

1 **Linking Species Functional Roles To Their Network Roles**

2 Camille COUX¹, Romina RADER², Ignasi BARTOMEUS³, Jason M. TYLIANAKIS^{1,4}

3
4 ¹Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag
5 4800, Christchurch 8140, New Zealand

6 ²Ecosystem Management, School of Environment and Rural Sciences, University of New England,
7 Armidale, NSW, Australia

8 ³Estación Biológica de Doñana (EBD-CSIC), Dpto. Ecología Integrativa, Avda. Américo Vesputio s/n
9 Isla de la Cartuja 41092, Sevilla, Spain

10 ⁴Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road,
11 Ascot, Berkshire SL5 7PY, UK

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20 CC wrote the manuscript and conducted analyses with inputs from JT and IB. RR designed and
21 conducted the field study with assistance from JT. RR and IB compiled the trait data. All authors
22 conceptualised the study and commented on the manuscript. JT secured funding.

23
24 CORRESPONDING AUTHOR:

25 Camille Coux

26 Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag

27 4800, Christchurch 8140, New Zealand

28

29 Email: camille.coux@orange.fr

30 Cell phone +64-22-186-5969

31 Fax +64-3-364-2590

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36 ABSTRACT

37 Species roles in ecological networks combine to generate their architecture, which contributes to
38 their stability. Species trait diversity also affects ecosystem functioning and resilience, yet it remains
39 unknown whether species' contributions to functional diversity relate to their network roles. Here
40 we use 21 empirical pollen transport networks to characterise this relationship. We found that, apart
41 from a few abundant species, pollinators with original traits either had few interaction partners or
42 interacted most frequently with a subset of these partners. This suggests that narrowing of
43 interactions to a subset of the plant community accompanies pollinator niche specialisation,
44 congruent with our hypothesised trade-off between having unique traits vs. being able to interact
45 with many mutualist partners. Conversely, these effects were not detected in plants, potentially
46 because key aspects of their flowering traits are conserved at a family level. Relating functional and
47 network roles can provide further insight into mechanisms underlying ecosystem functioning.

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51 INTRODUCTION

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53 The role biodiversity plays in ecosystem functioning has received much attention (Hooper *et al.*
54 2005), motivated by increasing species extinction rates (Pimm *et al.* 2014) and potential loss of
55 ecosystem services (Thompson & Starzomski 2007). Early findings that the positive biodiversity-
56 ecosystem functioning relationship (e.g. Tilman *et al.* 1996) was not universal (Thompson &
57 Starzomski 2007) drew attention to the redundancy of functional traits across species (Walker 1991).
58 The diversity of traits (i.e. ‘functional diversity’; Lavorel & Garnier 2002) has become a focus of
59 considerable research, as it can predict the rates of ecosystem processes more accurately than does
60 species richness (Reiss *et al.* 2009; Gagic *et al.* 2015), and differences in the redundancy of traits
61 within a community can yield various biodiversity-ecosystem functioning relationships (e.g.
62 saturating or sigmoidal).

63

64 Species’ traits define their functional role by accounting for the morphological, physiological and
65 phenotypic features that affect ecosystem processes or respond to the environment (Lavorel &
66 Garnier 2002). The originality and uniqueness of a species’ traits relative to others in the community
67 define its functional role and contribution to the community functional diversity, i.e. the total
68 diversity of traits displayed by all species (and which reflects a community’s functional “capacity”
69 (Laliberté & Legendre 2010) . The loss of species following land-use change has been shown to
70 reduce this functional diversity (Laliberté *et al.* 2010; Rader *et al.* 2014) and alter ecosystem
71 functioning and services (Larsen *et al.* 2005). Moreover, these losses may non-randomly select
72 certain species based on their ‘response’ traits (Larsen *et al.* 2005), and the interplay of response
73 and effect traits can produce non-random functional changes following environmental change
74 (Lavorel & Garnier 2002). We do not attempt here to infer response and effect trait correlations *a*
75 *priori*, but rather seek to understand how known response and effect traits will also affect the
76 propensity of species to interact, and thereby generate changes to interaction networks.

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78 Indeed, species traits are also known to influence ecological interactions to the point where whole
79 interaction-network topology can be predicted (Eklöf *et al.* 2013), and this topology can have
80 important impacts on resilience (Gao *et al.* 2016). For example, Montoya *et al.* (2015) assigned
81 species to functional groups based on their trophic function (e.g. pollination or decomposition) and
82 found that network modularity favoured higher functional group diversity. Furthermore, a species'
83 function within a community has also been defined relative to the traits of the species with which it
84 interacts (Dehling *et al.* 2016), based on the idea that interactions mediate morphological trait-
85 matching. Thus, the global structure of ecological networks, as well as the relative arrangement of
86 each species' interactions that define their network roles, may capture important elements not only
87 of species diversity, but also functional diversity (Poisot *et al.* 2013).

88

89 However, these functional and network roles may place different constraints on species traits, as the
90 benefits that emerge from functional originality could oppose those arising from acquiring
91 mutualistic interactions. In fact, the benefits of reduced competition that emerge through niche
92 partitioning and drive the functional diversification of species (Grime 2001) may reinforce individual
93 mutualisms through co-specialisations mediated by the cost-benefit balance for the involved
94 partners. Yet, this process may oppose the preservation of many mutualistic interactions in which
95 species are involved, and which constrain their traits to match those of a range of partners, thereby
96 potentially favouring interaction generalism (Fontaine *et al.* 2009). We therefore hypothesise a
97 trade-off between species traits being sufficiently unique to exploit different resources, while
98 remaining similar enough to maintain interactions with a higher number of mutualistic partners. In
99 addition, species relative abundances in a community may further complicate this trade-off, e.g. by
100 affecting species functional diversification through intra- and inter-specific competition (Chesson
101 2000), as well as the partner selection process, which is likely density-dependent (Fort *et al.* 2015).
102 Despite the fact that a network approach could encapsulate these previous trade-offs and thereby

103 improve our understanding of their relationships, it remains unknown whether functional roles of
104 species are related to their network roles (Reiss *et al.* 2009; Thompson *et al.* 2012).

105

106 Here we use empirical data from 21 pollen transport networks to characterise the network roles of
107 plant and pollinator species, and investigate whether these are linked to their functional roles.

108 Specifically, we test whether the position of a species in the network relates to its contribution to
109 community functional diversity (i.e. the uniqueness of its traits). We hypothesise that a species'

110 functional originality will be positively related to its degree of resource specialisation, because

111 specialists should have evolved original traits to better access a single resource, whereas generalists

112 should have average, widespread trait values that do not limit their ability to interact with other

113 species, even if generalist species could also be rare.

114

115

116 METHODS.

117

118 *Site description and experimental design*

119

120 Six replicates of each of four land-use types (in decreasing order of intensity): rotational cropping,
121 dairy farms, blackcurrant orchards and native gardens were sampled in the Canterbury plains region,
122 a highly modified agricultural landscape in the South Island of New Zealand (see Rader *et al.* 2014 for
123 site details). We chose this dataset because the gradient of land-use intensity has been shown to
124 generate a decline in community functional diversity (Rader *et al.* 2014), thereby ensuring that we
125 had a broad range in this predictor variable to test whether it was related to the pollen transport
126 network structure.

127

128 *Sampling methods*

129

130 At each of the 24 sites, insect pollinators were trapped for five days per month from November 2008
131 to 2009 using flight-intercept and pan traps. The two trapping methods were used to maximize the
132 diversity and sample size of insects captured. At the end of each day, insects were removed and
133 trapping materials replenished (see Rader *et al.* 2014 for further details of trapping methods).
134 Insects were sorted to species (Table S1) using existing collections, identification keys (Donovan
135 2007; Landcare Research, 2013) and assistance from expert taxonomists. The pollen found on the
136 underside of pollinator species was sampled by pressing insects onto a cube of gelatine–fuchsin (c. 3
137 mm × 3 mm × 3 mm) and slide mounted. Pollen grains were then counted manually under a
138 microscope using a pollen library of plant specimens collected at each site at the time of sampling
139 (as in Rader *et al.* 2011, see Appendix 1 in S.I. for more details on pollen identification and
140 quantification, and Table S2 for a list of plant species). Data were pooled across trap types (pan and
141 flight-intercept traps) and time (i.e. monthly trap collections for 1 year) to achieve the best
142 resolution possible when identifying interactions among species. Of the initial 24 sites, 3
143 communities were excluded due to their small sample sizes. Voucher specimens are housed at the
144 New Zealand Institute for Plant and Food Research in Lincoln, New Zealand.

145

146 *Trait measurement*

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148 Pollinator and plant traits, as well as some species-level behavioural responses to changing
149 environments comprising many traits, were compiled using existing published and unpublished
150 datasets from the Canterbury region (Tables S3, S4, S.I.). In some cases, the traits are fixed attributes
151 of a species, whereas others are continuous and vary among individuals within species. In the latter
152 case, we used mean values from ten representative specimens (Table S3) (Rader *et al.* 2014),
153 because our aim was to relate species traits with their roles in the interaction network, the nodes of
154 which represent species, rather than individuals.

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We recorded two traits pertaining to pollinator body size (length and width), which is known both to constrain the breadth of species' trophic niches and correlate negatively with reproductive rate (Stang *et al.* 2006) and also to moderate pollination efficiency (e.g., larger insects are hypothesised to have a higher pollen carrying capacity than smaller ones, Larsen *et al.* 2005; Hoehn *et al.* 2008). Likewise, the time spent on the inflorescence (in seconds) is a trait that could simultaneously influence pollination efficiency (Hoehn *et al.* 2008) and be an expression of a response to changes in resource quality (according to optimal foraging theory, Pyke 1978). We also estimated phenology using time of daily abundance peak as well as month of seasonal abundance peak for each insect species during the sampling season (i.e. daily and seasonal activity), as this will determine the amplitude of the match with the plants that flower at a given period, and phenology may respond to environmental changes such as climate (Bartomeus *et al.* 2011). Foraging behaviour can underpin pollination success, hence we recorded the diet preferences of adults (proportions of their diet made up of nectar versus pollen based on field observations; Rader *et al.* 2014) and the type of carrying structure used for pollen transport (corbicula, scopa or none). Moreover, diet preferences of larvae (whether their diet included nectar, plant matter, carrion, dung, parasitism of other insects, and/or predation of other insects) and nesting behaviour (social vs. solitary) are traits that have been shown to influence species responses to environmental changes such as land use or habitat fragmentation (Williams *et al.* 2010). Because we had no *a priori* reason to weight some traits more than others, we considered each trait to be of equal importance in its ability to influence a species' functional niche. However because body length and width are non-independent features relating to body size, we grouped them together by assigning them a weight of 1/2 throughout the analyses so that the 'body size' trait had an equal weight to all the other measured traits. For the same reason, the use of each kind of larval food resource was given a fractional weighting so that all components of larval diet summed to a single trait. See Table S3 in Appendix 1 of the S.I. for a summary of pollinator traits.

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182 For the plant community, we recorded morphological traits that pertained to plant type (grass, herb,
183 shrub or tree), inflorescence morphology (number of flowers per inflorescence, flower symmetry
184 e.g., actinomorphic or zygomorphic; branching organisation type e.g., spike, catkin, umbel,
185 capitulum or other), pollen and nectar access, and physiological characteristics (life span, sex,
186 fragrance, amount of nectar). We also kept a phenological record when flowering of each plant
187 occurred throughout the sampling season (presence/absence of flowers spanning spring, summer,
188 fall and winter), and as for pollinator body size, we gave each season a weight of 0.25 in order to
189 obtain one final 'season' trait (see Table S4, Appendix 1 of the S.I. for a record of plant traits).

190

191 The selected traits reflect the capacity for plants to adapt to changing environments as well as their
192 availability and attractiveness for pollinators ("pollination syndrome" traits, Fenster *et al.* 2004).

193

194 *Species functional originality and uniqueness*

195

196 For a given community, functional diversity is defined by the matrix comprising the trait attributes of
197 every species. These are used to calculate the coordinates of the species in a multivariate space,
198 where each trait corresponds to an axis (Petchey & Gaston 2006; Laliberté & Legendre 2010). The
199 functional niche (or phenotypic range) of the community depends both on the number of traits (i.e.
200 axes, which were constant in each of our networks) and on the range of trait values. The boundaries
201 of this functional niche are delimited by species with the most extreme trait values, and the centroid
202 corresponds to the 'average' trait values of all species of the community. We calculated two
203 different metrics: functional originality and uniqueness. Functional originality is the distance of a
204 species from that centroid, i.e. how its traits differ from the community trait average (Laliberté &
205 Legendre 2010, Buisson *et al.* 2013) within a given community. Functional uniqueness corresponds
206 to the distance of a species to its nearest neighbour. Species with a similar combination of trait

207 values are located closer together in trait space, and therefore the distance of a species to its
208 nearest neighbour is a good measure of its functional uniqueness (conceptually, it is the opposite of
209 functional redundancy, Walker 1991; Buisson *et al.* 2013). These two measures could at first glance
210 seem related, but in fact, two species can simultaneously be functionally original by having a
211 combination of traits differing from that of the community average, and still not be unique if they
212 are similar to each other in their trait combinations. This distinction would be particularly apparent if
213 species formed clusters in trait space, but these clusters were all distant from the centroid. Figure 1
214 is a 2-dimensional representation of this multivariate trait space, where species are represented by
215 points.

216

217 Species' relative abundances can be used to weight the average trait values when calculating the
218 functional trait space, thereby shifting the position of the centroid towards the most abundant
219 species (the red cross in Figure 1 is closer to larger points corresponding to abundant species). In this
220 quantitative measure of functional originality (Laliberté & Legendre 2010), rarer species displaying
221 different trait attributes contribute more to extending community diversity than do abundant
222 species, because that combination of traits itself is rarer in the community than if it had belonged to
223 an abundant species. In contrast, when only qualitative (species presence/absence) data are used,
224 the centroid is the unweighted average of community trait values, which sets each species on an
225 even ground and prevents abundant species with trait values that deviate from those of other
226 species from appearing less 'original' simply because they comprise a large proportion of the
227 individuals in the community. The coordinates of each species however remain identical whether the
228 community average is weighted or not; hence the measure of functional uniqueness is independent
229 of species' relative abundances and only changes with species presences or absences from a
230 community.

231

232 In our study, we used the weighted measure of originality for the pollinator community, for which
233 we had independent measures of abundances based on the number of insects caught in the traps.
234 This corresponds to a trait-centred approach that quantifies the occurrence of traits in a community
235 and fully endorses the underlying aim of functional diversity, which is to focus on traits rather than
236 species to quantify biodiversity and ecological processes (Mouillot *et al.* 2005; Petchey & Gaston
237 2006). We did not have independent measures of plant abundances (see below), and we therefore
238 used the unweighted measure of plant functional originality, which in comparison, corresponds to a
239 species-centred approach based on the number of species characterised by that trait. As species
240 form the nodes of our networks, they remain an important functional unit of our framework. We
241 provide the unweighted version of the analysis for the pollinator community for comparison in
242 Appendix 2, S.I.

243

244 We used the functional originality and uniqueness of each species as measures of their functional
245 role. With the traits measured for pollinator and plant species across the 21 out of the initial 24
246 sites, we calculated sets of coordinates for each species and the centroid for each site using a
247 Principal Coordinates Analysis (PCoA), as used in other studies of functional diversity (e.g. Buisson *et*
248 *al.* 2013; Mouillot *et al.* 2013b; Gagic *et al.* 2015). Even though species' coordinates were fixed
249 across sites, changes in species composition, as well as in pollinator relative abundances, shifted the
250 position of the centroid in each plant and pollinator community. This yielded different site-specific
251 measures of species originality and uniqueness, thereby defining their functional role within each
252 site. This approach allowed us to provide a measure of relative functional diversity that was scaled
253 and comparable across sites, because we essentially defined a maximal functional diversity (by fixing
254 the multivariate space of all species) against which to compare each local community's functional
255 properties. In this sense, a species can only be 'original' or 'unique' when compared with others in its
256 community, such that originality is not a fixed trait of a species but rather depends on its community
257 context. Therefore, functional originality is only conserved across different communities if a species

258 has a combination of traits so different from all the other species that it is seldom average, or if the
259 composition of other species is conserved. The primary aim of this approach was thus to obtain a
260 measure of a given species' contribution to functional diversity, relative to its community context,
261 rather than determining which particular traits were most important in driving the functional roles
262 of species in the networks (but see Appendix 3 of the S.I. for an evaluation of the most important
263 traits in our communities).

264 Each trait was standardised (mean = 0, variance = 1) for the estimation of functional originality, and
265 non-numerical traits were standardised according to Gower's (1971) standardisation by range prior
266 to their conversion into dissimilarity matrices for the computation of the PCoA. These calculations
267 were realised using version 1.0-12 of the dbFD function from the FD package (Laliberté & Legendre
268 2010; Laliberté & Shipley 2011); R version 3.2.2 (2015-08-14); analysis code can be found in
269 Appendix 4, and is accessible online at: https://github.com/CamilleCoux/Ntw_FD_roles.

270

271 *Interaction networks*

272 Two methods are commonly used to generate plant-pollinator interaction networks; (i) pollinator
273 visitation surveys conducted on focal plants and (ii) pollen transport networks. Visitation surveys
274 generally comprise high proportions of pollinator species linked to a single plant species, thus this
275 approach may overestimate ecological specialization (Bosch *et al.* 2009). In contrast, pollen
276 transport networks often reveal additional plant-pollinator links (that would otherwise have gone
277 undetected) due to the physical presence of pollen on a pollinator. Yet, this approach may
278 underestimate ecological specialization and be influenced by pollinator grooming behaviour and/or
279 body size (Harder 1990). Here, we used the records we obtained of pollinators and the pollen they
280 carried to construct weighted pollination networks where we quantified the interaction links by
281 recording the number of pollinator individuals of species *i* carrying pollen of a given plant species *j*.
282 From a pollinator's perspective, this measures the frequency with which a plant species is used; from

283 a plant's perspective, it is related to pollinator visitation frequency, but does not make any
284 assumptions about the value of carrying more pollen.

285

286 *Network structure description*

287

288 To evaluate the role occupied by each species in each pollination network, we calculated a set of
289 indices that described i) each species' potential range of interaction partners, and ii) any observed
290 relative preference for certain species within its range of potential partners. i) normalised degree
291 (ND) is the sum of interactions per species (normalised within networks to control for variation in
292 network size), and is a classic descriptor of a node's connectedness, which also correlates with many
293 other aspects of network topology (Gómez & Perfectti 2012). ii) Specificity (HS), as measured by
294 Shannon's entropy divided by the number of partners, measures the specialisation of species i on j ,
295 such that the evenness of a species' interactions are quantified within its range of partners. The
296 specificity of species i ranges between 1 for a perfect specialist and 0 for a perfect generalist.
297 Normalised degree is a binary metric; specificity was calculated based on quantitative (i.e. weighted)
298 interactions (calculation for ND : 'specieslevel' function, bipartite package 2.04; for HS: 'getspe'
299 function, package ESM 2.0.3-02, Poisot 2011). Combined, these indices describe each species'
300 connectedness and their relative use of each of their interaction partners. Thus, they describe many
301 crucial aspects of a species' role in a network, and also correlate strongly with other species-level
302 network indices, which are mostly variations on the number of interaction partners (resource range,
303 species strength, effective partners, nestedness rank) or generalism/specialism (node specialisation,
304 proportional generality, proportional similarity; Dormann 2011).

305

306 *Linking species traits with network roles and relative abundances*

307

308 For the pollinator community, we used linear mixed effects models (LMMs) to test whether the
309 network role of a pollinator species, as defined by its normalised degree (ND) or specificity (HS), was
310 predicted by its functional role, defined as its functional originality (i.e., its distance from the
311 centroid in multidimensional niche space) and uniqueness (its distance to its nearest neighbour). For
312 each model with either ND or HS as response variable, we used weighted originality or uniqueness as
313 fixed effects in separate models (see Appendix 5 of S.I. for correlation structures between predictor
314 variables), which yielded a total of 4 different models. A corresponding set of models was generated
315 for the plant community, except that we used the unweighted measure of originality as plant
316 abundances were not measured. We do not explicitly compare pollinators with plants, so this
317 difference could not confound our results for each level.

318

319 In addition to the measures of a species' functional role, we also included pollinator abundance in
320 both pollinator and plant models as fixed covariates to predict network role. Not only is pollinator
321 abundance a measure of sample size, but the abundance of a species is also an important part of its
322 ecology and can determine its functional importance in the community, so it could be one of the
323 mechanisms explaining the correlations between network and functional roles. One of the pollinator
324 species, *Lasioglossum sordidum*, was found to have an unusually high abundance in the first site.
325 After calculating its leverage, we considered it as a statistical outlier (Crawley 2007). We thus set its
326 abundance to 0 and removed it from the analysis such that other species of that community
327 remained unchanged by this removal (see Appendix 2, S.I. for more details, and results of the
328 analysis comprising the outlier). This did not qualitatively affect the results pertaining to originality
329 or uniqueness.

330

331 Although ND and HS metrics are both normalised to control for network size, we included the
332 product of the number of pollinator species by the number of plant species as a measure of network
333 size in our models to control for these potential artefacts. We tested for two-way interactions both

334 between functional role and pollinator abundance (in the pollinator models), and functional role and
335 network size (in all models) to control for any interference of these effects with either species
336 originality or uniqueness. Finally, to control for the non-independence between species from each
337 network, we included site as a random effect in each model. We also tested a final set of models in
338 which unweighted pollinator originality is used (Appendix 2, S.I.).

339

340 Best-fitting models were obtained after testing every possible subset of these models (with main
341 effects and interactions removed, adhering to the principle of marginality) by minimising Akaike's
342 Information Criterion (AIC). In cases where several competing models had a difference of less than 2
343 in AIC scores, which suggested their fit were not statistically different, we applied model averaging
344 techniques ('model.avg' function MuMIn package 1.15.1, (Barton 2015)). The results presented are
345 those of conditional averages.

346 All models were computed using the 'lme' function (nlme package 3.1-122, Pinheiro *et al.* 2014).

347

348

349 RESULTS

350

351 We obtained pollination networks ranging from 4 to 23 species, comprising 3 to 99 realised links,
352 which represents connectance values from 0.22 to 0.87. The mean normalised degree for the
353 pollinator community across all networks was equal to 0.42; that of plants 0.45. For specificity,
354 pollinators showed an average of 0.58 and a higher frequency of highly specific species focussing on
355 one plant. This effect was enhanced among the plants, which had an average specificity of 0.72.

356

357 The relationship between pollinator normalised degree and weighted originality was averaged
358 across 2 best-fitting models and revealed a significant negative effect of originality on a pollinator's
359 normalised degree, indicating that pollinator species with an original combination of traits relative to

360 the community average tended to have fewer interactions (Table 1a, Figure 1). However, a positive
361 interaction effect between abundance and weighted originality revealed that this effect was
362 compensated for in the few most abundant pollinator species with original traits (Figure 2, Table 1a).
363 In addition, we note here that this interaction effect was stronger than the weak, negative main
364 effect of abundance, such that abundant pollinators generally had more interactions than rare ones,
365 as would be expected based on sampling effort.

366

367 The relationship between pollinator specificity and weighted originality was also averaged across the
368 2 best-fitting models, and indicated a strong positive relationship. This suggested that pollinators
369 with unique traits that differed from the rest of the community focused preferentially on a limited
370 subset of their partners (Table 1b). As with normalised degree, there was also a significant
371 interaction effect between originality and abundance that moderated this relationship, as the most
372 abundant pollinators showed less specificity than those that had more average traits (Figure 3, Table
373 1b). However, as in the previous model, this interaction effect was stronger than the main effect of
374 abundance, and therefore abundant pollinators were overall less specific than rare pollinators.

375

376 When we examined functional uniqueness as a fixed effect, we found that the average of the 2 best-
377 fitting models contained a significant positive relationship with normalised degree, indicating that
378 species with unique trait combinations had more interaction partners than species that were
379 functionally similar (Table 1c). Although abundant pollinators had more interaction partners (Table
380 1c), as would be expected from greater sampling effort, there was no significant interaction between
381 abundance and uniqueness.

382

383 Finally, the three averaged best-fitting models considering the effects of pollinator uniqueness,
384 abundance and network size on pollinator specificity revealed a negative correlation between

385 uniqueness and specificity, indicating that pollinators with unique trait combinations interacted
386 more evenly with their plant partners (Table 1d, Figure 4).

387

388 Contrasting with the pollinator community, we did not find any significant relationships between
389 plant normalised degree and species' unweighted originality ($P=0.608$) or uniqueness ($P=0.627$). The
390 only significant effects concerned a negative correlation between normalised degree and network
391 size (coef. = -0.004 , $p=0.010$), simply indicating that plants interacted on average with
392 proportionately fewer pollinators in larger networks. Furthermore, we did not find any significant
393 effect of originality ($P=0.53$) or uniqueness ($P=0.472$) on plant specificity. This suggests that neither
394 the number of interactions with pollinator partners, nor the evenness in a plant's interactions with
395 its pollinators was influenced by how different the traits of a plant species were compared to the
396 community average or to its most functionally similar plant species counterpart.

397

398

399 DISCUSSION

400

401 We have found that the role of a pollinator in the interaction network was correlated with its
402 functional role, as defined by its functional originality and functional uniqueness compared with
403 other pollinator species present in the community. Our finding that species with trait profiles that
404 differed from the community average had fewer interaction partners and/or interacted most
405 frequently with only a subset of these (Table 1a, 1b) is congruent with our hypothesised trade-off
406 between having unique traits to avoid competition but needing to retain interaction partners. This
407 suggests that the functional specialisation of pollinators is reflected by the narrowing down of their
408 interactions to a subset of the plant community, possibly as a means to avoid competition between
409 pollinators for shared plant resources (Vamosi *et al.* 2014).

410

411 This benefit of reduced competition was most evident when we examined a pollinator's trait
412 difference from its functionally most similar counterpart in a given community (i.e. uniqueness). In
413 this case, the most functionally unique pollinators were those with the most interaction partners.
414 This suggests that competition for access to a shared resource is likely to be more intense between
415 two redundant species than between species that are functionally unique, and further satisfies the
416 idea that the number of interactions of a pollinator depends on its functional status in the
417 community. Thus, species' contributions to community functional diversity were correlated with a
418 combination of network metrics that captured both the range of interaction partners and the
419 quantitative preferential focus on particular partners.

420

421 Although functional roles were associated with certain network roles for pollinator species, this
422 relationship did not hold for plants. This absence suggests that original plant traits (particularly with
423 respect to floral structures and resource allocation to flowering) do not necessarily act as barriers to
424 interaction with pollinators, which may be partly due to the conservation of many categorical traits
425 (such as flower symmetry, inflorescence type) at the family level. Furthermore, this depicts a more
426 homogenous distribution of species in the trait space, where differences in plant originality and
427 uniqueness are less important than in the pollinator community, and are rather levelled out by the
428 use of presence/absence data for plant originality values.

429

430 In contrast, pollinator's relative abundances were associated with higher normalised degree and
431 lower specificity, which is to be expected given that abundant species have a larger probability to
432 randomly interact than rare species (Fort *et al.* 2015). Interestingly, there was a recurrent interaction
433 effect between abundance and pollinator originality, whereby the relationships between the latter
434 and normalised degree or specificity were reversed for abundant species. Therefore, the trade-off
435 between originality and interaction partner diversity may not apply to species that are successful
436 enough to be abundant, either because or in spite of their unique trait combinations. This was

437 frequently the case for certain pollinator species, such as *Apis mellifera* or *Lasioglossum sordidum*,
438 which appeared to have succeeded in being functionally original and retaining many interaction
439 partners in most of the communities in which they were recorded (Figure 5).

440

441 Most other species, however, were not as consistent in their network or functional roles across sites
442 (Figure 5; see also Figure S4, Appendix 6, S.I.). This context-dependency in the originality of any given
443 species suggests that the correlation between functional and network roles across sites are not
444 driven simply by the identity of a few key species with extreme traits that interact in a certain way.
445 Similarly, important variations in interaction turnover can also occur through time, and specialisation
446 can be highly variable (Brosi & Briggs 2013), which suggests the importance of context-dependency
447 in network roles. In an evolutionary sense, this suggests that it may be difficult for a species to
448 evolve traits that are novel across its entire spatial and temporal range of community contexts.
449 Furthermore, as our communities were sampled over an anthropogenic gradient (Rader *et al.* 2014),
450 it is likely that the importance of functions fulfilled by specific traits do not occupy the same rank in
451 different sites, which may be reflected here. Moreover, the spatial and temporal scales of differing
452 land uses would likely be sufficient to allow trait-based competitive exclusion of species, but not the
453 evolution of novel traits.

454

455 Our results provide an important step forward in merging the fields of interaction networks with the
456 functional diversity framework (Thompson *et al.* 2012; Poisot *et al.* 2013). Recently, Eklöf *et al.*
457 (2013) found that surprisingly few traits (< 10, similar to the number of traits used here) were
458 needed to predict interactions in different types of ecological networks. This linking of traits with
459 whole-network structure complements work linking network structure to ecosystem functioning
460 (e.g, Peralta *et al.* 2014) and the importance of functional trait diversity for ecosystem functioning
461 and resilience (Mouillot *et al.* 2013b). Our finding that there is a context-dependent relation
462 between network roles and trait originality of species opens up possibilities to predict the functional

463 responses of communities to realistic extinction sequences beyond simple trait-matching
464 mechanisms. For example, recent studies have linked the role of species in interaction networks to
465 their extinction risk, concluding that low interaction degree and rarity characterised species and
466 interactions most prone to extinction (Aizen *et al.* 2012). Mouillot *et al.* (2013) further found that
467 rare species displayed the least redundant functions. Combined with our findings, these results
468 suggest that the order in which species go extinct from networks may generate a more rapid decline
469 in functional diversity than would be expected if species went extinct at random, as has been
470 observed in highly-modified land uses (Rader *et al.* 2014). This merging of network and functional
471 diversity approaches highlights the trade-offs associated with niche differentiation within interacting
472 communities, and links species interactions with the response of ecosystem functioning to a
473 changing environment.

474

475

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644

645 TABLE AND FIGURE LEGENDS

646

647 **Table 1:** Linear Mixed-effects Model partial coefficient estimates from the averaged best-fitting
 648 models predicting either pollinator normalised degree (ND) or specificity (HS) and containing either
 649 weighted pollinator originality (distance to the weighted community centroid) or uniqueness
 650 (distance to the nearest neighbour). Non-significant results are shown only if they were retained in
 651 the model; significant results are shown in bold.

a: Weighted pollinator originality predicting ND

<i>(conditional average)</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>Pr(> z)</i>
(Intercept)	0.8149824	0.1000847	0.1018370	8.003	< 2e-16 ***
pol.abun ¹	-0.0009092	0.0004875	0.0004968	1.830	0.06723 .
size	-0.0038279	0.0026488	0.0027578	1.388	0.16512
w.pol.orig²	-0.4450986	0.1342180	0.1364670	3.262	0.00111 **
pol.abun :	0.0029684	0.0009967	0.0010156	2.923	0.00347 **
w.pol.orig					
size : w.pol.orig	0.0046083	0.0038590	0.0039334	1.172	0.24136

b: Weighted pollinator originality predicting HS

<i>(conditional average)</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>Pr(> z)</i>
(Intercept)	0.3621938	0.1232768	0.1252185	2.892	0.00382 **
pol.abun	0.0004899	0.0008335	0.0008410	0.582	0.56027
w.pol.orig	0.3607632	0.1617809	0.1641896	2.197	0.02800 *
pol.abun : w.pol.orig	-0.0028602	0.0013302	0.0013555	2.110	0.03485 *

c: Pollinator uniqueness predicting ND

<i>(conditional average)</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>Pr(> z)</i>
(Intercept)	0.0365432	0.1893075	0.1918268	0.191	0.8489
pol.abun	0.0004353	0.0002028	0.0002064	2.109	0.0349 *
pol.uniq³	0.493841	0.1953927	0.1983509	2.490	0.0128 *
size	-0.0014741	0.0008303	0.0008866	1.663	0.0964 .

d: Pollinator uniqueness predicting HS

<i>(conditional average)</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>Pr(> z)</i>
(Intercept)	1.0677128	0.2209953	0.2246114	4.754	2e-06 ***
pol.abun	-0.0002991	0.0010091	0.0010245	0.292	0.7703
pol.uniq	-0.5274807	0.2458298	0.2500764	2.109	0.0349 *
size	-0.0012802	0.0013282	0.0014184	0.903	0.3668
pol.abun:pol.uniq	-0.0013629	0.0022979	0.0023415	0.582	0.5605

1: pollinator abundance; 2: pollinator originality; 3: pollinator uniqueness

652

653

654

655 **Figure 1:** Representation of pollinator species from one site, conserving only the two first axes of
656 the PCoA used to calculate functional originality and uniqueness. Darker colours represent
657 pollinators of higher normalised degree. The size of each point corresponds to the square root of
658 pollinator abundances. When these abundances are accounted for, the location of the centroid
659 shifts towards the more abundant species (red cross); when only presence-absence of pollinators are
660 used, the centroid corresponds to the unweighted mean of species' traits, and occupies a central

661 position (black cross). As shown in Table 1a, the distances to the weighted centroid (i.e. pollinator
662 weighted originality) are shorter for species with higher normalised degree, and their nearest
663 neighbours (i.e. pollinator uniqueness) are further away than for species of lower normalised
664 degree. We show in the S.I. (Appendix 2) that pollinator originality in the unweighted centroid is not
665 significantly different for pollinators of higher or lower normalised degree.

666

667 **Figure 2:** Partial residual plots from the pollinator model representing the effect of pollinator
668 functional originality on its number of interactions (normalised degree, ND) for fixed values of
669 pollinator abundances (for presentation, whereas in analyses abundance was treated as a continuous
670 variate). In each panel, points correspond to partial residuals versus raw values of originality;
671 pollinator abundance is fixed to the 10th, 50th and 90th quantiles (1, 21 and 202 respectively), while
672 network size is kept constant at the median (45) to calculate the fitted values (lines). Residuals were
673 taken from a model that included site as a random effect, to show relationships within sites.

674

675 **Figure 3:** Partial residual plots from the pollinator model representing the effect of pollinator
676 functional originality on specificity (HS) for fixed values of pollinator abundances. In each panel,
677 points correspond to partial residuals versus raw values of originality; pollinator abundance is fixed
678 to the same values as in Figure 1 to calculate the fitted values (lines). No other variables were
679 included in the best-fitting models, except for site, which remained as a random effect.

680

681 **Figure 4:** Partial residual plots from the pollinator model representing the effect of pollinator
682 uniqueness (distance to the nearest neighbour) on its number of interactions (normalised degree,
683 ND). Points correspond to raw values of pollinator uniqueness versus their partial residuals. The line
684 represents the fitted values of the model accounting for the random effect of site.

685

686

687 **Figure 5:** Variation in originality (left) and normalised degree (right) across sites according to
688 pollinator identity. Raw values are shown to indicate the frequency of each species occurrences
689 across sites. Species are ordered according to their increasing mean originality in both figures.