

1 **A common framework for identifying linkage rules across different types of**
2 **interactions.**

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20 Running headline: Linkage rules in interaction networks

21

22

23 **Summary**

24

25 1. Species interactions, ranging from antagonisms to mutualisms, form the architecture
26 of biodiversity and determine ecosystem functioning. Understanding the rules

27 responsible for who interacts with whom, as well as the functional consequences of

28 these interspecific interactions, is central to predict community dynamics and stability.

29 2. Species traits *sensu lato* may affect different ecological processes by determining

30 species interactions through a two-step process. First, ecological and life-history traits

31 govern species distributions and abundance, and hence determine species co-

32 occurrence and the potential for species to interact. Second, morphological or

33 physiological traits between co-occurring potential interaction partners should match for

34 the realization of an interaction. Here, we review recent advances on predicting

35 interactions from species co-occurrence, and develop a probabilistic model for inferring

36 trait matching.

37 3. The models proposed here integrate both neutral and trait-matching constraints,

38 while using only information about known interactions, thereby overcoming problems

39 originating from under-sampling of rare interactions (i.e. missing links). They can easily

40 accommodate qualitative or quantitative data, and can incorporate trait variation within

41 species, such as values that vary along developmental stages or environmental

42 gradients.

43 4. We use three case studies to show that the proposed models can detect strong trait

44 matching (e.g. predator-prey system), relaxed trait matching (e.g. herbivore-plant

45 system) and barrier trait matching (e.g. plant-pollinator systems).

46 5. Only by elucidating which species traits are important in each process (i.e. in
47 determining interaction establishment and frequency), can we advance in explaining
48 how species interact and the consequences of these interactions for ecosystem
49 functioning.

50

51 **Key words:** Trait matching, functional traits, interaction networks, pollination, predation,
52 herbivory, parasitism, mutualisms, trophic interactions.

53

54 **Introduction**

55

56 Species interactions form the architecture of biodiversity (Bascompte & Jordano 2007).

57 There is growing recognition that community structure, stability and functioning depend

58 not only on which species are present in a community, but also on how they interact

59 (Tylianakis *et al.* 2008). Complex networks of biotic interactions such as predation,

60 parasitism and mutualism provide essential information related to conservation

61 (Carvalho, Barbosa & Memmott 2008; Tylianakis *et al.* 2010), community stability and

62 ecosystem functioning (Thompson *et al.* 2012; Peralta *et al.* 2014), and evolutionary

63 processes (Jacquemyn *et al.* 2011; Fenster *et al.* 2015). These insights would be not

64 possible from simple species occurrence data or analysis of pairwise interactions.

65 Despite the growing literature describing species interaction networks, we still have a

66 poor understanding of how network structure comes to exist.

67

68 There are few generalizable observations of how species interactions respond to

69 environmental changes (Tylianakis *et al.* 2008). Therefore, understanding what

70 determines the occurrence of pairwise interactions, and, at a higher level, the structure
71 of ecological networks, is a key challenge for ecologists. Overcoming this challenge
72 requires the identification of the mechanisms responsible for who interacts with whom.
73 Natural selection promotes adaptations to increase species efficiency (Castellanos et al.
74 2003). Reciprocal trait adaptations between partners, which have positive demographic
75 consequences, lead to increased interaction strength among co-evolved members
76 (Sargent and Ackerly 2008). Hence, there is a great expectation that incorporating a
77 trait-based approach can help us explain general mechanisms driving pairwise
78 interactions. We refer here to traits in a broad sense, comprising adaptations that define
79 organisms in terms of their ecological role, how they interact with the environment and
80 with other species (Díaz & Cabido 2001). Most traits studied so far for predicting
81 species interactions fall into morphological adaptations (e.g. body size), but
82 physiological (e.g. chemical defenses) or behavioral (e.g. diel) adaptations can also
83 drive species interactions. Moreover, traits should be precise and measurable attributes
84 of the species. Recent studies indeed suggest that ecological networks of different
85 types (e.g. from antagonistic to mutualistic) could be described from the traits of the
86 interacting species (Eklöf *et al.* 2013). The ability of these methods to predict novel
87 interactions following species invasions or following range shifts is, however, limited.
88
89 Traits are implicated in ecological dynamics at several concatenated levels of
90 community organization (Fig. 1), and therefore could influence the occurrence of
91 interactions in multiple ways. Some traits determine species distributions in a multi-
92 dimensional environmental space, and thus impact co-occurrence in space and time.

93 Since the occurrence of an interaction requires the presence of the two species, traits
94 involved in phenological matching or habitat filtering could constrain interactions. Life-
95 history traits impact demography, abundance and biomass, thereby affecting the
96 probability of encounter. Then, provided they encounter each other in space and time,
97 the compatibility between traits of the two species (i.e. trait-matching constraints) will
98 also determine whether or not they interact. Finally, the intensity and the impact of an
99 interaction will determine the functioning of the network, and also feed back to
100 determine species abundances and dynamics. How efficient an interacting species is on
101 a per capita basis is also likely to be mediated by its behavioural or physiological traits
102 and how these match with those of the other species. Of course, these levels interact
103 with each other through evolutionary processes. Most work to date has focused on
104 morphological trait matching and little, if any, has tackled several of these stages at a
105 time (see the review in Morales-Castilla et al. 2015). Our first objective here is to review
106 what we know about each of these processes and assess their success and limitations
107 at predicting interactions. Our second objective is to propose a way forward to evaluate
108 trait matching in a way that is not confounded with species co-occurrences, and how
109 this can be integrated into a larger framework, from species occurrences to ecosystem
110 functioning.

111

112 **Traits governing species encounters in space and time.**

113

114 Habitat filtering constrains the pool of co-occurring species in a region or microhabitat.
115 Sharing habitat-filtering traits, like tolerance to drought or thermal preference, may

116 hence be a prerequisite for two species to interact. Even in large and diffuse networks
117 such as the global planktonic interactome, 18% of the variance in community
118 composition (taxon presence and abundance) can be explained by environment alone,
119 and these co-occurrences can be used successfully to predict interactions between taxa
120 (Lima-Mendez *et al.* 2015). Microhabitat characteristics can also influence sessile
121 organisms even within close proximity, as shown by interactions among mycorrhizas
122 and plants, where rooting depth could preclude co-occurrence between shallow rooted
123 plants and fungi restricted to lower soil horizons. In fact, the concept of “habitat
124 associations” as a driver of interactions has been pointed to as the sole explanation for
125 these interactions (Zobel & Öpik 2014), suggesting that both partners interact simply
126 because they respond independently to different environmental factors.

127

128 At broader spatial scales, species turnover along ecological gradients can also be
129 responsible for a large fraction of network variation in space (Poisot *et al.* 2012). Range
130 overlap determines the location and the total area over which two species can
131 eventually interact. This can be used to better understand the consequences of range
132 shifts on the local food-web structure (Albouy *et al.* 2014). Species distribution models in
133 combination with ecological and life-history traits (D’Amen *et al.* 2015) can be used to
134 predict co-occurrence and potential interactions in response to global changes (Albouy
135 *et al.* 2014, Morales-Castilla *et al.* 2015).

136

137 Similar to species distribution in space, species encounter will be determined by the
138 synchrony of their activity periods at different temporal scales (i.e. daily, seasonal,
139 interannual). Mismatch of phenology has been widely called to explain undetected

140 interactions that are not possible to occur (i.e. forbidden interactions; Olesen *et al.* 2011;
141 Encinas-Viso, Revilla & Etienne 2012; Olito & Fox 2015), that is, species present in the
142 same location that do not interact because they do not overlap in their seasonal activity
143 periods. Phenological overlap during the season has therefore been used as a proxy for
144 interaction probability (Bartomeus *et al.* 2013). While phenology is usually studied as
145 the timing when species are active during a season (e.g. plant flowering period), daily
146 fluctuations of activity can also be important for defining when interactions among
147 partners can occur. A clear example is the distinction between crepuscular vs. diurnal
148 species (Herrera 2000), but more subtle fluctuations of activity depending on daily
149 temperature may be also relevant (Rader *et al.* 2013). In addition, some species may
150 interact only with partners in a given life-history stage, for example, some
151 ectomycorrhizal fungi may require host trees to be at least several years old and do not
152 interact with seedlings. This highlights the importance and complexity of the temporal
153 constraints on co-occurrence.

154

155 Given that species co-occur in space and time, their abundance also determines the
156 frequency at which they will interact (Canard *et al.* 2014). Abundant species are simply
157 more likely to encounter each other than rare ones. This mechanism has been called
158 neutral because it does not rely on any niche differentiation. Thus, models that use
159 species abundances to predict encounter probabilities have found that abundance alone
160 can explain considerable variance in key aspects of network structure (Vázquez *et al.*
161 2007; Krishna *et al.* 2008; Olito & Fox 2015). Abundance is determined primarily by life-
162 history traits (e.g. fecundity, longevity, mortality). For plant communities, there is some
163 consensus over which traits relate to abundance or dominance in the community, such

164 as maximal height and position along the slow-fast continuum (e.g. leaf economic
165 spectrum; Wright *et al.* 2004). Therefore, trait distributions over environmental gradients
166 have been used to predict plant abundance and community structure (Shipley, Vile &
167 Garnier 2006; Laughlin *et al.* 2012). Similarly, it is possible to relate life-history traits to
168 animal abundances. For instance, species with fast life cycles (usually small, with high
169 reproduction rates and short longevity) tend to be more abundant than large species
170 with slow life histories (White *et al.* 2007), and large species can decline more rapidly
171 following habitat change (Larsen, Williams & Kremen 2005). As a result, abundance can
172 be largely related to body size and position in the interaction network (Woodward *et al.*
173 2005). Overall, the relationships between traits, abundance and probability of encounter
174 defines the neutral expectations for interacting. This relationship is complex, for
175 example, because the encounter probability changes both as function of species traits
176 (e.g. landscape use) and as a function of abundance (e.g. through density-dependent
177 foraging).

178

179 **Trait matching**

180

181 Trait matching between interacting partners has been identified for a variety of
182 organisms. Plant corolla length and pollinator proboscis length is a classic example
183 (Kritsky 1991). However, most pollinators are quite generalists and while species may
184 have specialized morphology, it does not prevent them from utilizing a diversity of
185 resources (Waser *et al.* 1996). Bird beak size and fruit size has also been shown to be
186 tightly related to dispersal success (Galetti *et al.* 2013). In fishes, predator mouth gap
187 and prey size are also strong determinants of predatory interactions (Cunha & Planas

188 1999). More complex relationships have been found for plants too, with the role of
189 specific leaf area in plant-plant interactions changing from facilitation to competition,
190 depending on resource availability (Gross *et al.* 2009). Trait-matching constraints have
191 been described for most interacting species, ranging from arbuscular mycorrhizas and
192 plants (Chagnon *et al.* 2013) to plants and herbivores (Deraison *et al.* 2015).

193

194 Trait matching between individuals operates in addition to neutral processes to impact
195 pairwise interactions. Despite advances in these respective fields (e.g. null model
196 analysis: Vázquez, Chacoff & Cagnolo 2009; trait matching analysis: Dehling *et al.*
197 2014; Spitz, Ridoux & Brind'Amour 2014, Crea *et al.* 2015), we still lack a common
198 analytical framework with which to evaluate the contribution of species traits to pairwise
199 interactions, and at the higher level to the structure of interaction networks.

200

201 Even though neutral and trait-based null models can predict the general structure of
202 interaction networks, such models often are poor at predicting the occurrence and
203 intensity of individual interactions (Vázquez *et al.* 2009; Olito & Fox 2015). Such models
204 are useful because they free us from species identities and allow us to detect
205 generalities, but there is no guaranty that synthetic network properties do not arise from
206 the wrong reason. Another major problem that may preclude disentangling trait-based
207 processes is that traits could influence interactions directly via trait matching, or
208 indirectly via environmental matching. Hence, even if the variance between neutral and
209 trait matching components is successfully partitioned, this would ignore the fact that
210 some of the 'neutral' variance was generated by species traits via their effect on
211 distribution and abundance (as we outlined in the previous section). Thus, the influence

212 of abundance versus traits can be seen as a path diagram where traits directly affect
213 interactions and also affect abundances, which affect interactions (Fig. 1). We propose
214 a framework that aims to integrate, rather than separate both processes.

215

216 A significant challenge before such an analysis can be achieved is to access completely
217 sampled networks with which to validate models. Empirical network data however have
218 inherent uncertainties associated with the way in which they are sampled. Specifically,
219 sampling completeness is rarely achieved when collecting interaction networks (Chacoff
220 *et al.* 2012, Bartomeus 2013), and hence, some unobserved interactions may indeed
221 occur (i.e. false absence of interactions). This would be less of a problem if the
222 proportion of interactions that are sampled were constant, but this sampling efficiency
223 can vary with local environmental conditions (Laliberté & Tylianakis 2010), species
224 abundance and frequency, and of course, sampling effort. Thus, to truly understand the
225 importance of trait matching for determining species interactions, the absence of an
226 interaction in an empirical dataset cannot be used to infer true absence of that
227 interaction in nature. The nature of the data therefore impedes the direct evaluation of
228 probabilistic models (e.g. Rohr *et al.* 2010; Crea *et al.* 2015) and requires methods to
229 estimate absences (Bartomeus 2013) or the development of model fitting procedures
230 based on observed interactions only.

231

232 Another challenge is that null models based on *a priori* rules for interactions have to be
233 constructed using assumptions of which traits are critical for interaction establishment.
234 Constructing and interpreting biologically meaningful null models that can isolate the
235 targeted process to be studied is not an easy task (Vázquez & Aizen 2003). As an

236 alternative, recent attempts to understand trait matching by statistically modeling
237 empirical data are promising (e.g., models incorporating imperfect detectability:
238 Bartomeus 2013; fourth corner analysis: Dehling *et al.* 2014; linear models: González-
239 Castro *et al.* 2015; Dirichlet-multinomial regression: Crea, Ali & Rader 2015), but such
240 models are still unable to integrate the relative contribution of neutral vs. trait-based
241 process.

242

243 A final caveat is that most models are constrained to use mean trait values at the
244 species level, neglecting variability among individuals of the same species. However,
245 intraspecific trait variation, which can result from life-history stage, sexual dimorphism,
246 or stochastic, environmental, genetic or epigenetic forces (Bolnick *et al.* 2011), has
247 been shown to affect specific interactions such as competition, as well as overall
248 ecological dynamics (González-Suárez & Revilla 2013).

249

250 **A probabilistic method for evaluating trait matching**

251

252 To overcome the limitations pointed out above, we model the probability of interaction
253 among pairs of individuals given their traits, based on a framework developed by Gravel
254 and colleagues (Gravel *et al.* 2013). The method also has the advantage to build
255 directly on the established theory of ecological network structure (Williams & Martinez,
256 2000; Eklof *et al.* 2013), by contrast with the above listed methods that are essentially
257 phenomenological. We propose a method to evaluate trait-matching relationships while
258 taking into account abundance of the interacting partners. The fitting procedure uses
259 information about observed interactions only, thereby overcoming problems caused by

260 under-sampling of rare interactions leading to false absences of interactions. The
261 approach implies that sampling effort is enough to adequately describe most true
262 interactions in trait-space and no false positives are recorded (i.e. recording interactions
263 as true when they do not occur). A previous sensitivity analysis however revealed it to
264 be robust to sampling effort (Gravel *et al.* 2013). The parameters are estimated by
265 maximum likelihood and the fitted model can be used to predict unobserved interactions
266 based on species traits and abundances. Several models, corresponding to different
267 hypotheses, can be fit directly to raw data and accommodate complex trait matching
268 response functions to either qualitative or quantitative interaction data. Finally, they can
269 incorporate intraspecific trait variation, avoiding the loss of realism in species with trait
270 values that vary along developmental stages or environmental gradients. In that way we
271 provide a common toolbox to understand trait-matching rules across a variety of
272 interaction types.

273

274 We are interested in evaluating from empirical data a function describing the probability
275 of an interaction between species i and j based on their respective sets of traits T_i and
276 T_j . Building upon the model developed by (Gravel *et al.* 2013), we aim to evaluate the
277 parameters of a model that will relate the probability with which an interaction occurs to
278 the set of traits of the two species:

279

$$280 \quad P(L_{ij} = 1 | T_i, T_j) \quad (1)$$

281

282 Which reads as the probability of observing an interaction L between species i and j

283 given the traits T_i and T_j . The function describing this probability could take any form.
284 For the sake of the example here, we will consider a Gaussian shaped function (i.e. a
285 function that assumes an unimodal relationship between T_i and T_j) to represent the trait-
286 matching interaction (also termed interaction niche; Williams, Anandanadesan & Purves
287 2010, see below). Other functions, such as a high order polynomial or even regression
288 trees, could be considered as well. The Gaussian function is however convenient
289 because it is easy to integrate and further it matches the niche model of network
290 structure (Williams *et al.* 2010; Eklof *et al.* 2013).

291
292 Equation 1 could be fit directly to empirical data by maximum likelihood. To do so, the
293 required data should contain information on presence and absence of interactions (e.g.
294 Rohr *et al.* 2010). The problem we are facing, however, is that records of the true
295 absence of interactions are often not available in most datasets of ecological
296 interactions, and when available, there might be considerable uncertainty in these
297 absences (i.e. false negatives due to insufficient sampling). We therefore derive a
298 likelihood function using Bayes theorem to fit Eq. 1 indirectly, using only information
299 about the observed interactions. Parameters are still evaluated by maximum likelihood
300 (using simulated annealing, as described in the supplementary information), but one
301 could eventually develop the method further to compute the posterior distribution of
302 parameters.

303
304 The data contains information about the traits of species i and of species j only for
305 observed interactions $L_{ij} = 1$. We consequently revise the problem and model the

306 probability of observing trait T_i , knowing the trait T_j and the occurrence of the interaction

307 L_{ij} :

308

309
$$P(T_i|L_{ij} = 1, T_j) \quad (2)$$

310

311 Which could be interpreted as the probability that we pick trait T_i from the trait

312 distribution we model, given we know there is an interaction between species i and j

313 and the trait T_j . This equation provides the likelihood for any observation of an

314 interaction based on the traits of the two species. We now use Bayes' theorem,

315 $p(A|B)p(B) = p(B|A)p(A)$, to decompose Eq. 2, yielding the following distribution of

316 the trait of one species, given the trait of the second species and the observation of the

317 interaction:

318

319
$$P(T_i|L_{ij} = 1, T_j) = \frac{P(L_{ij} = 1|T_i, T_j) P(T_i)}{P(L_{ij} = 1|T_j)} \quad (3)$$

320

321 The first term from the numerator is the trait-matching model, described at Eq. 1. It is

322 the model for which we aim to evaluate parameters. $P(T_i)$ is the probability density

323 function for the trait T_i . It corresponds to the probability of observing this trait in the

324 regional pool. It could be weighted by abundance because the most abundant species

325 are more likely to be sampled. The denominator is the marginal distribution of the trait-

326 matching function, computed as the integral of the numerator over the whole distribution

327 of the trait T_i :

328

329 $P(L_{ij} = 1|T_j) = \int_{-\infty}^{\infty} P(L_{ij} = 1|T_i, T_j) * P(T_i) dT_i$ (4)

330

331 As a side product, the denominator informs us of the generality of the species j . This
332 integral might be tricky to compute analytically, depending on the form of Eq. 1 and the
333 distribution of trait T_i , but most software offer easy ways to compute it numerically.

334

335 The model given at Eq. 3 should not be confounded with the more traditional use of the
336 Bayes theorem in statistics. The resulting distribution describes the probability of
337 observing an interaction given a trait, while in statistics, the distribution describes the
338 probability of observing a set of parameters given the data. Here the parameters are
339 estimated by simulated annealing and there is only a single set of parameters yielding
340 the maximum likelihood. True confidence intervals for parameter estimates are hard to
341 evaluate for non-linear models with complex likelihood surfaces, but could nonetheless
342 be evaluated numerically. The Eq. 3 could also be implemented in a Bayesian fitting
343 procedure to obtain a posterior distribution of parameters for Eq. 1 (Eq. 3 being the
344 likelihood of the Bayes theorem), but this would be out of the scope of the current study.

345

346 The model could be simplified to account only for the effect of abundance (trait
347 distributions) to reveal the importance of the trait-matching constraint. A neutral model
348 in this framework is found when an interaction is equally probable, irrespective of the
349 traits of the two species involved in the interaction (i.e. Eq. 1 is set as a constant).

350 Alternatively, one could want to compare to the situation where interactions are purely

351 determined by trait-matching constraints. In this situation, we consider the distribution of

352 the trait ($P(T_i)$) uniform within the range of the observed traits. The Eq. 3 remains the
353 same for all three models and could be used to compute the likelihood for each of them.
354 Equations for the pure neutral and trait-matching models, and a multi-trait expansion, as
355 well as all of the R code necessary to perform this analysis are provided in the
356 supplementary material (see Appendix S1 in Supporting Information) and as an R
357 package found at https://github.com/ibartomeus/trait_match.

358

359 We re-analyzed three datasets on different systems ranging from antagonistic to
360 mutualistic interactions to illustrate the overall principle of the method. First, we use data
361 from (Barnes *et al.* 2008) on the diet of marine fish species. The traits are the individual
362 (log transformed) body size of the predator fish species (M_{pred}) and the individual body
363 size of preys $P(M_{prey})$. We know that larger fish typically feed on smaller ones because
364 they must catch and handle the prey with their mouth. The frequency distribution of prey
365 size will indeed influence the distribution of the body mass in the diet of the predator. A
366 predator will tend to feed most often on the most abundant preys, which is a neutral
367 component to the interaction probability. The predator does not select from that
368 distribution randomly, however, but rather it targets only a specific range (given by Eq.1
369 ; the niche component). Both the available prey size distribution, $P(M_{prey})$, and the
370 resulting prey size distribution, $P(M_{prey}|L, M_{pred})$, are illustrated in figure 2B for a given
371 predator species. The resulting prey distribution has to be somewhere between the
372 regional prey distribution and its preferred prey size. The model therefore integrates
373 both neutral and trait-matching constraints.

374

375 We consider the following Gaussian function to represent the probability of an
376 interaction given the size of the predator and the prey:

377

$$378 \quad P(L_{ij} = 1 | M_{pred}, M_{prey}) = \exp \frac{-(\alpha_0 + \alpha_1 * M_{pred} - M_{prey})^2}{2(\beta_0 + \beta_1 * M_{pred})^2} \quad (5)$$

379

380 Where α_0 , α_1 , β_0 and β_1 are fitted parameters describing the linear relationship between
381 the predator size, its optimum ($\alpha_0 + \alpha_1 M_{pred}$) and the range ($\beta_0 + \beta_1 M_{pred}$) of its
382 preference function. This formulation considers there is an optimal prey size for the
383 predator and the probability an interaction occurs reduces with any deviation from it
384 (Williams et al. 2010). The optimum also increases linearly with predator size. The same
385 reasoning could also be applied to mutualistic interactions, considering there is an
386 optimal corolla length for a pollinator of a given tongue length. One tricky issue might be
387 to gather information about the prey trait distribution. The distribution of prey traits might
388 be influenced by the interactions if there is a feedback of predators on prey abundance,
389 and in the best situation we need to tease that effect apart. Here we assume that the
390 distribution of the data provides an adequate representation of the distribution of
391 potential prey sizes because of the large number of observed interactions (> 33 000)
392 and their diversity. We thus consider a normal distribution of (log) prey size and
393 computed the average and the standard deviation.

394

395 The predator-prey example provides a case where trait matching is a strong driver of
396 interactions because of a strong predator-prey body size relationship (likelihood = -

397 21223). The parameters of the fitted model can subsequently be used for predicting
398 interactions among species that co-occur, but have not been observed to interact (e.g.
399 due to incomplete sampling) or more interestingly, for species that currently do not co-
400 occur but may do so in the future, for example as a consequence of range shifts under
401 climate change (Albouy *et al.* 2014) or species invasions.

402

403 Next, we use the same models on experimental data on the relationship between
404 grasshopper incisive strength and leaf dry matter content (Deraison *et al.* 2015). In this
405 case, both traits are species averages. We first find weak trait matching for binary data
406 (who eats whom at the species-level; likelihood = -213; Fig 3A). However, weighting the
407 interactions by consumption frequency removes bias in parameter estimates and the fit
408 of the model is considerably improved (likelihood = -5383). We thus find that strong-
409 mandibled grasshoppers prefer plants with higher content of dry matter, as reported in
410 the original paper (Fig 3B).

411

412 The model could also be evaluated using traits measured at the individual level. In the
413 last example, we related pollinator tongue length with plant nectar holder depth in
414 visitation networks from Bartomeus, Vilà & Santamaría (2008). Individual pollinator
415 tongue length was inferred using the allometric relationship with body inter-tegular span
416 within each bee family (Cariveau *et al.* 2015), while species average flower size was
417 considered for plants. Individual trait data for pollinators allows capture of the inter-
418 individual differences when evaluating parameters of trait-matching functions. In
419 addition, this model uses independent information to describe the trait abundance
420 distribution of plant species. In the past examples, abundance was inferred from the

421 network of interactions, but in this case, independent transect measures of percent plant
422 cover in the site are available (Bartomeus *et al.* 2008). We find that the model can be
423 interpreted as a trait-barrier, where small-tongued individuals cannot access deep
424 flowers, but long-tongued species can access both deep and shallow flowers (likelihood
425 = -705; Fig. 4). However, under such weak constraints (most pollinators can access
426 most plants), abundance is the main determinant of interaction probability. For
427 comparison, using pollinator species trait averages instead of individual values produce
428 a similar model, but with a worst likelihood (-726), indicating that there is a gain from
429 using detailed data when available.

430

431 **Discussion and conclusions**

432 Quantifying the trait-matching relationships across species may help us to understand
433 how networks are structured. For example, the nested structure of plant-pollinator
434 networks may be driven from species abundance (Vázquez *et al.* 2009) or from barriers
435 to certain interactions (Stang, Klinkhamer & van der Meijden 2006). In contrast, the
436 strong trait-matching observed in plant-herbivore interactions (e.g. plant defenses
437 limiting herbivory for all but a few tolerant species) can produce more modular networks
438 where interactions depart more from the null expectation based solely on abundance
439 (Thébault & Fontaine 2010). Even within plant-pollinator interactions, bird-plant
440 networks are more specialized than insect-plant networks, which is also reflected in
441 their degree of trait-matching (Maglianesi, Böhning-Gaese & Schleuning 2015). Our
442 framework is however limited to pairwise interactions and future work will have to
443 investigate how the distribution of traits in a community constrains the emergent
444 network properties. Moreover, trait-matching constraints describe potential interactions,

445 but may not always reflect realized interactions (Poisot, Stouffer & Gravel 2015). The
446 future development of a bayesian approach to evaluate the distribution of parameters
447 will help quantifying the uncertainty of predicted interactions.

448

449 Parameterized trait-matching functions not only provide a better understanding of the
450 drivers of interactions, but they also allow prediction of novel interactions following
451 deliberate introductions (e.g. of crop species or biological control agents) or
452 unintentional invasions and range shifts (Morales-Castilla *et al.* 2015). Proxies of trait
453 similarity, like phylogenetic distance, have already been successfully used to predict
454 interactions of exotic species (Pearse & Altermatt 2013) and adding traits has the
455 potential to enhance this approach. Species losses and gains following local and global
456 changes are threatening most ecosystems, and it is simply impossible to measure all
457 potential interactions in the field. Tools are consequently required to assess how the
458 interaction network will rewire. We know that exotic species invading a community get
459 easily integrated into the recipient network of interactions (Albrecht *et al.* 2014), and that
460 after species turnover in a community, the remaining species reshuffle their interactions
461 to adjust to the new composition (Kaiser-Bunbury *et al.* 2010). Our predictive ability in
462 these situations is however still limited.

463

464 Careful selection of the right set of traits to run the analysis is, however, a critical step.
465 We have seen that traits constraining interactions could potentially comprise all
466 morphological and physiological species characteristics, and hence, are quite specific
467 for each interaction type. A good *a priori* knowledge on the biology of the species and
468 type of interaction involved is needed to select the right trait combinations. For example,

469 we also explored whether body size drives host-parasite relationships using the
470 Tylianakis, Tscharntke & Lewis (2007) dataset, but in this case all models performed
471 poorly because the largest parasitoid is smaller than the smallest host, which allows all
472 types of body size combinations. Alternatively, spurious trait matches could be found
473 when some traits are correlated. For instance, traits like body size correlate
474 allometrically with several other morphological traits (Woodward *et al.* 2005) and might
475 therefore provide a wrong causal explanation of the interactions. One strong limitation
476 for some interactions, such as fungi and plants, is that the traits governing interactions
477 remain somewhat unclear (Tedersoo *et al.* 2008; Martínez-García *et al.* 2015). The
478 challenge for the future will be to determine and quantify the actual traits governing
479 these interactions, including their variability among individuals or genets.

480

481 Another challenge outlined in Fig. 1 and still unresolved is inferring functioning from a
482 network of interactions (Duffy *et al.* 2009; Thompson *et al.* 2012). Species interactions
483 are driving several ecosystem processes and functions (e.g. animal pollination, fruit
484 dispersion) as well as energy fluxes (e.g. predation, parasitism). Inferring the function
485 from traits however requires incorporating the interaction efficiency (the per capita
486 strength of a single interaction link; Vázquez *et al.* 2015), which in turn may be also trait-
487 or abundance-mediated, and can depend on the extent of matching (e.g. pollinators with
488 short tongues may be able to visit, but inefficiently pollinate long flower corollas), or on
489 morphological, physiological or behavioural traits (e.g. large pollinators deposit more
490 pollen; Hoehn *et al.* 2008; Fig 1). Empirical evidence measuring interaction efficiency is
491 still scarce.

492

493 In conclusion, different traits can inform us about how species form networks of
494 interactions. For some interaction types, like mycorrhizal fungal interactions, traits
495 affecting co-occurrence can be the most relevant for understanding the occurrence of
496 interactions. Conversely, for other interaction types, like those between predators and
497 prey, morphological and physiological traits may be the main determinants of who
498 interacts with whom. Understanding which mechanisms are driving pairwise interactions
499 is key to predict how communities will respond to global change. Interactions regulated
500 by co-occurrence will be more likely to be affected by climate change (e.g. changing
501 phenologies and distributions), while changes in dominance following disturbance may
502 redistribute the interactions in neutral-driven networks. Non-random species extinctions
503 are also expected to affect more drastically interactions regulated by strong trait
504 matching (Larsen, Williams & Kremen 2005). There are still too many unknowns to draw
505 general conclusions about how communities are structured by traits and what
506 implications this has for ecosystem functioning, but we are now armed with appropriate
507 analytical tools to move beyond the mere description of interactions and run predictive
508 analysis of network assembly and dynamics.

509

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515

516 **SUPPORTING INFORMATION**

517 Additional supporting information may be found in the online version of this article.

518 Appendix S1: niche, neutral and multi-trait derivations

519 Appendix S2: R code as .zip

520 Please note: Wiley Blackwell are not responsible for the content or functionality of any

521 supporting information supplied by the authors. Any queries (other than missing material) should

522 be directed to the corresponding author for the article.

523

524 **References:**

525 Albouy, C., Velez, L., Coll, M., Colloca, F., Loc'h, F., Mouillot, D. & Gravel, D. (2014)

526 From projected species distribution to food-web structure under climate change.

527 *Global change biology*, **20**, 730–741.

528 Albrecht, M., Padrón, B., Bartomeus, I. & Traveset, A. (2014) Consequences of plant

529 invasions on compartmentalization and species' roles in plant--pollinator networks.

530 *Proceedings of the Royal Society of London B: Biological Sciences*, **281**,

531 20140773.

532 Araújo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011) Using species co-

533 occurrence networks to assess the impacts of climate change. *Ecography*, **34**,

534 897–908.

535 Barnes, C., Bethea, D.M., Brodeur, R.D., Spitz, J., Ridoux, V., Pusineri, C., Chase,

536 B.C., Hunsicker, M.E., Juanes, F., Kellermann, A. & Others. (2008) Predator and

537 prey body sizes in marine food webs: Ecological Archives E089-051. *Ecology*, **89**,

538 881–881.

539 Bartomeus, I. (2013) Understanding linkage rules in plant-pollinator networks by using
540 hierarchical models that incorporate pollinator detectability and plant traits. *PloS*
541 *one*, **8**, e69200.

542 Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N. & Winfree, R. (2013)
543 Biodiversity ensures plant-pollinator phenological synchrony against climate
544 change. *Ecology letters*, **16**, 1331–1338.

545 Bartomeus, I., Vilà, M. & Santamaría, L. (2008) Contrasting effects of invasive plants in
546 plant-pollinator networks. *Oecologia*, **155**, 761–770.

547 Bascompte, J. & Jordano, P. (2007) Plant-Animal Mutualistic Networks: The Architecture
548 of Biodiversity. *Annual review of ecology, evolution, and systematics*, **38**, 567–593.

549 Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M.,
550 Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011) Why
551 intraspecific trait variation matters in community ecology. *Trends in ecology*
552 *& evolution*, **26**, 183–192.

553 Cadotte, M.W., Carscadden, K. & Mirotnick, N. (2011) Beyond species: functional
554 diversity and the maintenance of ecological processes and services. *The Journal of*
555 *applied ecology*, **48**, 1079–1087.

556 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014)
557 Empirical evaluation of neutral interactions in host-parasite networks. *The American*

558 *naturalist*, **183**, 468–479.

559 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P.,
560 Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C.,
561 Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012)
562 Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

563 Cariveau, D.P., Nayak, G., Bartomeus, I., Zientek, J., Ascher, J. & Winfree, R. (2015)
564 The allometry of bee tongue length and its uses in ecology and evolution. *PLoS One*.
565 In review.

566 Carvalheiro, L.G., Barbosa, E.R.M. & Memmott, J. (2008) Pollinator networks, alien
567 species and the conservation of rare plants: *Triniaglauca* as a case study. *The*
568 *Journal of applied ecology*, **45**, 1419–1427.

569 Castellanos, M. C., Wilson, P. & Thomson, J. D. (2003) Pollen transfer by
570 hummingbirds and bumblebees, and the divergence of pollination modes in
571 *Penstemon*. *Evolution* **57**, 2742–2752.

572 Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J. & Padrón, B.
573 (2012) Evaluating sampling completeness in a desert plant–pollinator network. *The*
574 *Journal of animal ecology*, **81**, 190–200.

575 Chagnon, P.-L., Bradley, R.L., Maherali, H. & Klironomos, J.N. (2013) A trait-based
576 framework to understand life history of mycorrhizal fungi. *Trends in plant science*,
577 **18**, 484–491.

578 Crea, C., Ali, R. A. & Rader, R. (2015) A new model for ecological networks using
579 species-level traits. *Methods in Ecology and Evolution*. In press. doi: 10.1111/2041-
580 210X.12471

581 Cunha, I. & Planas, M. (1999) Optimal prey size for early turbot larvae (*Scophthalmus*
582 *maximus* L.) based on mouth and ingested prey size. *Aquaculture* , **175**, 103–110.

583 Dehling, D.M., Töpfer, T., Schaefer, H.M., Jordano, P., Böhning-Gaese, K. &
584 Schleuning, M. (2014) Functional relationships beyond species richness patterns:
585 trait matching in plant–bird mutualisms across scales. *Global ecology and*
586 *biogeography*, **23**, 1085–1093.

587 Deraison, H., Badenhausser, I., Börger, L. & Gross, N. (2015) Herbivore effect traits and
588 their impact on plant community biomass: an experimental test using grasshoppers.
589 *Functional ecology*, **29**, 650–661.

590 Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M.
591 (2007) The functional role of biodiversity in ecosystems: incorporating trophic
592 complexity. *Ecology letters*, **10**, 522–538.

593 Duffy, J.E., Srivastava, D.S., McLaren, J., Sankaran, M., Solan, M., Griffin, J.,
594 Emmerson, M. & Jones, K.E. (2009) Forecasting decline in ecosystem services
595 under realistic scenarios of extinction. *Biodiversity, ecosystem functioning and*
596 *human wellbeing: an ecological and economic perspective*. Oxford University
597 Press, Oxford, British, 60–77.

598 Díaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity mattersto

599 ecosystem processes. *Trends in ecology & evolution*, **16**, 646–655.

600 D'Amen, M., Dubuis, A., Fernandes, R.F., Pottier, J., Pellissier, L. & Guisan, A. (2015)
601 Using species richness and functional traits predictions to constrain assemblage
602 predictions from stacked species distribution models. *Journal of biogeography*, **42**,
603 1255–1266.

604 Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B.,
605 de Sassi, C., Galetti, M., Guimarães, P.R., Lomáscolo, S.B., Martín González,
606 A.M., Pizo, M.A., Rader, R., Rodrigo, A., Tylianakis, J.M., Vázquez, D.P. & Allesina,
607 S. (2013) The dimensionality of ecological networks. *Ecology letters*, **16**, 577–583.

608 Encinas-Viso, F., Revilla, T.A. & Etienne, R.S. (2012) Phenology drives mutualistic
609 network structure and diversity. *Ecology letters*, **15**, 198–208.

610 Fenster, C.B., Reynolds, R.J., Williams, C.W., Makowsky, R. & Dudash, M.R. (2015)
611 Quantifying hummingbird preference for floral trait combinations: The role of
612 selection on trait interactions in the evolution of pollination syndromes. *Evolution*, **69**,
613 1113–1127.

614 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M.,
615 Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tschardtke, T., Weisser, W. &
616 Bommarco, R. (2015) Functional identity and diversity of animals predict ecosystem
617 functioning better than species-based indices. *Proceedings of the Royal Society of*
618 *London B: Biological Sciences*, **282**, 20142620.

619 Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca,

620 F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, P.R., Jr,
621 Brancalion, P.H., Ribeiro, M.C. & Jordano, P. (2013) Functional extinction of birds
622 drives rapid evolutionary changes in seed size. *Science*, **340**, 1086–1090.

623 González-Castro, A., Yang, S., Nogales, M. & Carlo, T.A. (2015) Relative importance of
624 phenotypic trait matching and species' abundances in determining plant-avian seed
625 dispersal interactions in a small insular community. *AoB plants*, **7**.

626 González-Suárez, M. & Revilla, E. (2013) Variability in life-history and ecological traits is
627 a buffer against extinction in mammals. *Ecology letters*, **16**, 242–251.

628 Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013) Inferring food web
629 structure from predator–prey body size relationships. *Methods in ecology and*
630 *evolution*, **4**, 1083–1090.

631 Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding, K.N. & Lavorel, S. (2009)
632 Linking individual response to biotic interactions with community structure: a trait-
633 based framework. *Functional ecology*, **23**, 1167–1178.

634 Herrera, C.M. (2000) Flower-to-seedling consequences of different pollination regimes
635 in an insect-pollinated shrub. *Ecology*, **81**, 15–29.

636 Hoehn, P., Tschardtke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional
637 group diversity of bee pollinators increases crop yield. *Proceedings of the Royal*
638 *Society of London B: Biological Sciences*, **275**, 2283–2291.

639 Jacquemyn, H., Merckx, V., Brys, R., Tyteca, D., Cammue, B.P.A., Honnay, O. &

640 Lievens, B. (2011) Analysis of network architecture reveals phylogenetic
641 constraints on mycorrhizal specificity in the genus *Orchis* (Orchidaceae). *The New*
642 *phytologist*, **192**, 518–528.

643 Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010) The
644 robustness of pollination networks to the loss of species and interactions: a
645 quantitative approach incorporating pollinator behaviour. *Ecology letters*, **13**, 442–
646 452.

647 Krishna, A., Guimaraes, P.R., Jr, Jordano, P. & Bascompte, J. (2008) A neutral-niche
648 theory of nestedness in mutualistic networks. *Oikos*, **117**, 1609–1618.

649 Kritsky, G. (1991) Darwin's Madagascan Hawk Moth Prediction. *American*
650 *Entomologist*, **37**, 206–210.

651 Laliberté, E. & Tylianakis, J.M. (2010) Deforestation homogenizes tropical parasitoid-host
652 networks. *Ecology*, **91**, 1740-1747.

653 Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered
654 community structure rapidly disrupt ecosystem functioning. *Ecology letters*, **8**, 538–
655 547.

656 Laughlin, D.C., Joshi, C., van Bodegom, P.M., Bastow, Z.A. & Fulé, P.Z. (2012) A
657 predictive model of community assembly that incorporates intraspecific trait
658 variation. *Ecology letters*, **15**, 1291–1299.

659 Lima-Mendez, G., Faust, K., Henry, N., Decelle, J. & Colin, S. (2015) Determinants of
660 community structure in the global plankton interactome. *Science*.

661 Loreau, M. (1998) Biodiversity and ecosystem functioning: a mechanistic model.
662 *Proceedings of the National Academy of Sciences of the United States of America*,
663 **95**, 5632–5636.

664 Loreau, M. (2010) Linking biodiversity and ecosystems: towards a unifying ecological
665 theory. *Philosophical transactions of the Royal Society of London. Series B*,
666 *Biological sciences*, **365**, 49–60.

667 Maglianesi, M.A., Böhning-Gaese, K. & Schleuning, M. (2015) Different foraging
668 preferences of hummingbirds on artificial and natural flowers reveal mechanisms
669 structuring plant–pollinator interactions. *The Journal of animal ecology*, **84**, 655–
670 664.

671 Martínez-García, L.B., Richardson, S.J., Tylianakis, J.M., Peltzer, D.A. & Dickie, I.A.
672 (2015) Host identity is a dominant driver of mycorrhizal fungal community
673 composition during ecosystem development. *The New phytologist*, **205**, 1565–
674 1576.

675 Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015) Inferring biotic
676 interactions from proxies. *Trends in ecology & evolution*, **30**, 347–356.

677 Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P.
678 (2011) Missing and forbidden links in mutualistic networks. *Proceedings of the*
679 *Royal Society of London B: Biological Sciences*, **278**, 725–732.

680 Olito, C. & Fox, J.W. (2015) Species traits and abundances predict metrics of plant–
681 pollinator network structure, but not pairwise interactions. *Oikos*, **124**, 428–436.

682 Pearse, I.S. & Altermatt, F. (2013) Predicting novel trophic interactions in a non-native
683 world. *Ecology letters*, **16**, 1088–1094.

684 Peralta, G., Frost, C.M., Rand, T.A., Didham, R.K. & Tylianakis, J.M. (2014)
685 Complementarity and redundancy of interactions enhance attack rates and spatial
686 stability in host-parasitoid food webs. *Ecology*, **95**, 1888–1896.

687 Poisot, T., Canard, E., Mouillot, D., Mouquet, N., Gravel, D. & Jordan, F. (2012) The
688 dissimilarity of species interaction networks. *Ecology letters*, **15**, 1353–1361.

689 Poisot, T., Mouquet, N. & Gravel, D. (2013) Trophic complementarity drives the
690 biodiversity–ecosystem functioning relationship in food webs. *Ecology letters*, **16**,
691 853–861.

692 Poisot, T., Stouffer, D.B. & Gravel, D. (2015) Beyond species: why ecological interaction
693 networks vary through space and time. *Oikos*, **124**, 243–251.

694 Rader, R., Reilly, J., Bartomeus, I. & Winfree, R. (2013) Native bees buffer the negative
695 impact of climate warming on honey bee pollination of watermelon crops. *Global
696 change biology*, **19**, 3103–3110.

697 Rohr, R.P., Scherer, H., Kehrl, P., Mazza, C. & Bersier, L.-F. (2010) Modeling food
698 webs: exploring unexplained structure using latent traits. *The American naturalist*,
699 **176**, 170–177.

700 Sargent, R.D. & Ackerly, D.D. (2008) Plant-pollinator interactions and the assembly of
701 plant communities. *Trends in Ecology and Evolution*, **23**:123-130

702 Shipley, B., Vile, D. & Garnier, E. (2006) From plant traits to plant communities: a
703 statistical mechanistic approach to biodiversity. *Science*, **314**, 812–814.

704 Spitz, J., Ridoux, V. & Brind’Amour, A. (2014) Let’s go beyond taxonomy in diet
705 description: testing a trait-based approach to prey–predator relationships. *The*
706 *Journal of animal ecology*, **83**, 1137–1148.

707 Stang, M., Klinkhamer, P.G.L. & van der Meijden, E. (2006) Asymmetric specialization
708 and extinction risk in plant–flower visitor webs: a matter of morphology or
709 abundance? *Oecologia*, **151**, 442–453.

710 Tedersoo, L., Jairus, T., Horton, B.M., Abarenkov, K., Suvi, T., Saar, I. & Kõljalg, U.
711 (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet
712 sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *The*
713 *New phytologist*, **180**, 479–490.

714 Thébault, E. & Loreau, M. (2003) Food-web constraints on biodiversity-ecosystem
715 functioning relationships. *Proceedings of the National Academy of Sciences*, **100**,
716 14949–14954.

717 Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Jr, Hladysz, S., Kitching, R.L.,
718 Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B. & Tylianakis, J.M.
719 (2012) Food webs: reconciling the structure and function of biodiversity. *Trends in*
720 *ecology & evolution*, **27**, 689–697.

721 Thébault, E. & Fontaine, C. (2010) Stability of ecological communities and the
722 architecture of mutualistic and trophic networks. *Science*, **329**, 853–856.

- 723 Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change
724 and species interactions in terrestrial ecosystems. *Ecology letters*, **11**, 1351–1363.
- 725 Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of
726 species interaction networks. *Biological conservation*, **143**, 2270–2279.
- 727 Tylianakis, J.M., Tschardtke, T. & Lewis, O.T. (2007) Habitat modification alters the
728 structure of tropical host–parasitoid food webs. *Nature*, **445**, 202–205.
- 729 Vázquez, D.P. & Aizen, M.A. (2003) Null Model Analyses of Specialization in Plant-
730 Pollinator Interactions. *Ecology*, **84**, 2493–2501.
- 731 Vázquez, D.P., Chacoff, N.P. & Cagnolo, L. (2009) Evaluating multiple determinants of
732 the structure of plant-animal mutualistic networks. *Ecology*, **90**, 2039–2046.
- 733 Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R.
734 (2007) Species abundance and asymmetric interaction strength in ecological
735 networks. *Oikos*, **116**, 1120–1127.
- 736 Vázquez, D.P., Morris, W.F. & Jordano, P. (2005) Interaction frequency as a surrogate
737 for the total effect of animal mutualists on plants. *Ecology letters*, **8**, 1088–1094.
- 738 Vázquez, D.P., Ramos-Jiliberto, R., Urbani, P. & Valdovinos, F.S. (2015) A conceptual
739 framework for studying the strength of plant-animal mutualistic interactions.
740 *Ecology letters*, **18**, 385–400.
- 741 Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996) Generalization
742 in Pollination Systems, and Why it Matters. *Ecology*, **77**, 1043–1060.

- 743 White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between
744 body size and abundance in ecology. *Trends in ecology & evolution*, **22**, 323–330.
- 745 Williams, R.J., Anandanadesan, A. & Purves, D. (2010) The probabilistic niche model
746 reveals the niche structure and role of body size in a complex food web. *PloS one*,
747 **5**, e12092.
- 748 Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*,
749 **404**, 180–183.
- 750 Winfree, R., W Fox, J., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015) Abundance
751 of common species, not species richness, drives delivery of a real-world ecosystem
752 service. *Ecology letters*, **18**, 626–635.
- 753 Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. &
754 Warren, P.H. (2005) Body size in ecological networks. *Trends in ecology &*
755 *evolution*, **20**, 402–409.
- 756 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-
757 Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E.,
758 Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C.,
759 Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H.,
760 Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G.,
761 Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum.
762 *Nature*, **428**, 821–827.
- 763 Zobel, M. & Öpik, M. (2014) Plant and arbuscular mycorrhizal fungal (AMF)

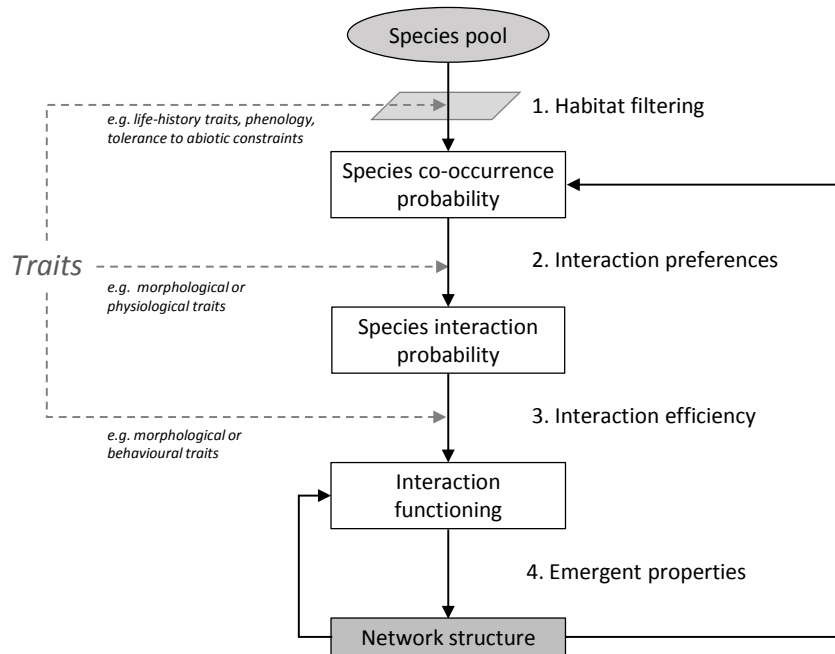
764 communities--which drives which? *Journal of vegetation science*, **25**, 1133–1140.

765 **Data Accessibility:** All data and R code to perform analysis can be found in the
766 appendix and at https://github.com/ibartomeus/trait_match ([10.5281/zenodo.46382](https://doi.org/10.5281/zenodo.46382))

767

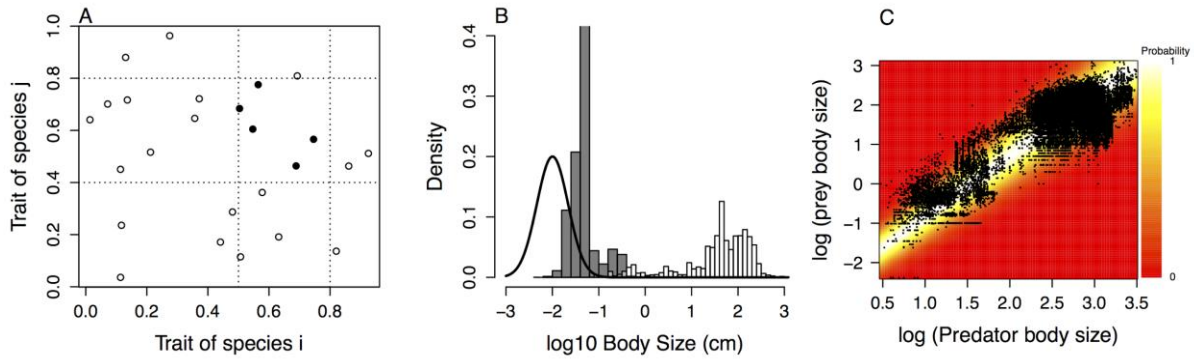
768 **Figures:**

769 **Figure 1**



770

771 Figure 1. Species traits may influence the structure of interaction networks in three
772 different ways. 1) Trait-based environmental filtering may determine species
773 abundances in space and time, which will affect probability of encounter. 2) Given
774 species co-occurrence, trait matching according to species interaction preferences will
775 shape interaction probability. 3) Species traits might also influence the per capita
776 efficiency and impact of an interaction, and thereby influence network functioning. In
777 addition, 4) emergent properties inherent to the structure of the network will influence
778 network functioning and feedback on community dynamics.

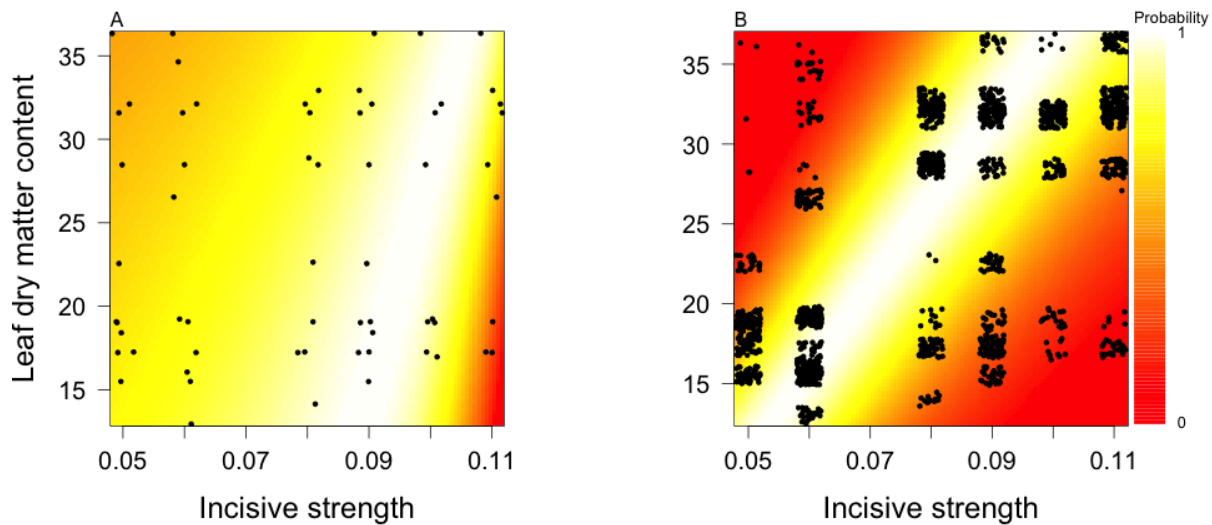


779

780

781 Figure 2. Illustration of the quantitative framework to evaluate a trait-matching
 782 probabilistic function. A) Conceptual representation of a trait-matching constraint.
 783 Interactions (in black) are feasible only when both species have traits that are
 784 compatible. However, we often do not have reliable information on the species that are
 785 present, but are not observed to interact (white dots). Dotted lines indicate the trait
 786 ranges of compatibility between the species B) Representation of the density function
 787 for available body size in the (Barnes *et al.* 2008) dataset (white bars), the trait-
 788 matching function (black line) and the observed distribution of prey size for the predator
 789 *Nototheniops larseni* (black bars). C) Representation of the observed interactions (black
 790 dots) and the prediction for the maximum likelihood estimate of the trait-matching
 791 function (from low probability in red to high probability in white).

792 **Figure 3**



793

794 Figure 3. Representation of the fitted interaction probability for grasshopper and plant

795 interactions unweighted (A) and weighted (B) by frequency of interaction (from low

796 probability in red to high probability in white). The probability of interaction between a

797 grasshopper and a plant follows a positive relationship between incisive strength and

798 plant leaf dry matter content. Note that the overlapping data in B has been jittered to

799 appreciate the different frequencies of particular interactions. The likelihood for (A) is

800 similar to the neutral model, while much better in (B), indicating that the frequency of

801 interactions must be taken into account to better reveal the trait-matching constraint.

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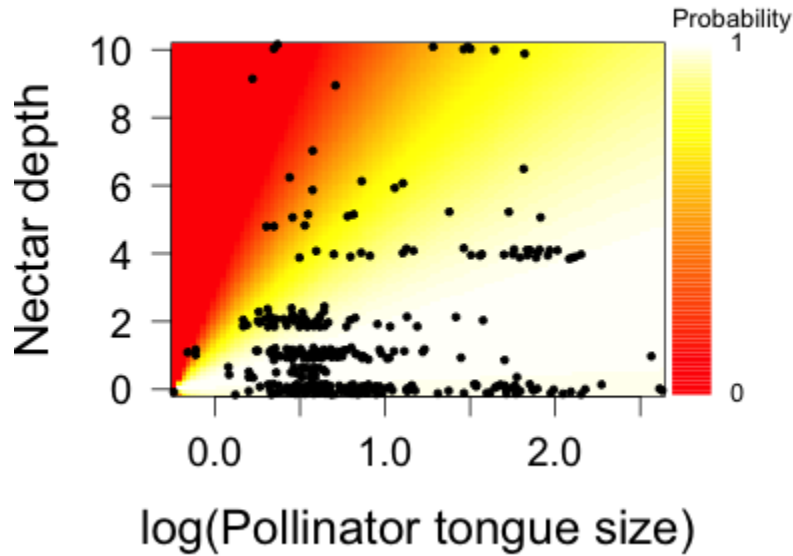
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808 **Figure 4**



809

810 Figure 4. Representation of the fitted interaction probability plant and pollinators

811 weighted by the frequency of interactions (from low probability in red to high probability

812 in white). Only a few interactions among small tongue sized bees and long corolla depth

813 flowers are realized (red area), while the rest of interactions are explained mainly by

814 abundance.

815