

Opinion

2 The Labile Limits of Forbidden Interactions

Juan P. González-Varo ^{1,2,*} and Anna Traveset ³

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¹ Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK

6 ² Integrative Ecology Group, Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC), Sevilla, Spain

8 ³ Mediterranean Institute of Advanced Studies, IMEDEA (CSIC-IUB), Esporles, Mallorca, Spain

10 * Correspondence: jpg62@cam.ac.uk (J.P. González-Varo).

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14 **Forbidden links are defined as pairwise interactions that are prevented by the biological**
16 **traits of the species. Here, we focus on the neglected importance of intraspecific trait**
18 **variation in the forbidden link concept. We show how intraspecific trait variability at**
20 **different spatiotemporal scales, and through ontogeny, reduces the expected prevalence of**
22 **forbidden interactions. We also highlight how behaviour can foster interactions that, from**
24 **traits, would be predicted as forbidden. We therefore discuss the drawbacks of frameworks**
26 **recently developed to infer biotic interactions using available trait data (mean values).**
28 **Mispredictions can have disproportionate effects on inferences about community dynamics.**
30 **Thus, we suggest including intraspecific trait variability in trait-based models and using**
32 **them to guide the sampling of real interactions in the field for validation.**

What are forbidden interactions and why do they matter?

26 Biotic interactions across trophic levels govern the dynamics of communities and the
28 functioning of ecosystems [1-5]. Interspecies relationships not only determine energy
30 fluxes [6], but also mediate key ecological functions such as mycorrhizal-mediated mineral
32 nutrition [7], animal-mediated pollination and seed dispersal [8]. When sampling such
34 interactions in the field, the norm is that certain pairwise interactions remain undetected,
36 named the missing and forbidden links [9,10]. **Missing links** (see Glossary) are possible
38 but hardly observable interactions, whereas **forbidden links** are pairwise interactions that
are prevented by biological **traits** of the species [9,10], such as their size, morphology,
phenology, physiology–biochemistry or habitat specificity. For instance, large-sized food
items, like animal preys or fruits, can preclude consumption by small-gaped eaters [11-15],
whereas non-overlapping phenologies impede the temporal encounter between potentially
interacting species [10]. Indeed, both morphology and phenology explain a huge fraction of
unobserved interactions in pollination and frugivory networks [10]. By constraining the
number of possible interactions, forbidden interactions are of major importance for the

40 structure and functioning of ecological networks, including **food webs** and **bipartite**
41 **networks** of mutualistic and antagonistic systems [16-22].

42 Largely motivated by the ongoing biodiversity crisis, ecologists have recently
43 stressed the need for inferring biotic interactions at wide geographical scales [15,23-26],
44 acknowledging interactions are key for predicting species distributions in response to
45 global change pressures [27-29]. To cope with this demand, Morales-Castilla *et al.* [24]
46 have recently presented a new conceptual framework to infer pairwise interactions in
47 unknown systems, that is, the elements that build up complex networks of ecological
48 relationships. The framework is based on **trait matching**, particularly, on the use of
49 available trait data (e.g. body size) to establish forbidden links [24]. A critical question that
50 arises from such predictive attempts is: how accurately can we establish forbidden links
51 using available trait information? In other words, how reliably can we infer different types
52 of pairwise interactions using available trait data?

53 Here, we focus on the neglected importance of intraspecific trait variability in the
54 forbidden link concept, which is usually considered as a categorical fact (forbidden or not)
55 rather than as a trait-matching continuum. Matching traits can vary dramatically within a
56 species across space (see Box 1), between individuals within populations and between
57 populations within its whole distribution range [30-33]. But matching traits can vary even
58 more in time (Box 1), between years and through the ontogenetic stages of individuals. We
59 show how intraspecific trait variability at different spatiotemporal scales reduces the
60 expected prevalence of forbidden interactions (Box 1), thereby increasing **species degree**
61 and overall **network connectance**. We also highlight that behaviour can foster pairwise
62 interactions that would rarely be expected from trait data. Consequently, we discuss the
63 potential limits and drawbacks of using mean values available from trait databases [34-36]
64 to infer pairwise interactions and community dynamics. Although the trait-matching

approach can be useful for elucidating general patterns within already sampled systems, we
66 argue that it could fail to detect key interactions that allow species co-occurrences and drive
critical ecological functions.

68

How accurately can we assign forbidden links using available trait data?

70 The forbidden link concept has proved useful to explain *a posteriori* interaction degree and
some emergent properties of empirical networks [10,21,37]. In these analyses, forbidden
72 links are regarded as immutable realities within the studied systems, i.e. as structural zeros
in the adjacency matrices of interacting species [10,21,24]. This rigid view has probably
74 been fostered by strong trait-matching evidence from networks in which interaction
sampling was coupled with trait measurements [10,21,37]. However, it is widely
76 recognized that empirical networks represent temporal snapshots (weeks, months, or at best
a few years) of complex interactions sampled at a particular site [38]. Because traits are a
78 suitable *post hoc* explanation of interaction patterns in these ‘well-known’ snapshots [37],
can we then use traits to accurately infer pairwise interactions in unknown systems?

80 The framework proposed by Morales-Castilla *et al.* [24] relies on the use of available
trait information (or phylogenetic distance as a surrogate for trait similarity if information
82 on traits is unavailable). Global databases of **functional traits** are currently accessible for
different taxonomic groups, including plants, birds, mammals, reptiles and amphibians [34-
84 36]. These data consist of trait mean values, which should ideally represent averages for all
individuals of each species across its whole distribution range. The reality is that trait
86 means usually account for a small number of individuals measured at a particular location
in a certain moment. But more limiting than their representativeness is the fact that trait
88 means neglect the existing intraspecific variation, thus, they underestimate the degree of
trait matching by overestimating the incidence of forbidden interactions (Figure 1, Box 1).

90 The latter can lead to serious misinterpretations about the dynamics and functioning of the
inferred ecosystems.

92 Conspecific individuals differ in the multiple traits that produce their phenotypes.
Such variability was indeed the essence for the Darwin's theory of evolution by natural
94 selection and is considered to be crucial in many ecological and evolutionary processes [39-
41]. Intraspecific trait variability enhances average interaction degree of species and
96 network connectance (Figure 1, Box 1), thereby robustness to secondary extinctions
[42,43]. In the following sections, we address the role of different sources of intraspecific
98 variation on the degree of trait matching between species. Moreover, we discuss the
importance of behaviour in allowing interactions that would be predicted as forbidden on
100 the basis of available traits.

102 ***Matching traits vary in space and time***

The most pervasive cases of intraspecific trait variation are among-individual differences in
104 age and sex [39,44]. We specifically focus on ontogenetic trait variation in the next section,
since traits and interactions can vary tremendously between individuals of different age or
106 life stage. Sexual dimorphisms typically entail differences in size or shape, which can lead
each gender to interact with different species [45,46]. For instance, males and females of
108 the purple-throated carib hummingbird (*Eulampis jugularis*) feed on two different
Heliconia species whose flowers match to the shape and length of the bill of each gender
110 [45]. In the Eurasian sparrowhawk (*Accipiter nisus*), the body size of females (185–342 g)
is about double that of males (110–196 g) [47]. As a result, females prey on birds up to 150
112 g (occasionally up to 500 g), mainly thrushes (Turdidae), starlings (Sturnidae) and pigeons
(Columbidae), whereas males normally prey on birds up to 40 g, including tits (Paridae),
114 finches (Fringillidae), sparrows (Passeridae) and buntings (Emberizidae) [48]. Both
examples illustrate how sexual dimorphism increases intraspecific trait variability, thus,

116 interaction degree at the species level. Hence, some interactions can be forbidden for one
gender but possible for the other. Yet, sex-dependent trophic niches with bimodal trait
118 distribution are reduced to a single value in trait databases: the mean.

Furthermore, intraspecific trait variability can also be huge among individuals of the
120 same sex and age. Species traits vary in space at different hierarchical levels or spatial
scales [30,32,33], among individuals within populations and among populations across the
122 species ranges (see Figure I in Box 1). In the case of plants, traits even vary within the same
individual (see Figure II in Box 1), among leaves, flowers and fruits, organs that mediate
124 several interactions with different types of feeding animals (herbivores, pollinators,
florivores, seed dispersers and seed predators) [31,49]. Phenotypes result from the
126 interaction between individuals' genes and local environmental conditions, each source of
variation having a specific relative weight in determining the expression of different traits
128 [50]. Therefore, those traits that strongly depend on the local environment are prone to vary
in time, between phenological events under different climate conditions (Box 1). For
130 instance, water deficits reduce the size and alter the chemical composition of fruits [51].
Consequently, these traits can hugely vary between consecutive years even in the same
132 individual plant, thus, in the same population, which increases uncertainty even when using
local trait data to infer local interactions (Box 1). Despite its importance, intraspecific trait
134 variability in time has been largely overlooked in community ecology [25,41].

Regardless of whether the main source of variation is genetic or environmental, trait
136 variability makes individuals of a given species (or plant organs) non-interchangeable from
the perspective of their interacting partners (see Figure II in Box 1). Actually, different bird
138 species have been reported to consume fruits of specific size distributions within the same
plant species according to their gape widths [13,52]. Similarly, different flower visitors and
140 herbivores have been documented to visit different individual plants according to their

flowering phenology, morphology and flower scent [53]. At the species level, the result of
142 particular individuals (or plant organs) interacting with particular partner species is an
increase in the possibilities of trait matching (see Figure II in Box 1), that is, a broader
144 ‘interaction niche’ generated by between-individual niche differences [39]. Whenever
inheritable, such differences can also be the basis of evolutionary changes after the loss or
146 gain of partner species [13].

Conversely, a framework that uses trait means to infer biotic interactions assumes
148 that all individuals, thereby all populations, are interchangeable. This assumption can lead
to important predictive errors associated to (i) the representativeness of available trait data
150 and (ii) the neglect of intraspecific variation. First, trait means account for individuals
sampled in one or a few locations during a particular moment. How well do these subsets
152 represent a species average across its entire distribution? For example, mean diameter in
myrtle (*Myrtus communis*) fruits can range from 7.3 to 10.4 mm, depending on which
154 population and year the fruits were sampled (see Figure I in Box 1). Hence, using a trait
mean obtained at a particular ‘site–year’ combination to infer interactions at different
156 locations can lead to under- or overestimation of forbidden links, depending on the sign of
the extrapolation error (e.g. from population L to M or vice versa; Figure I in Box 1).
158 Secondly, using trait means raises concerns about the predicted prevalence of forbidden
interactions when neglecting intraspecific variability. In the same example, myrtle fruits are
160 predicted as fully prevented for Sardinian warblers (*Sylvia melanocephala*) when using
mean diameters as interaction threshold, but such interaction is expected across myrtle
162 populations when using minimum values as threshold (see Figure I in Box 1). Accordingly,
there is empirical evidence that, indeed, Sardinian warblers regularly consume myrtle fruits
164 in different regions [10,54,55]. The myrtle and the Sardinian warbler are common and
locally abundant species in the studied sites, and abundance is a critical factor promoting

166 both the establishment and strength of interactions through increasing interspecies
encounter rates [25,56], even when such interactions are predicted to be unlikely from
168 traits.

170 ***Ontogeny enlarges intraspecific trait variability***

Traits can hugely vary between the life stages of one species, which promotes stage-
172 specific interactions [44,57]. The first life stage of most organisms (e.g. seeds in plants, and
eggs or newborn in animals) is normally tiny compared to adults. Thenceforth, ontogeny
174 normally entails an increase in body size, thereby an allometric shift of interacting partners
[12,57-59]. Keeping species roles as predators and prey, ontogeny not only allows young
176 prey individuals to be consumed by smaller predator species (e.g. Figure 2a), but also adult
and young predator individuals to feed on different prey species according to their size
178 [12,14,58,59]. Therefore, ontogeny generates a broader niche space for both consumers and
resources, allowing interactions that would be assigned as forbidden if we only look at the
180 adult traits. Besides, individuals of some species can increase in weight by several orders of
magnitude during their life, shifting their role from being a prey of certain species to being
182 a predator of another species (Figure 2b). These vast shifts can promote reciprocal
predation among species of the same trophic level and even cannibalism [14,57,59,60]. For
184 instance, an egg of Nile crocodile (*Crocodylus niloticus*) weights ~0.1 kg while an adult
typically exceeds 200 kg, i.e. four orders of magnitude larger [61,62]. Ontogenetic variation
186 allows animals of ca. 1–10 kg such as monitor lizards (Varanidae), herons (Ardeidae) and
ravens (Corvidae) to prey on the eggs and juveniles of this apex predator (Figure 2a), with
188 profound effects on its demography [61,63]. Interestingly, ontogeny can reverse the
direction of predation when adult predators can feed on those species which predate on
190 their early life stages, leading to feeding loops (Figure 3). Such loops are remarkably
common and can be of major importance for community dynamics [14,57,59,60].

192 It is not difficult to envisage that ontogenetic variability can generate an enormous
uncertainty when attempting to predict biotic interactions using available trait means of
194 adult individuals, which might lead us to wrong inferences about community dynamics. For
instance, reciprocal predation through life-stage-specific interactions promotes coexistence
196 between native Mohave tui chub (*Siphateles bicolor mohavensis*) and invasive western
mosquitofish (*Gambusia affinis*) [14]. Gravel *et al.* [26] have recently proposed
198 distinguishing ‘subspecies’ by size (ontogenetic) categories to build trait-based networks,
which would describe more accurately those pairwise interactions involving species with
200 size structured populations. A major limitation to this approach is the lack of available trait
data for species’ life-stages other than the adult [34-36].

202

Behaviour can allow ‘forbidden’ interactions

204 Species interactions that initially appear unlikely can eventually be established at ecological
timescales through changes in animal behaviour. Animal innovations (i.e. animals behaving
206 in an innovative way) have been described in a number of taxa, particularly in resource-
poor or novel environments [64]. For example, Laland & Reader [65] found that food-
208 deprived guppies (*Poecilia reticulata*) are more likely to develop foraging innovations than
non-food-deprived individuals. Tinker *et al.* [66] found analogous results in California sea
210 otters (*Enhydra lutris nereis*) at a resource-limited site, where individuals specialized on
different preys by acquiring specific behavioural skills. Birds are especially innovative in
212 their foraging techniques [67] and recent experiments have demonstrated that the
information can spread rapidly among individuals in the population through social network
214 ties [68]. The kelp gulls (*Larus dominicanus*) at Peninsula Valdés provide an excellent
example. In the 1970s, kelp gulls began to feed on skin and blubber of living southern right
216 whales (*Eubalaena australis*) by pecking on their backs [69]. Since then, the percentage of
living right whales (mothers and calves) with gull lesions has increased from 2% to 99% in

218 the 2000s, and wounding is now considered a major cause of whale mortality [70]. The gull
population grew rapidly in the last decades parallel to the human population on the nearby
220 mainland [69]. Rapid population growth is a common feature of biological invasions, and
this example shows that the outcomes can be surprising in terms of interspecies
222 interactions. Even more unexpected is the emergence of interactions between the sharp-
beaked finch (*Geospiza difficilis*) and different booby species (*Sula* spp.) on the small,
224 isolated and food-limited islands of Wolf and Darwin (see Figure 2c). This finch feeds on
insects and small seeds in the Galapagos Islands, but on Wolf and Darwin the so-called
226 vampire finch also feeds on the blood and eggs of these seabirds [71]. Information on bill
traits alone would rarely predict this strange but critical interaction for the sharp-beaked
228 finch at the extreme of the archipelago.

Besides promoting interactions, behaviour can also modify the sign of pairwise
230 interactions, from mutualistic (positive) to antagonistic (negative) or vice versa, leading to
partner dualities. For instance, scatter-hoarding birds and mammals are seed predators but
232 they also provide effective seed dispersal by moving caches that are eventually forgotten or
released if the animal dies [72]. In the Neotropics, agoutis (*Dasyprocta punctata*) are
234 actually claimed to have been responsible for the persistence of large-seeded species that
were once dispersed by megafauna which went extinct more than 10,000 years ago [73]
236 (Figure 2d). It is not always simple to foresee in which cases an animal species will behave
as a mutualist or antagonist, but we must bear in mind that such changes in the sign of
238 interactions can have important implications for community dynamics.

240 **Concluding Remarks and Future Directions**

The thresholds delimiting forbidden interactions are labile as a result of intraspecific trait
242 variability, which can be substantial. We have illustrated that only using available trait data

(i.e. means) underestimates species degree (thus, network connectance) through
244 overestimating the incidence of forbidden links. Also, that available trait means might not
be representative across the species ranges, which can lead to both over- and
246 underestimations of interactions inferred locally. Recently developed probabilistic models
now allow incorporating intraspecific trait variability to predict interactions [26,56].
248 However, the challenge to accurately infer biotic interactions in unknown or novel
ecosystems is to gather detailed trait data for multiple species, well replicated across their
250 ranges and ontogenetic stages, and then, to make these data available alongside descriptive
statistics of intraspecific trait variability. Although promising, this enterprise is clearly
252 colossal. Alternatively, one could quantify intraspecific trait variability in well-sampled
species (e.g. Box 1) and transfer an equivalent amount of variance to taxonomically or
254 phylogenetically close species lacking such detailed data (see Outstanding Questions). In
sum, we recommend incorporating intraspecific trait variability in models predicting
256 networks of biotic interactions.

Even with detailed trait information available, there are still many sources of
258 uncertainty affecting the establishment of pairwise interactions. On the one hand, predicted
but not recorded interactions (false positives) could reflect mismatches in non-
260 morphological or phenological traits (such as physiology or biochemistry), or reflect
cognitive constraints, which can block the formation of inferred interactions [e.g. 74]. On
262 the other hand, in novel scenarios, behavioural innovation can promote interactions
predicted as forbidden (false negatives). Evidence shows that these ‘outliers’ matter,
264 especially when they affect common or keystone species with a disproportionate role in
community dynamics and ecosystem functioning (see Outstanding Questions).

266 It is therefore essential to be aware that reducing the enormous complexity behind
biotic interactions to trait-matching models can critically limit our inferences. Yet, inferred

268 networks might serve as ‘maps’ to guide sampling of real interactions. Particularly, they
could help to focus sampling effort on predicted links (included the forbidden ones) that
270 seem to be key for the target communities, in order to validate network-model predictions
(see Outstanding Questions). Novel techniques (e.g. DNA barcoding, GPS tagging, camera
272 trapping) are now revolutionizing the sampling of biotic interactions, unravelling
unprecedented information about the functions they entail [52,73,75]. We thus need
274 synergies between trait-based models and empirical studies if we are to understand how
interspecies relationships shape the fate of communities and ecosystems.

276

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288

Figure 1. Frequency Distribution of Matching Traits (e.g. Body Size or Phenology) in a Consumer and a Resource Species. Interaction is possible whenever $x_{\text{consumer}} \geq x_{\text{resource}}$. (a) Mismatching between both trait means and intraspecific variability prevent interaction, leading to a totally forbidden link. (b) Mismatching occurs between trait means but intraspecific variability allows interaction, leading to a partially forbidden link. The difference between (a) and (b) – thus, our ability to infer interactions – may depend on how broadly intraspecific trait variability has been assessed in space and time (see Box 1).

Figure 2. Examples of How Ontogenetic Variability and Behaviour Promote Interspecific Interactions or Change their Sign. (a) Small groups of golden jackals (*Canis aureus*), which are two orders of magnitude smaller than an adult blue wildebeest (*Connochaetes taurinus*), can hunt wildebeest calves [62]. (b) The Nile monitor (*Varanus niloticus*), three orders of magnitude smaller than an adult Nile crocodile (*Crocodylus niloticus*), is the main predator of crocodile eggs [61]. (c) The Galápagos sharp-beaked finches (*Geospiza difficilis*) mainly feed on insects and small seeds, but on the small and food-limited islands of Wolf and Darwin, they cut wounds on seabirds (boobies *Sula* spp.) to drink their blood; they also push and roll seabird eggs into rocks to break them and feed on them [71]. (d) The Central American agouti (*Dasyprocta punctata*), a seed predator (antagonist) of the black palm (*Astrocaryum standleyanum*), can effectively disperse its seeds through scatter-hoarding, acting as a mutualistic partner [73]. Photos reproduced with permission from Todd Gustafson (a), Anup Shah (b), Pete Oxford (c) and Christian Ziegler (d).

Figure 3. Feeding Loop Generated by Ontogenetic Reversal of Predation. Arrows, from prey to predator, denote predation. (a) Species level diagram showing reciprocal predation between species *j* and *k*. (b) Life-stage level diagram showing how reciprocal predation is mediated by stage-specific interactions between both predators during their ontogeny: species *j* is a prey of species *k* during its earlier life stages, but it becomes a predator of species *k* in the adult stage. We could hardly infer the role of species *k* as predator of species *j* using trait data of adult individuals (e.g. body size).

Box 1. Spatiotemporal variation in trait matching

Assessing spatiotemporal variation in size matching between the fruits of the Mediterranean myrtle (*Myrtus communis*) and the gape of the five most abundant frugivore species in Circum-Mediterranean woodlands during fruit ripening (see details in Appendix S1). We assess variation in fruit diameter among populations and years across the distribution range of the plant (Figure I), and among individual plants and between consecutive years within three of these populations (Figure II) (see sections A and B, respectively, in Appendix S1). A gape width smaller than a fruit diameter involves the incapability of the frugivore to swallow the fruit [11,13], and thus a forbidden interaction. However, different forbiddance thresholds in fruit diameter – mean, first quartile (Q_{25}), 5th percentile (P_{05}) or minimum – can lead to different prevalences of forbidden interactions. These thresholds represent the capability of an average individual of each frugivore species (mean gape width) to consume fruits of average size (mean), or to consume at least 25% (Q_{25}), 5% (P_{05}), or some (minimum) of available fruits. We use this mixed and conservative approach, using mean values for the frugivores but intraspecific variability for the plant [41], owing to the lack equivalent geographical variation for gape width data [10,76-78] (see section C in Appendix S1). We show how fruit diameter varies geographically and temporally, among populations and between years within populations (Figure I). Due to geographical variation (15% variance), some populations are predicted as forbidden for narrow-gaped frugivores while others do not (Figure I). But due to interannual variation (22% variance), some populations are predicted as forbidden some years but not others (e.g. populations D and M in Figure I). We also show how forbidden links largely drop when using less restrictive thresholds. For example, when using mean fruit diameter as threshold, *S. melanocephala* results a forbidden frugivore in 100% of population-year combinations, but only in 26% when using the minimum diameters (Figure I). Accordingly, empirical information from different frugivory studies shows that all five species – even those with the smallest gape widths – actually consume myrtle fruits in different sites [10,54,55].

Figure I

Similarly, we show how fruit diameter varies among individuals within populations and between consecutive years (Figure II). Due to among-individual variation (56% variance), some plants are predicted as forbidden for narrow-gaped frugivores while others do not. But due to interannual variation (31% variance), some plants are predicted as forbidden some years while not in others (Figure II). Again, the prevalence of forbidden links depends on the forbiddance thresholds chosen (Figure II).

Figure II

Figure I. Geographical and Temporal Variation in Trait Matching. (a) Boxplot (median, quartiles and 5th/95th percentiles) showing variation in fruit diameter across 18 populations of Mediterranean shrub *Myrtus communis*, some of them sampled in different years (27 population-year combinations) (Appendix S1). Black dots denote means. White dots denote minimum values. Horizontal lines denote the mean gape width (mm) of the five most abundant frugivore species in Circum-Mediterranean woodlands during the winter (*Er*: *Erithacus rubecula*; *Sa*: *Sylvia atricapilla*; *Sm*: *Sylvia melanocephala*; *Tm*: *Turdus merula*; *Tp*: *Turdus philomelos*), period when *M. communis* ripe its fruits. (b) Map of the Mediterranean Basin with the location of the study *M. communis* populations. The distribution of *M. communis* is shown in dark-grey (redrawn from Migliore *et al.* [79]).

Figure II. Intra- and Interindividual Variation in Trait Matching. Boxplot showing variation in fruit diameter among marked myrtle plants in two consecutive years (grey and white boxes, respectively) and in three different populations. Black dots denote means. Grey and white dots denote minimum values. Horizontal lines denote the mean gape width (mm) of the five most abundant frugivore species in Mediterranean woodlands during the winter (bird species acronyms as in Figure I).

Glossary

Bipartite network: ecological network comprising two trophic levels (e.g. host and parasitoids, plants and pollinators, or plants and frugivores) with the links between species representing trophic interactions (i.e. fluxes of matter and energy) and ecological functions (e.g. pollination, seed dispersal) [8,9].

Connectance: the fraction of pairs of species that interact in an ecological network [42,80]. In food webs, $C = L/S^2$, where L is the number of interactions (links) and S the number of species in the community. In bipartite networks, $C = L/S_r S_c$, where S_r and S_c are the number of species in each trophic level (resources and consumers; e.g. plants and pollinators).

Food web: ecological network comprising multiple trophic levels (e.g. primary producers, herbivores, predators, detritivores) with the links between species representing trophic interactions (i.e. fluxes of matter and energy) [17].

Forbidden link: pairwise interaction that is prevented by the biological traits of the species [9,10].

Functional trait: any trait affecting, directly or indirectly, the performance and fitness of individuals [41].

Missing link: possible but hardly observable pairwise interaction (e.g. between rare species), thus, a result of under-sampling [10].

Species degree: the number of different species a certain species interacts with in an ecological network [9,42].

Trait: any morphological, physiological, phenological or behavioural feature measurable at the individual level [41].

Trait matching: phenotypic expression of functional traits that allow a particular interspecific interaction (Figure 1).

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Figure I – Box 1

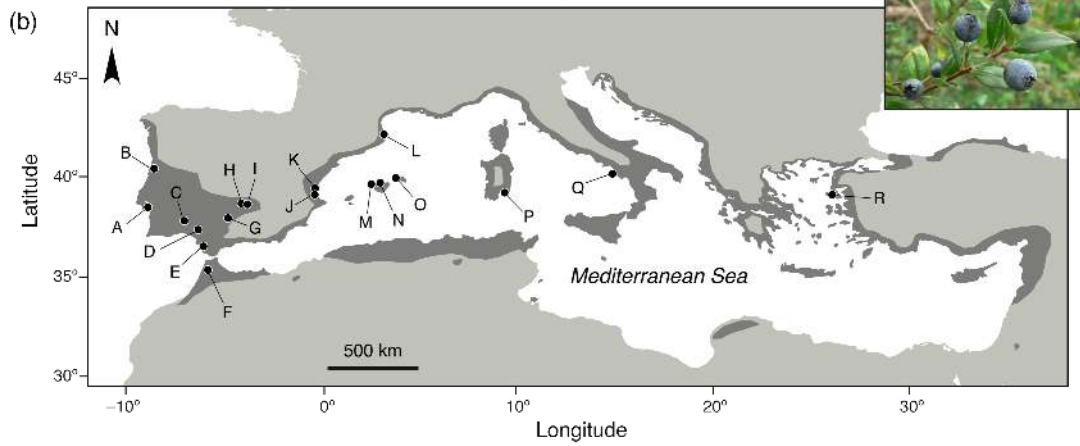
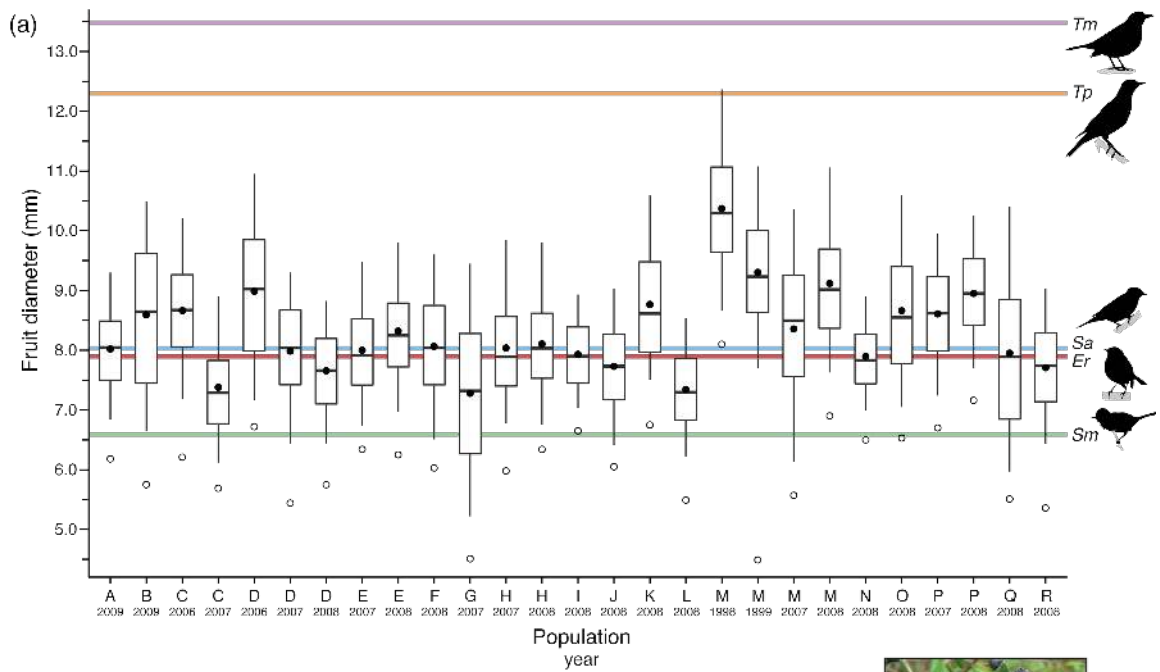


Figure II – Box 1

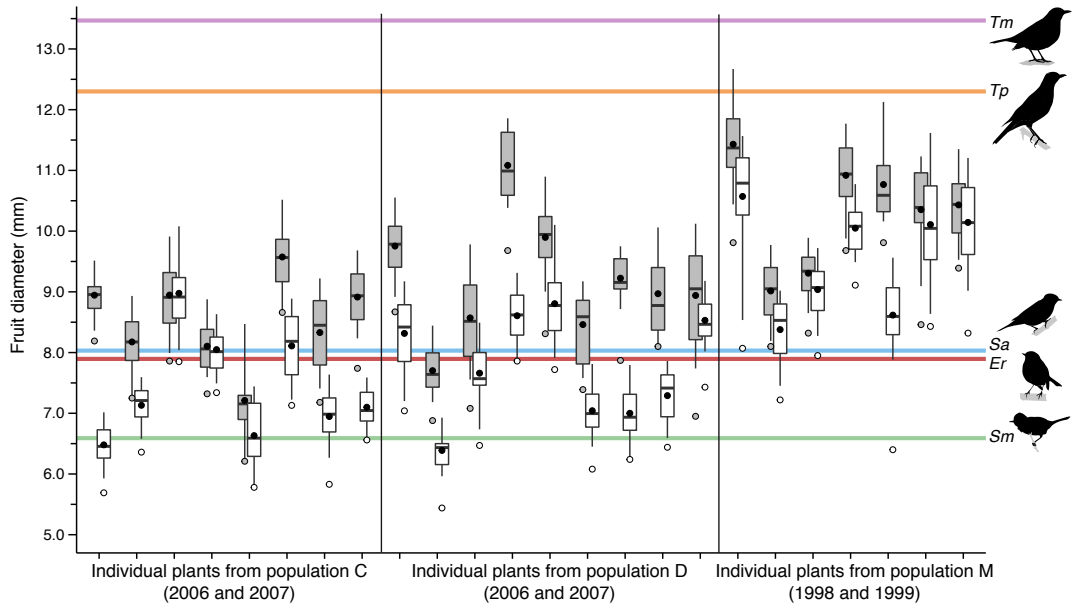


Figure 1

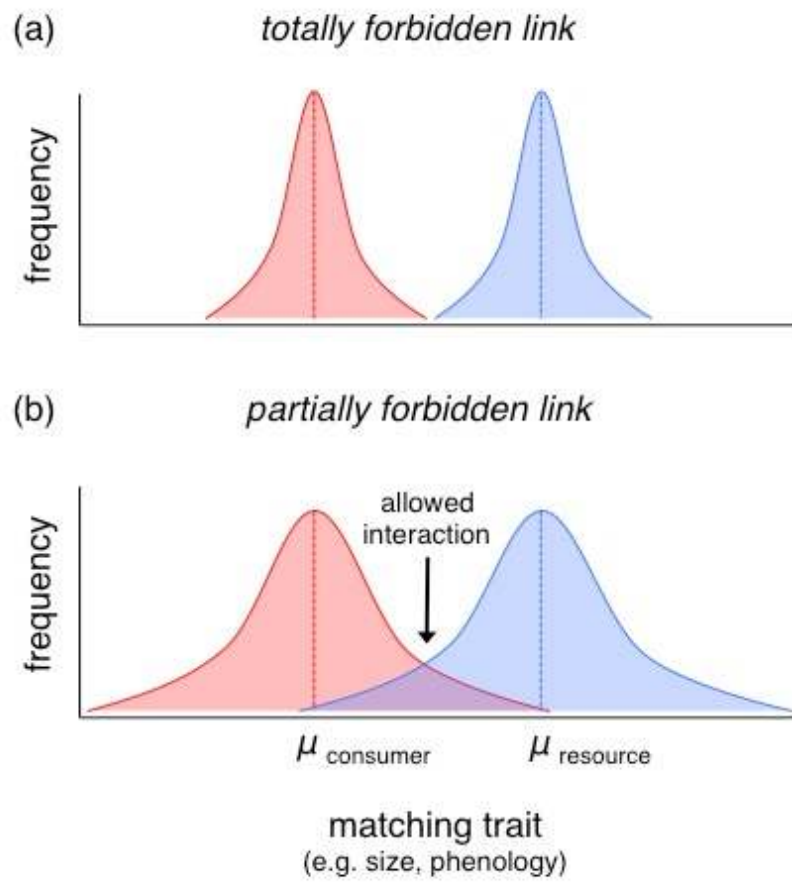


Figure 2



Figure 3

