species fitness (red line).

625   Importantly, systems with low fitness differences may face larger perturbations. For

626   instance, species can coexist in case E but it can be less resistant to perturbations compared

627   to case D given that the position of the vector of species' fitness is close to the exclusion

628   region.

Box 1: Conceptual parallelism between conditions leading species coexistence for niche and network theory

For a pair of species in competition, the coexistence conditions according to niche theory are defined by:

$$\underbrace{\sqrt{\frac{\alpha_{11}\alpha_{22}}{\alpha_{12}\alpha_{21}}}}_{(1-\text{Niche difference})^{-1}} > \underbrace{\frac{r_1}{r_2}\sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}}}_{\text{Fitness difference}} > \underbrace{\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}}_{1-\text{Niche difference}} \qquad (1)$$

where $r_1 > 0$ corresponds to the intrinsic growth rate (demographic parameter) of species 1, and $\alpha_{12} > 0$ represents the competitive per capita effect of species 2 on the per capita growth rate of species 1. This equation states that the fitness difference (i.e., the ratio between intrinsic growth rates modulated by what is known as the competitive response ratio) of the two species has to fall between a lower and an upper bound computed from the niche difference (i.e., range of values defined by the ratio between inter and intra-specific competition). Note that these inequalities can be also simply written as $\alpha_{11}/\alpha_{21} > r_1/r_2 > \alpha_{21}/\alpha_{22}$. Moreover, such inequalities have also to assume that the niche difference is smaller than one, i.e.,

$$\alpha_{12}\alpha_{21} < \alpha_{11}\alpha_{22} \qquad (2)$$

which guarantees that the equilibrium point is dynamically stable (the system returns to its original equilibrium point after a pulse perturbation) in a Lotka-Volterra competition model of the form:

$$\begin{cases} \dfrac{dN_1}{dt} = N_1\left(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2\right) \\ \dfrac{dN_2}{dt} = N_2\left(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2\right) \end{cases} \qquad (3)$$

where N_1 and N_2 correspond to the abundance of species 1 and 2, respectively. Note that, the inequalities in Equation 1 correspond to an equilibrium point called feasible because all species have positive abundances (i.e., $N_1^* > 0$ and $N_2^* > 0$) [35, 52-54, 99]. In contrast, the

651   inequality of Equation 2 only grants the dynamical stability (in fact in that specific case the

652   global stability) by having intra-specific competition stronger than interspecific

653   competition. Note that feasibility is a necessary condition for species persistence in a

654   Lotka-Volterra model [54].

655

656   Let us explain how dynamical stability and feasibility conditions arise in multi-trophic

657   systems by taking as an example a two-trophic level system describing the mutualistic

658   interactions between a set of plants (P) and a set of pollinators (A). Note that similar

659   conclusions are obtained by considering antagonist interactions such as a prey-predator

660   system. This mutualistic system can be described by the following set of dynamical

661   equations:

662

$$
\begin{cases}
\dfrac{dP_i}{dt} = P_i\left(r_i^{(P)} - \sum_j \alpha_{ij}^{(P)} P_j + \sum_j \gamma_{ij}^{(P)} A_j\right) \\[2ex]
\dfrac{dA_i}{dt} = A_i\left(r_i^{(A)} - \sum_j \alpha_{ij}^{(A)} A_j + \sum_j \gamma_{ij}^{(A)} P_j\right)
\end{cases}
$$

663   (4)

664   where the variables P_i and A_i denote the abundance of plant and animal species i,

665   respectively. The parameters of this mutualistic model correspond to the values describing

666   intrinsic growth rates (r_i), within-guild competition ($\alpha_{ij}>0$), and the benefit received via

667   mutualistic interactions between trophic levels ($\gamma_{ij}>0$). All these interaction strengths can,

668   in turn, be embedded in a two-by-two block matrix $\beta = \begin{bmatrix} \alpha^{(P)} & -\gamma^{(P)} \\ -\gamma^{(A)} & \alpha^{(A)} \end{bmatrix}$. The conditions for

669   feasibility depend on both the species interactions defined by β and the demographic

670   parameters of species r (analogous to equation (1) above) [71]. Note that the conditions for

671   dynamical stability are more complex [40]. Indeed, several meaningful notions of stability

672   have been defined in ecology, such as Volterra-dissipative, D-stability, sign-stability, and

673   local stability. Sign-stability, Volterra-dissipative, and D- stability are only determined by

674   the interaction matrix β. Sign-stability has the property of granting global stability only on

675   the description of who eats whom and not on the strength of the trophic interactions.

676   Volterra-dissipative implies the global stability of a feasible equilibrium, while D-stability

677   grants only local stability. Finally, local stability involves also the equilibrium densities and

678   therefore the intrinsic growth rates. The relations among these notions of stability (and

679   more) are well represented by Logofet's flower [53].

680 **Box 2: Emerging properties of the integration of niche and network theory**

681 For multi-trophic dynamical systems of the general form $dN_i/dt = N_i f_i(N)$, an $n \times n$ block

682 matrix emerges for describing species interaction across n trophic levels:

683
$$\beta = \begin{bmatrix} \alpha_1 & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & \alpha_2 & \cdots & \gamma_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_{n1} & \gamma_{n2} & \cdots & \alpha_n \end{bmatrix},$$

684 where the diagonal blocks (α_i) correspond to the within-trophic level (i) interactions (i.e.

685 competition, intraguild predation, facilitation) and the other blocks (γ_{ij}) represent the between-

686 trophic level interactions (effect of trophic level j on i in the form of mutualism or antagonism

687 interactions). As β is a block matrix, each element of the matrix represents a submatrix of

688 species interaction. For instance, α_1 is a matrix describing all species interaction within the

689 trophic level 1, and γ_{12} is another matrix describing all interactive effects of species from the

690 trophic level 2 on species from the trophic level 1.

691

692 Stable coexistence of all species ($N_i^* > 0$) across trophic levels depends on whether this

693 interaction matrix β and the demographic parameters r_i satisfies together both the stability and

694 feasibility conditions [53, 54, 71]. There are different classes of dynamical stability. For

695 instance, local stability is the property of the system to return to the equilibrium point after a

696 small pulse perturbation (changes in species abundances), whereas global stability is concerned

697 with external perturbations of any given magnitude converging to the same equilibrium point.

698 Each class demands specific properties to be fulfilled by the interaction matrix β in

699 combination with the species demographic parameters r_i [53, 71], and which class of stability

700 should be studied depends on both the research question and knowledge about the system. The

701 feasibility of a multi-trophic system corresponds to the conditions allowing all species to have

702 positive abundances, which also depends on both the interaction matrix β and the demographic

703 parameters r_i [35, 52-54, 71]. The figure below illustrates the conditions of feasibility in a

704 three-species system. The green area on the sphere represents the range of demographic

705 parameters leading to feasibility given the interaction strengths matrix. To some extent, Fig. i

706 of the extension of modern coexistence theory to multispecies coexistence; the border of the

707 green area is the multispecies analogous of the fitness and niche difference inequality (Box 1,

708 Equation 1) that applies to species pairs only.

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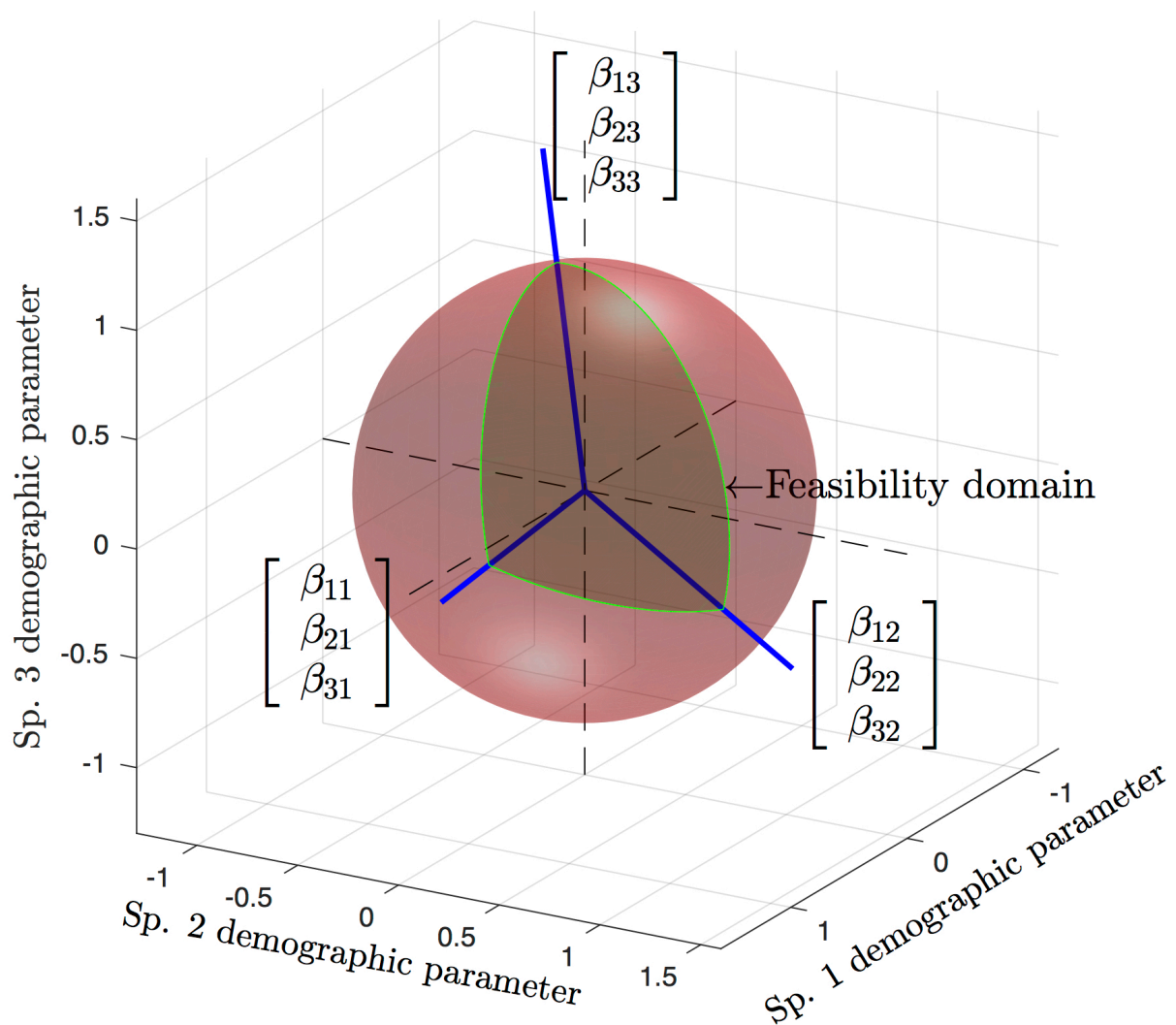
Figure i: Illustration of the feasibility domain for a multi-trophic system. The figure shows the

711 normalized domain of demographic parameters (feasibility domain relative to the unit sphere)

712 that a two-trophic system (e.g., two pollinators and one plant) can theoretically have to be

713 compatible with all species having positive abundances. This normalized feasibility domain

714   (green spherical triangle) is constrained by the intra- and interspecific interaction matrix (β).

715   The columns of the interaction matrix (e.g. [β_{11}, β_{12}, β_{13}]) give the boundaries of the feasibility

716   domain (three blue lines). The larger this volume is, the larger the set of demographic values

717   compatible with feasibility, and the larger the likelihood of species coexistence across trophic

718   levels [55, 71].

Box 3: An example of how to integrate niche and network theories with experimental and observational data

Our approach to evaluate how between trophic interactions drive niche and fitness differences within trophic levels and vice versa involves three steps.

Step. 1: Depart from a relatively simple system of equations. Here it is composed of two annual population models describing changes in population size with time in plants (seeds, $P_{i,t+1}$) and pollinators (eggs, $A_{i,t+1}$). Both models are mirror images including an equal number of parameters with the same biological meaning,

$$\begin{cases} P_{i,t+1} = P_{i,t}\left((1 - g_i)s_i + \dfrac{\lambda_i g_i (1 + \sum_k \gamma_{ik} A_{k,t})}{1 + \sum_j \alpha_{ij} g_j P_{j,t}}\right) \\ A_{i,t+1} = A_{i,t}\left((1 - e_i)t_i + \dfrac{\nu_i e_i (1 + \sum_k \delta_{ik} P_{k,t})}{1 + \sum_j \theta_{ij} e_j A_{j,t}}\right) \end{cases},$$

(5)

where each model is the summation of two components. The first component describes the possibility of a storage effect process, and the second component describes per capita fecundity. Specifically, this second component describes how mutualisms enhances the species intrinsic ability to produce off spring reduced by the competitive effects exerted by other species within the same guild.

Step. 2: Estimates species vital rates. Estimate per capita growth rate in the absence of species interaction (plants (λ's), pollinators (ν's)), is best described as the intercept of the statistical models built for step 3 (see below). Additional efforts are needed to estimate rates of seed germination (g's) or larva survival (e's), and the storage effect as the survival of the species' life stages that do not produce offspring within a year (e.g. soil seed bank in plants (s's) and non-reproductive adult mortality in some pollinators (t's)).

743

744 Step. 3: Estimate species interaction matrix. To estimate species intra- and inter-specific

745 competitive interactions within trophic levels (plants ($\boldsymbol{\alpha}$'s), pollinators ($\boldsymbol{\theta}$'s), the best approach

746 is to fit a series of statistical models describing for each species its per capita growth rate as a

747 function of competitor's relative abundance. For mutualistic interactions (pollinator's effect on

748 plants ($\boldsymbol{\gamma}$'s), plants' effect on pollinators ($\boldsymbol{\delta}$'s)), do the same but describe

749 species' per capita growth rate as a function of mutualistic's relative abundances (Fig. ii).

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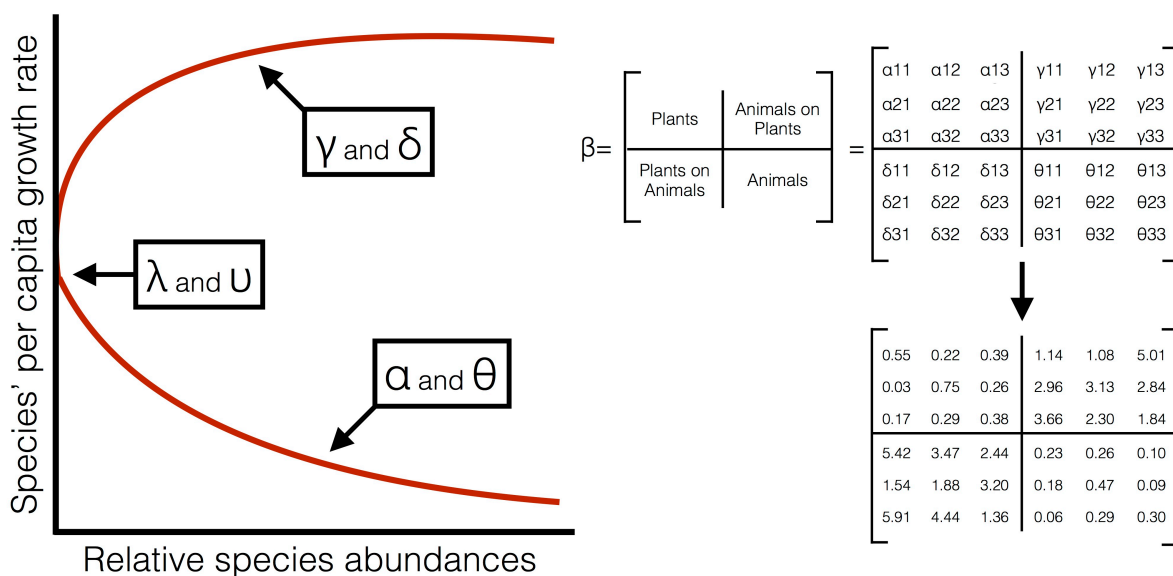
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753 **Figure ii:** Competitive relationships between species including itself are expected to take a

754 negative exponential form [59, 66], whereas mutualistic relationship is expected to be

755 functionally saturating best described by non-inflicted curves [100]. With this information is

756 possible to then build the β matrix summarizing species interactions across trop

Glossary box

Ecological network: A synthesis of biotic interaction between organisms present in a community in which species represented by nodes are connected by pairwise inter-specific interactions.

Equalizing mechanisms: Mechanisms that reduce the likelihood of species exclusion within trophic levels by promoting similar fitness between competitors.

Equilibrium point: A fixed state at which species abundances are constant over time.

Dynamical stability: The property of an ecological system to return to an original equilibrium point after a pulse perturbation.

Intrinsic growth rate: The rate at which a population increases in size in the absence of density dependent regulation.

Feasibility: The property of an ecological system to hold an equilibrium point with positive abundances in all its constituent species.

Feasibility domain: The range of conditions (e.g., demographic parameters) compatible with all species having positive abundance.

Feedback: The process by which the output of a system is routed back as an input of another system forming a loop.

783 **Fitness:** The species ability to mature and produce offspring.

784

785 **Fitness differences:** According to Chesson (2000), average fitness differences

786 between species are an equalizing mechanism of species coexistence that reduce

787 competitive imbalance between competitors. In the absence of niche differences

788 determine the superior competitor in a community.

789

790 **Multi-trophic network:** A network representing patterns of multiple interaction types

791 between species including competition, mutualistic, or antagonistic relationships. Also

792 known as multiplex networks.

793

794 **Niche:** The environmental conditions and resources a species requires for living and

795 reproducing.

796

797 **Niche differences:** According to Chesson (2000), niche differences are a stabilizing

798 mechanism of species coexistence by causing intra-specific competition to exceed inter-

799 specific competition.

800

801 **Per capita growth rate:** The relative contribution to the population increases in size

802 per individual.

803

804 **Species dynamics:** Changes in species' population over space and time.

805

806 **Trophic level:** A level of organization within the food chain of an ecosystem, whose

807 organisms obtain resources in a similar way

808