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23   **Abstract**

24   **Aim** Understanding the relative contribution of different species interactions in shaping community

25   assembly has been a pivotal aim in community ecology. Biotic interactions are acknowledged to be

26   important at local scales although their signal is assumed to weaken over longer distances. We

27   examine the relationship between positive, neutral, and negative pairwise bird abundance

28   distributions and the phylogenetic and functional distance between these pairs after first controlling

29   for habitat associations.

30   **Location** France and Finland.

31   **Methods** We used results from French and Finnish land bird monitoring programs from which we

32   created three independent data sets (French forests, French farmlands, Finnish forests). Separately

33   for the three data, we fitted linear mixed-effects models for pairwise abundance values across years

34   per point count station to infer the association between all common species pairs while controlling

35   for geographic distribution and habitat associations, and saved pairwise regression coefficients for

36   further analyses. We used a null model approach to infer whether the observed associations (effect

37   sizes) differ from random. Finally, using quantile regression we analyzed the relationships between

38   functional dissimilarity/phylogenetic distance and effect sizes.

39   **Results** Our results show both negative and positive species interactions although negative

40   interactions were twice as common as positive interactions. Closely-related species were more likely

41   to show strong associations, both negative and positive, than more distant species across broad

42   spatial scales. For functional dissimilarity the results varied across data sets.

43   **Main conclusions** Our results emphasize the potential of functional and phylogenetic proximity in

44   generating both negative and positive species associations, which can produce pervasive patterns

45   from local to geographical scales. Future assembly studies should refrain from strict dichotomies

46   such as compensatory dynamics versus environmental forcing and instead consider the possibility of

47   positive interactions.

48   **Introduction**

49   A fundamental and long-standing goal in community ecology has been to understand the complexity

50   of dependencies among species, and thereby the mechanisms by which communities are assembled.

51   Since the 1950's (MacArthur, 1958; Hutchinson, 1959) interspecific competition and niche

52   partitioning have been the focus of explanations for species coexistence and community assembly

53   patterns (Diamond, 1975; Connor & Simberloff, 1983; Cornell, 1985; Cornell & Lawton, 1992).

54   Experimental evidence also shows that competition is undeniably an important factor for community

55   assembly (Connell, 1983; Schoener, 1983; Goldberg *et al.*, 1992; Gurevitch *et al.*, 2000). However, it

56   is not the only one. A growing body of literature demonstrates the importance of facilitative or

57   positive non-trophic interactions (Bertness & Callaway, 1994; Cardinale *et al.*, 2002; Bruno *et al.*,

58   2003). Moreover, interactions often result from combinations of positive, negative and neutral

59   relationships (Seppänen *et al.*, 2007) potentially generating asymmetric interactions (Mönkkönen *et*

60   *al.*, 1999). Indeed, Gross (2008) concluded that the joint effects of different interactions may be the

61   most important factor for community assembly, the key-question being the relative contribution of

62   each interaction.

63   Species interactions may affect species abundances in communities leading to patterns in space,

64   which are independent of habitat characteristics. Negative interactions, such as competition, are

65   predicted to cause segregated distributions (Gotelli *et al.*, 2010). Positive interactions, predicted to

66   result in aggregated distributions, are well known among plants and sessile animals (Bertness &

67   Callaway, 1994; Bruno *et al.*, 2003), but in mobile animals, the prevalence and mechanisms of

68   positive interactions are poorly known. Recent findings about information use in animals imply a

69   likely mechanism. While assessing the best site or resources for reproduction, individuals may use

70   the presence, behavior or success of, not only conspecifics (Danchin *et al.*, 2004), but also competing

71   heterospecific individuals (Seppänen *et al.*, 2007) as cues to decide where to settle. Heterospecific

72   information use and attraction to heterospecifics and potential competitors has been demonstrated

73   from ants to apes (Seppänen *et al.*, 2007), including in breeding site choices of birds (Mönkkönen *et*

74   *al.*, 1990; Thomson *et al.*, 2003; Seppänen & Forsman, 2007; Loukola *et al.*, 2013; Kivelä *et al.*, 2014).

75   Another source producing positive species associations is the benefits of certain keystone species,

76   such as beavers and woodpeckers, which free or create new resources for other species and result in

77   positive species spatial associations (Heikkinen *et al.*, 2007; Belmaker *et al.*, 2015).

78   Although biotic interactions, and particularly competition, have a long history in the study of

79   community patterns their importance is often neglected at broad spatial scales where speciation,

80   extinction and geographic dispersal are expected to be the main driving processes (Gaston &

81   Blackburn, 2000). Recently, Araújo and Rozenfeld (2014) modelled spatial consequences of all types

82   of species interactions (continuum from positive to negative) and concluded that, in particular,

83   positive species interactions can be manifested from local to larger scales. Indeed, a few empirical

84   studies have revealed both aggregated and segregated distribution patterns among ecologically

85   similar species, likely resulting from both competitive and positive interactions, independent of

86   habitat characteristics, at broad spatial scales (Gotelli *et al.*, 2010; Ricklefs, 2012).

87   The strength of species associations may depend on functional and phylogenetic similarity of species

88   involved. Both heterospecific information use and the limiting similarity principle predict that

89   species associations are most intense, but in opposite directions, among functionally similar species

90   (Fig. 1). Heterospecific information use predicts positive associations between species that use

91   similar resources, i.e. are functionally similar, because the information value decreases with

92   increasing ecological distance (Seppänen *et al.*, 2007), while limiting similarity predicts mutual

93   avoidance between similar species due to costs of competition (MacArthur & Levins, 1967).

94   However, it is likely that both competition and heterospecific information use are context

95   dependent and the net outcome of an association between similar species depends on the costs of

96   competition and benefits of information use (Mönkkönen *et al.*, 1999; Seppänen *et al.*, 2007).

97   Therefore, associations between functionally similar species may be strong, either positive or

98   negative and the strength of the association may decrease with decreased species similarity. The

99   likelihood of finding such a relationship depends, however, on the traits considered (Trisos *et al.*,

100   2014). Using phylogenetic information can be a relevant approach to avoid a priori trait selection.

101   Similar patterns are indeed also likely for phylogenetic distance providing that trait conservatism

102   renders closely related species also ecologically more similar (Mouquet *et al.*, 2012). In this case,

103   phylogenetically closely related species should also show both the strongest positive and negative

104   associations, and phylogenetically distant species should show neutral associations. So far, however,

105   empirical tests of this hypothesis have yielded mixed results (Violle *et al.*, 2011; Godoy *et al.*, 2014).

106   Earlier research on general mechanisms of community assembly commonly separated the effects of

107   competitive interactions from environmental forcing causing positive covariation among species

108   abundances and provided support for environmental variation rather than competition driving the

109   variation in species abundances (Houlahan *et al.*, 2007; Mutshinda *et al.*, 2009; Ricklefs, 2012).

110   However, some of the positive covariation may be due to positive interactions between species,

111   over and above habitat filtering and productivity. Moreover, even if environmental forcing generally

112   prevails over competitive interactions, negative interactions may not be trivial. Thus both negative

113   and positive interactions can leave a signature on community assembly that affects both historical

114   and ecological distribution patterns. In this article, we study (i) whether there are positive or

115   negative associations among bird species in local communities, independently of habitat

116   characteristics, and consequent community patterns at large geographical scales, and (ii) whether

117   these positive or negative associations are related to functional similarity and/or phylogenetic

118   distance of the species. We predict that functional dissimilarity/phylogenetic distance and the

119   strength of the associations form a 'funnel plot' where the strongest associations, either positive or

120   negative, are between functionally similar or phylogenetically close species whereas the associations

121   grow weaker with increasing dissimilarity/distance (Fig. 1). We use comprehensive bird census data

122   from French forests and farmlands as well as Finnish forests, and analyze the three datasets

123   separately to test for consistency of results across habitat types and geographic areas. Using these

124   three datasets separately offers a possibility to test the same question on the same group of species

125   originating from quite different kinds of landscapes and climatic conditions. Consistent patterns

126   would imply generality and call for further scrutiny of underlying mechanisms.

127

128   **Material and methods**

129   *Data*

130   Data were extracted from two independent datasets from France and Finland. They are very well

131   suited for the study because together they cover a wide extent (with a relatively small grain size) and

132   consequently also a wide spectrum of climatic and environmental conditions, and they are both of

133   high quality gathered over multiple years and multiple sites. The French Breeding Bird Survey is a

134   large-scale, multi-year and multi-plot monitoring program of the French avifauna. The program

135   followed a standardized protocol from 2001 to 2012 (Jiguet *et al.*, 2012) where 2x2 km sampling

136   plots are randomly selected within 10-km radius areas, which ensures a representative sampling of

137   existing habitats. In each plot, 10 point count stations were evenly distributed. At each station, the

138   observer recorded all birds heard and seen during 5 minutes, in two sessions during the breeding

139   season. For each species in each point count station and each year, the maximum number of

140   individuals recorded during the two sessions is retained as a proxy for the local abundance of that

141   species in that plot and year.

142   In Finland, point counts have been conducted as part of the national common bird monitoring

143   scheme between 1984 and 2011 (Laaksonen & Lehikoinen, 2013). Each census route included 20

144   point count stations located in the habitat that is uniform within 50-m radius of the station. The

145   habitat of each point was classified into 17 different habitat categories. Stations within a route were

146   at least 250 m apart in forested habitats and 350 m apart in open habitats to avoid pseudo-

147   replication. Due to very short and synchronized breeding season of boreal birds, a route was

148   censused only once per season. At each station, an observer counted, for 5 mins, all the observed

149   land birds during late spring – early summer (May 20 – June 20 in south-central Finland, May 30 -

150   June 30 in northern Finland). In both monitoring projects, surveys were conducted early in the

151   morning (typically between sunrise and 10 am), which is when the birds were most active, and only

152   on days with good weather conditions (no rain or heavy wind).

153

154   *Data handling*

155   Original French data included plots sampled for at least two years, i.e. 1,914 plots and 19,140 point

156   count stations. Finnish data included 286 routes and 5,760 stations. From these data we first created

157   three independent data sets by selecting the point count stations situated in forests or in farmlands

158   only (French farmlands, French forests, Finnish forests; Finnish farmland data were too small for the

159   analysis). The aim was to remove most of the variation in bird abundances resulting from habitat

160   structures (habitat filtering). Indeed, one of the obvious sources of species segregation or

161   aggregation is the main habitat type in which a given plot is monitored. A negative association

162   between farmland birds and forest birds would be interpreted as a signal of competition although

163   those two groups simply do not co-occur. The three datasets contain about 2,900–9,000 point count

164   stations but a rather narrow range of habitats (Table 1). We analyzed the three datasets separately

165   to test for the consistency of results across habitat types and geographic areas.

166   We excluded all waterbirds and birds of prey since point count census at the local point count

167   station level provides reliable information on species abundances only for land birds with relatively

168   small home ranges. We also excluded very rare species that were present in less than 2% of the

169   point count stations. After filtering, our data included 43,000-206,000 observations for 76-83 species

170   (Table 1), for which we calculated average abundance values across years per point count station.

171   The same species occurred in multiple data sets: the number of shared species was 67 in French

172   forest and farmland data, 51 in French and Finnish forest data, and 45 in French farmland and

173   Finnish forest data.

174   The matrix of pairwise functional distances was produced from 22 functional traits (Appendix S1 in

175   Supporting Information) using methods described in Devictor *et al.* (2010). These traits encompassed

176   life-history traits and feeding habits (Petchey *et al.*, 2007) and were identified as being important in

177   determining the response of bird species to environmental change and in determining the

178   contribution of bird species to ecosystem functions (Sekercioglu, 2006). From these traits, we

179   calculated the Gower distance to represent pairwise trait distances estimated from the species trait

180   matrix (Legendre & Legendre, 1998). As we aim to remove habitat-induced distances between

181   species we calculated a separate matrix for each set of species (French farmlands, French forests,

182   Finnish forests). Gower distance accounts for both continuous and qualitative traits (Mouchet et al.,

183   2008) and were measured with the function 'daisy' of the R package 'cluster' (Maechler *et al.*, 2016).

184   All pairwise distances were standardized by dividing original distance values with the range of

185   values.

186   We extracted pair-wise phylogenetic distances directly from a dated molecular phylogenetic tree

187   assembled by Thuiller *et al.* (2011) and then used ultrametric distances from this tree representing

188   relative phylogenetic distances among species using the function 'cl_utrametric in the R package

189   'clue' (Hornik, 2005). Phylogenetic information was not available for 7 species in Finnish forest

190   dataset, and thus we performed analyses of phylogenetic distance on 69 species.

191   *Statistical analyses*

192   We adopt the pairwise approach to analyze species effects on each other's abundance, i.e., consider

193   a species pair as the fundamental unit in interactions. The procedure has advantages over the matrix

194   method i.e. where a target of interest is the whole community i.e. presence-absence matrix that has

195   been used since the beginning of the studies of co-occurrence patterns (Diamond, 1975; Connor *et*

196   *al.*, 2013). Most communities contain many potential species pairs each of which may exhibit

197   positive, negative or random associations. Therefore, single metrics that summarizes an entire

198   assemblage can mask the type and strength of pairwise interactions and it is therefore instructive to

199   analyze individual pairs of species (Boulangeat *et al.*, 2012; Veech, 2013; Blois *et al.*, 2014). We

200   relate species abundances against each other to reveal signals of positive, neutral and negative

201   associations, after controlling for variation in bird abundances due to geographic distribution and

202   corollary climatic variation as well as finer habitat associations, beyond the main habitat type (i.e.

203   forest and farmland). We fitted a linear mixed-effects model for each species pair to infer the

204   association between species$_i$ and species$_j$ while controlling for geographic distribution and finer

205   habitat associations within the main habitat type (forest or farmland; see Appendix S2 for a detailed

206   flowchart of the analyses). First, the biogeographic zone was entered into the model as a random

207   factor to control for large scale variation in climatic conditions. In each dataset, we assigned the

208   point count stations to biogeographical zones according to information from European

209   Environmental Agency (2015) for France and Järvinen & Väisänen (1980) for Finland (see Table 1 for

210   zones). Second, we included site (a dummy variable for a point count plot or route) nested within

211   the biogeographic zone, to control for small scale variation in environmental conditions among plots

212   or routes. We then added a second-order trend surface ($X + Y + X^2 + Y^2 + XY$; X = longitude and Y =

213   latitude) to control for the geographic (e.g. temperature and precipitation related) variation in

214   species abundances. Although a minimum of third order trend surface is generally recommended

215   (Legendre & Legendre, 1998) random effects (zone and site) already control for spatial

216   autocorrelation at the scale of biogeographic zone and at very small spatial scales. Moreover, the

217   models with a third-order trend surface tended to be over-parameterized leading to model

218   convergence problems. Including second-order trend surfaces ensures that our pairwise regression

219   analysis operates on local scale variation in species abundances. Fourth, we entered habitat type of

220   the point count station (Table 1) to further control for species habitat preferences. Because we

221   analyzed forest and farmland data separately (i.e. narrowed down the variation in habitat structures

222   prior to analysis) and entered farmland type (ploughed meadow, unploughed meadow, mixed

223   farmland, open field, permanent crop) or forest type (e.g. deciduous, coniferous or mixed forests in

224   France; spuce, pine, deciduous or mixed forests in Finland) as a random factor, our analysis

225   effectively controls for fine scale habitat filtering. Fifth, we entered community size (summed

226   abundances of all species, excluding $species_i$ and $species_j$) as a fixed effect controlling for the

227   possibility that species abundances may covary with total community size because of independent

228   responses to productivity. Finally, we added the abundance of $species_j$ as a fixed effect. We log-

229   transformed ($\log(n+1)$) all abundances prior to analyses and saved pairwise regression coefficients

230   for further analyses. Estimating pairwise associations using Poisson distribution yielded too many

231   convergence problems and was not feasible due to a very high number of models. Note that using

232   Poisson distribution should not change the general conclusions derived from our framework based

233   on log-transformed abundances (Ives, 2015).

234   To infer whether the observed associations differ from what could be observed on the basis of

235   randomly distributed individuals we used a null model approach. First, we defined a regional species

236   pool as all observed species and their abundances, separately for each habitat in each

237   biogeographical zone. Next, we randomly sampled the observed number of individuals from the

238   regional species pool while preserving the abundance of each species and observed total abundance

239   in each point count station. In other words, we kept the size of the regional habitat-specific species

240   pools and the size of the local communities fixed, and within these constraints we randomized the

241   composition of local communities at point count stations (see Crist *et al.*, 2003, for a similar

242   approach). This type of randomization makes a plausible assumption that species habitat

243   associations, their relative abundances in regional pools and local community size are real ecological

244   properties worth retaining while relaxing deterministic pairwise associations. Then we fitted the

245   linear mixed-effect model described above for the randomized datasets. We repeated this

246   procedure 1000 times and calculated the standardized effect size as the difference between

247   observed pairwise regression coefficient and mean expected coefficient, divided by the standard

248   deviation. Thus, the effect size measures the direction (positive or negative) and strength of species

249   interactions in the datasets, independent from what one expects by chance and sampling artefacts.

250　Because the effect sizes within species pairs (effect of species$_i$ on species$_j$, and *vice versa*) were

251　strongly correlated (Spearman's rho = 0.943, *n* = 3,403, *P* < 0.001; Spearman's rho = 0.956, *n* = 2,926,

252　*P* < 0.001; Spearman's rho = 0.960, *n* = 2,850, *P* < 0.001; in French farmlands, French forest, and

253　Finnish forests, respectively) we used the mean of the effect sizes of each species pair (ES$_{mean}$) as an

254　observation unit in the analysis. Given that these observations are not independent (every species is

255　represented in multiple species pairs) we used bootstrap method to calculate standard errors

256　(Koenker, 2013).

257　We considered pairwise species effect sizes "strong" when absolute effect size values were >2 (i.e.

258　observed association deviated more than two standard deviations from the expected) and "weak"

259　when effect size values were <2. We predicted a relationship between the magnitude of the effect

260　sizes, both positive and negative, and functional dissimilarity/phylogenetic distance. The magnitude

261　should decrease with increasing dissimilarity/distance. To test this, we used quantile regression

262　(Cade & Noon, 2003) for all quantiles from 1 to 99% quantiles (τ ranges from 0.01 to 0.99) at

263　intervals of 1%. We predicted that the regression between effect size and dissimilarity/distance

264　would result in a negative coefficient in the upper (>50%) quantiles (reflecting smaller positive effect

265　sizes with increasing dissimilarity/distance) and a positive coefficient in the lower (<50%) quantiles

266　(reflecting smaller negative effect sizes with increasing dissimilarity/distance). If these predictions

267　are verified, the shape of the relationship should be a 'funnel plot' with higher numbers of positive

268　and negative associations for lower values of functional dissimilarity or phylogenetic distance (Fig.

269　1). To infer whether this is truly the case we plotted the coefficient of each of the quantile regression

270　as a function of the quantile (τ) in question, and expect to see a negative relationship. As we do not

271　have a specific hypothesis about the overall relationship in the data we do not concentrate on the

272　general tendency, i.e. 50% quantile, but on upper vs lower quantiles. We performed linear mixed-

273　effect models with package 'lme4' (Bates *et al.*, 2014) and quantile regression with 'quantreg'

274　(Koenker, 2013) in R Version 3.0.3 (R Development Core Team, 2014), and the iterations for the null

275　model approach with Taito supercluster provided by CSC - IT Center for Science Ltd

276   (https://research.csc.fi/research-home). The R script for calculating the effect sizes is provided as

277   Appendix S3. Other analyses we performed with IBM SPSS Statistics 22.0 (IBM, Armonk, New York,

278   USA).

279

280   **Results**

281   We observed both positive and negative regression coefficients among species pairs tested in all

282   three datasets. The means of the observed coefficients were positive (0.02) and the distribution of

283   coefficients were highly similar in the three datasets (see Appendix S4). Likewise, the effect sizes

284   (ES_{mean}) were centered close to zero. A large proportion of pairwise species effect sizes can be

285   considered strong as absolute effect size values larger than two (i.e. observed association deviated

286   more than two standard deviations from the expected) constituted 83, 63 and 41% of all pairwise

287   effect sizes in French farmland (n=6,806), French forest (n=5,852) and Finnish forest dataset

288   (n=5,700), respectively. In all three datasets, strong negative associations were approximately twice

289   as common as strong positive associations: 57 vs 26% in French farmland, 39 vs 23% in French forest,

290   and 27 vs 15% in Finnish forest data. Thus, birds are not distributed randomly with respect to each

291   other in local communities, when controlling for habitat filtering and productivity, and we found

292   asymmetry between positive and negative associations with prevalence of the latter.

293   The relationship between functional dissimilarity and the mean of the effect sizes for species pairs

294   (ES_{mean}) showed differences among the three datasets. In French farmlands there was no

295   relationship in the lower quantiles but a negative relationship in the upper quantiles whereas in

296   French forests there was only a trend in both lower and upper quantiles (Fig. 2a,b). By contrast, in

297   Finnish forests there was a positive relationship in the lower quantiles and a negative relationship in

298   the upper quantiles (Fig. 2c). Thus, in French farmlands the level of aggregation increased with

299   decreasing functional similarity, in Finnish forests both the level of segregation and aggregations

300   increased with decreasing functional similarity, while in French forests there were no relationships.

301   Phylogenetic distance and ES_{mean} showed significant relationships in both ends of the quantile

302   spectrum in French farmlands and forests (Fig. 3a,b). Thus, both aggregated and segregated

303   distributions of species abundances increased as a function of decreasing phylogenetic distance. In

304   Finnish forests, there was a positive relationship between phylogenetic distance and ES_{mean} in the

305   lower quantiles but no relationship in the upper quantiles (Fig. 3c).

306

307   **Discussion**

308   Bird species showed both spatial aggregation and segregation in their abundances, independently of

309   habitat structures. Even though overall mean effect sizes of species associations in the local

310   communities were centered on zero, we found the majority of species were relatively strongly

311   associated with each other. This highlights the importance of both negative and positive biotic

312   interactions in affecting community assembly. Our study using natural communities across a wide

313   geographic area yielded results that are consistent with the results of the local manipulative

314   experiments: negative associations are common but also positive associations frequently occur

315   (Bertness & Callaway, 1994; Gurevitch *et al.*, 2000; Forsman *et al.*, 2002; Martorell & Freckleton,

316   2014; but see Gotelli & Ulrich, 2010). Moreover, our results suggest that high functional and

317   phylogenetic similarities can be important determinants increasing the probability of both negative

318   and positive associations. Also, we found that in bird communities strong negative associations were

319   twice as common as strong positive associations. This is in line with empirical results of Gotelli *et al.*

320   (2010) who showed strong predominance of spatially segregated over aggregated distributions

321   within foraging and congeneric guilds in Danish avifauna.

322   Species abundance is affected by a multitude of factors, such as habitat, productivity and

323   geographical position. Our pairwise approach controlled for the effects of habitat, first, by restricting

324   the analysis only to a limited set of habitat classes (Table 1) and, second, by entering habitat class as

325   a factor in the model. Moreover, we entered biogeographic zone, sampling site, and second order

326   trend surface in abundances to control for the effects of geographic factors such as species

327   geographic distributions and climate related variation. Finally, we controlled for the community size,

328   i.e. species independent responses to productivity. Yet our analysis revealed strong signals of

329   positive abundance associations. Thus, species abundances were probably affected also by positive

330   biotic interactions between species, and these interactions were strong enough to show up as

331   aggregated distributions. The recurrent finding that species abundances in natural communities tend

332   to covary positively rather than negatively has commonly been attributed to environmental forcing

333   (Houlahan *et al.*, 2007; Mutshinda *et al.*, 2009; Ricklefs, 2012). Our results suggest that a proportion

334   of this positive covariation is likely due to positive interactions. Therefore, dominance of positive

335   covariation over compensatory dynamics in community dynamics does not necessarily imply low

336   frequency of species interactions. Future studies testing assembly theories should therefore refrain

337   from using strictly dichotomist approaches such as compensatory dynamics versus environmental

338   forcing, but also consider the possibility of positive interactions and underlying processes such as

339   conspecific or heterospecific information use.

340   In all three datasets, closer species pairs with respect to phylogenetic distances are those showing

341   stronger segregation in their abundances. Neutral associations, however, were found throughout

342   the phylogenetic distance spectrum. Thus, a part of phylogenetically close bird species indeed seem

343   to compete more strongly than distantly related species which plausibly leads to avoidance of such

344   species in habitat selection. In Finnish forest bird assemblages, but not in the two French datasets,

345   the signal of spatial segregation increased also with increasing functional similarity. In concordance

346   with the prediction of heterospecific information use (Seppänen *et al.*, 2007), the signal of spatial

347   aggregations was stronger for pairs consisting of similar species and grew weaker with increasing

348   dissimilarity. However, whether the pattern was detected for phylogenetic distance, functional

349   dissimilarity or both showed variation among datasets: in French forests aggregation was related to

350   phylogenetic distance, in Finnish forests to functional dissimilarity, and in French farmlands to both.

351   In summary, segregated abundances were related to phylogenetic distance in all of the three cases,

352   to functional dissimilarity in only one, whereas aggregated abundances were related both to

353   phylogenetic distance and functional dissimilarity in two cases. Thus, the phylogenetic signal in

354   segregated abundances was stronger than that of functional (ecological) similarity. This suggests that

355   the traits we used for functional dissimilarity might not be those that actually affect species

356   competitive environment but more relevant in terms of heterospecific information use, whereas

357   phylogenetic signal encompass traits of direct relevance in both respects. This result also raises the

358   issue of trait selection in trait-based analysis. It is likely that a part of the results is dependent on the

359   particular combination of trait used. A finer examination of pairwise associations i.e. whether

360   segregated versus aggregated associations are influenced by a specific combination of traits,

361   whether there is any specific trait enhancing coexistence or whether aggregations are

362   phylogenetically clustered, would be an interesting extension of our approach.

363   Another reason why species pairs consisting of phylogenetically closely related species showed

364   strong segregation in their abundances could result from allopatric speciation. Phylogenetic

365   overdispersion, which is often attributed to negative biotic interactions, may instead be consistent

366   with a neutral model of allopatric speciation (Pigot & Etienne, 2015). If allospecies rarely co-occurred

367   in the bird assemblages we studied, and differ somewhat in their functional traits, one could see a

368   pattern where phylogenetic distance is more directly driving negative abundance associations than

369   functional similarity. Allopatric speciation does not, however, provide an explanation for

370   phylogenetic and functional patterning of positive abundance associations. It is possible, and even

371   probable, that for some species pairs the costs of competition and benefits of information use adds

372   up to show as a neutral association. Hence, it is important to bear in mind that small effect sizes in

373   our study do not necessarily indicate no or weak interactions.

374   Our approach where we simultaneously addressed both negative and positive interactions, and

375   provided support for both, may help to understand why earlier work has found mixed results

376   concerning the role of phylogenetic and ecological distance in species interactions (Violle *et al.*,

377   2011; Godoy *et al.*, 2014). Our results support a common expectation in the community assembly

378   literature that due to competition, close relatives and functionally similar species should show

379   segregated patterns in abundance (Webb *et al.*, 2002). But more interestingly, our results suggest

380   that close relatives and functionally similar species also may also aggregate, which is reflected as

381   positive associations among species' abundances. The likely mechanism is the use of social

382   information (Seppänen *et al.*, 2007) and/or facilitative interactions among species (Bruno *et al.*,

383   2003). It is evident that both clustering and overdispersion of co-occurring species within

384   communities may occur simultaneously. Our results challenge the implicit assumption pertinent to

385   community phylogenetics that assembly through positive associations decreases with increasing

386   assembly by competition (see Gerhold *et al.*, 2015). Thus, the relative balance of positive and

387   negative interactions in community assembly cannot be quantified by a single parameter of

388   phylogenetic (or functional) dispersion.

389   We acknowledge the fact that only experimental set-ups can truly prove the strength and the sign of

390   the interaction between a species pair. It is clear that the data used here do not capture all the small

391   scale habitat characteristics which may affect species aggregation and segregation patterns. Indeed,

392   a detailed data of environmental conditions might attenuate the coefficients we found. On the other

393   hand, it has been shown that even when modeling forest bird species distributions with a very

394   detailed forest structure data the density of a bird species remains a significant predictor of the

395   density of a close relative (Kosicki *et al.*, 2015).

396   Social information use and subsequent aggregated distribution in local communities result in

397   variation in local species diversity at a given site that deviates from diversity predicted by

398   environmental factors only, creating both hot and cold spots of species diversity in the landscape

399   (Seppänen *et al.*, 2007). Interspecific competition resulting in segregated distribution may also

400   create similar deviations from predictions. Our results suggest that such diversity anomalies should

401   carry phylogenetic/functional signal. Species´ interactions may render a proportion of suitable

402   habitat patches unoccupied by the species also because dispersal among patches in the landscape

403   may be affected by the presence of close relatives and/or functionally similar species. Consequently,

404   colonization and extinction in fragmented landscapes is no longer a sole function of landscape

405   patterns and species dispersal abilities but hinges also on other species' ability to persist in

406   fragmented landscapes. Given that interspecific social information use is widespread (Seppänen *et*

407   *al.*, 2007), from the point of view of species' conservation, it is important to keep in mind that the

408   effect of close relatives and ecologically similar species may also be positive.

409   Predicting species responses to various global changes has become crucial due to the ongoing

410   biodiversity crisis. Our results accompany earlier literature (e.g. Araújo & Rozenfeld, 2014)

411   suggesting that a failure to incorporate species interactions may account for the mixed results of

412   earlier species distribution modeling efforts that ignore interactions.

413

423

424   **Supporting Information**

425   Additional supporting information may be found in the online version of this article at the

426   publisher's web-site.

427   **Appendix S1** Functional traits

428   **Appendix S2** Detailed flowchart of the analyses

429   **Appendix S3** R script for calculating the effect sizes

430   **Appendix S4** Frequency distributions for observed coefficients, mean expected coefficients and effect sizes

431

432

433   **Biosketch**

434   Mikko Mönkkönen is a professor in applied ecology at the University of Jyväskylä, Finland. His main

435   research interests are community and landscape ecology, conservation biology and environmental

436   economics.

437

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590

591   Table 1 Biogeographic zones, habitat types, and number of point count stations, observations and species

592   included in each of the three datasets (French farmlands, French forests, Finnish forests)

Data set	Biogeographic zone	Habitat type	# point count stations	# observations	# species
French farmlands	Alpine	Ploughed meadow	60	1,291	74
		Unploughed meadow	70	1,372	75
		Mixed farmland	91	1,963	76
		Open field	122	2,485	76
		Permanent crop	380	7,358	78
	Atlantic	Ploughed meadow	496	11,930	81
		Unploughed meadow	595	14,666	82
		Mixed farmland	1,168	28,456	82
		Open field	1,759	34,626	82
		Permanent crop	259	6,306	80
	Continental	Ploughed meadow	506	12,228	82
		Unploughed meadow	1,306	33,795	82
		Mixed farmland	859	21,436	82
		Open field	976	19,763	81
		Permanent crop	128	3,125	79
	Mediterranean	Ploughed meadow	37	726	67
		Unploughed meadow	134	2,637	73
		Mixed farmland	49	1,095	70
		Open field	6	177	55
		Permanent crop	25	538	60
	Total		**9,026**	**205,973**	**83**
French forests	Alpine	Deciduous woodland	94	1,543	69
		Coniferous woodland	113	1,806	61
		Mixed woodland	161	2,952	67
	Atlantic	Deciduous woodland	1,136	25,670	77
		Coniferous woodland	216	4,537	74
		Mixed woodland	274	6,715	74
	Continental	Deciduous woodland	1,519	33,458	75
		Coniferous woodland	311	6,144	76
		Mixed woodland	440	9,227	75
	Mediterranean	Deciduous woodland	181	3,054	71
		Coniferous woodland	138	2,490	71
		Mixed woodland	187	3,282	75
	Total		**4,770**	**100,878**	**77**
Finnish forests	Hemi- and south boreal	Spruce forest	592	9,288	76
		Pine forest	563	9,322	76
		Deciduous forest	320	5,325	75
		Mixed forest	900	15,289	75
	Mid-boreal	Spruce forest	51	737	56
		Pine forest	134	1,887	68
		Deciduous forest	30	437	55
		Mixed forest	90	1,262	64

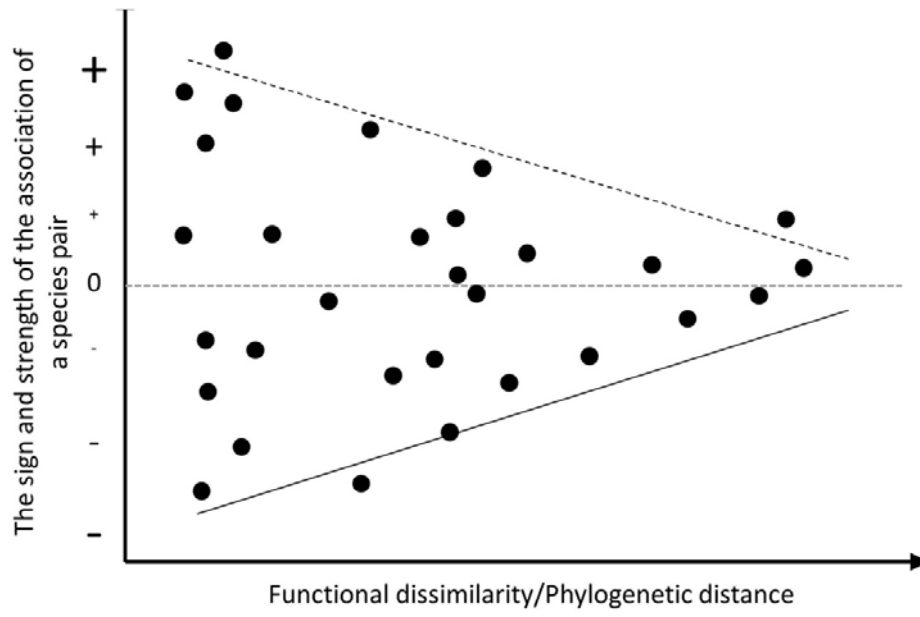|				
North boreal	Spruce forest	30	427	48
	Pine forest	109	1,081	50
	Deciduous forest	21	328	43
	Mixed forest	77	936	53
Total		**2,917**	**46,319**	**76**

593

594   **Figure captions**

595   **Figure 1** Schematic figure of the relationship between increasing functional dissimilarity/phylogenetic distance

596   (x-axis), and the sign [positive (+), neutral (0), negative (-)] and the strength (increases with increasing symbol

597   size) of the association of a species pair (y-axis). Every black dot represents an imaginary pair of species. Both

598   heterospecific information use (black dashed line) and the limiting similarity principle (solid line)

599   predict that species associations are most intense among functionally and phylogenetically similar

600   species, but in opposite directions. Heterospecific information use predicts positive association

601   between functionally/phylogenetically similar species. Since the information value decreases with

602   increasing functional similarity/phylogenetic distance so does the strength of the association. The

603   limiting similarity predicts functionally/phylogenetically similar species to have negative association

604   whereas functional dissimilar/phylogenetically distant species show neutral associations. The net

605   outcome of an association between similar species depends on the costs of competition and benefits

606   of information use and may thus result in a neutral association, and altogether they form a 'funnel

607   plot'.

608   **Figure 2** Left-hand panels show the relationship between increasing functional dissimilarity and the strength

609   and the sign of an association of the abundances of each species pair in French farmlands (a), French forests

610   (b), and Finnish forests (c). The strength and the sign of an association of the abundances is measured as the

611   mean of the standardized effect sizes (the difference between observed pairwise regression

612   coefficient and mean expected coefficient, divided by the standard deviation) between a species pair

613   (see text for further information). In a case of statistically significant relationship the regression line

614   for the quantile regressions in lower ($\tau = 0.05$) and/or upper ($\tau = 0.95$) quantiles are shown. Right-

615   hand panels show the relationship between all quantiles (τ) at intervals of 0.01 and the coefficient

616   from the quantile regressions (standard errors are shown in grey). Positive coefficients denote a

617   positive relationship in a given quantile between increasing functional dissimilarity and the strength

618   of an association of the abundances whereas negative coefficients denote a negative relationship.
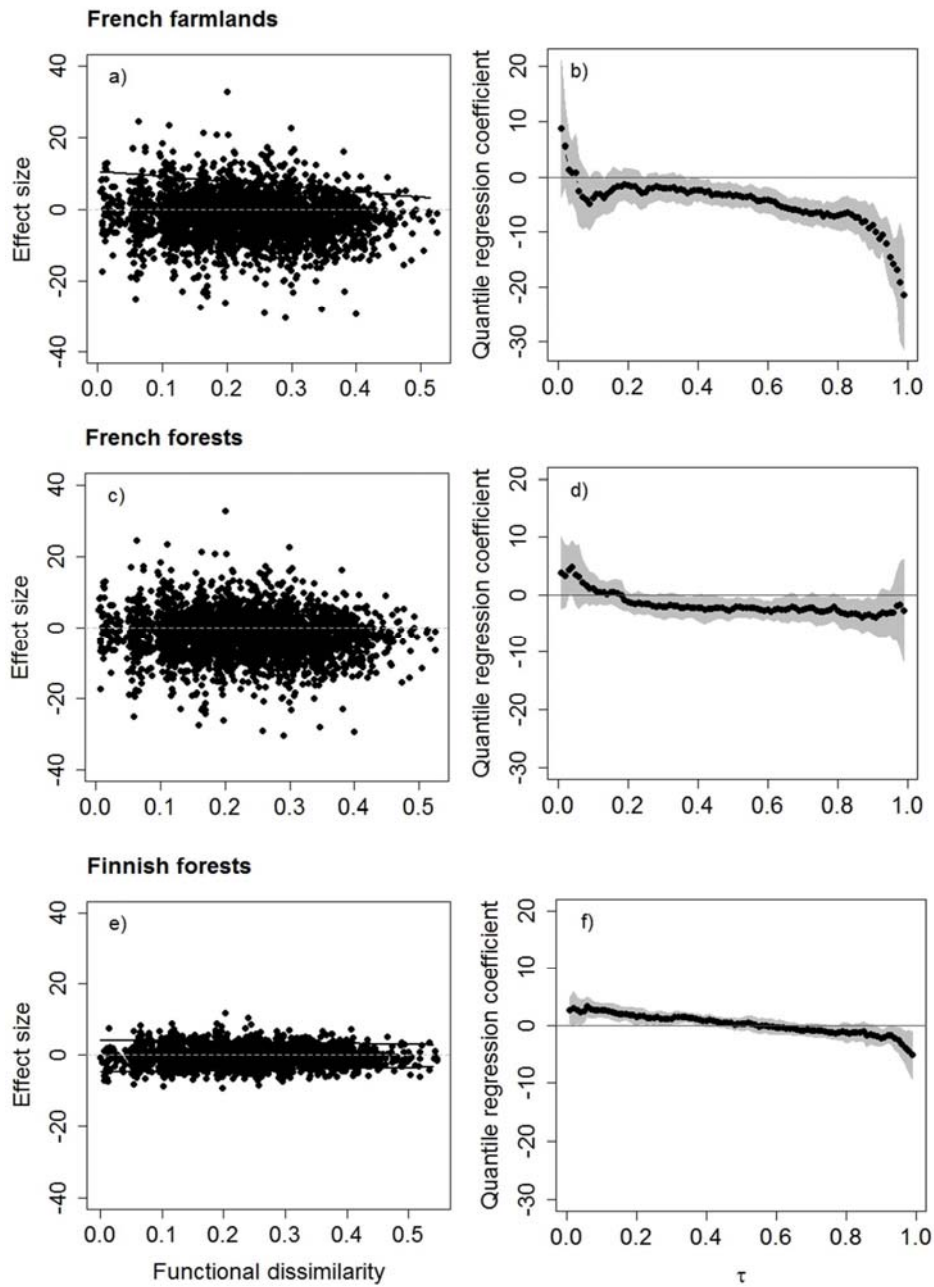
619   **Figure 3** Left-hand panels show the relationship between increasing relative phylogenetic distance and the

620   strength and the sign of an association of the abundances of a species pair in French farmlands (a), French

621   forests (b), and Finnish forests (c). The strength and the sign of an association of the abundances is measured

622   as the mean of the standardized effect sizes (the difference between observed pairwise regression

623   coefficient and mean expected coefficient, divided by the standard deviation) between a species pair

624   (see text for further information). In a case of statistically significant relationship the regression line

625   for the quantile regressions in lower ($\tau = 0.05$) and/or upper ($\tau = 0.95$) quantiles are shown. Right-

626   hand panels show the relationship between all quantiles (τ) at intervals of 0.01 and the coefficient

627   from the quantile regressions (standard errors are shown in grey). Positive coefficients denote a

628   positive relationship in a given quantile between increasing relative phylogenetic distance and the

629   strength of an association of the abundances whereas negative coefficients denote a negative
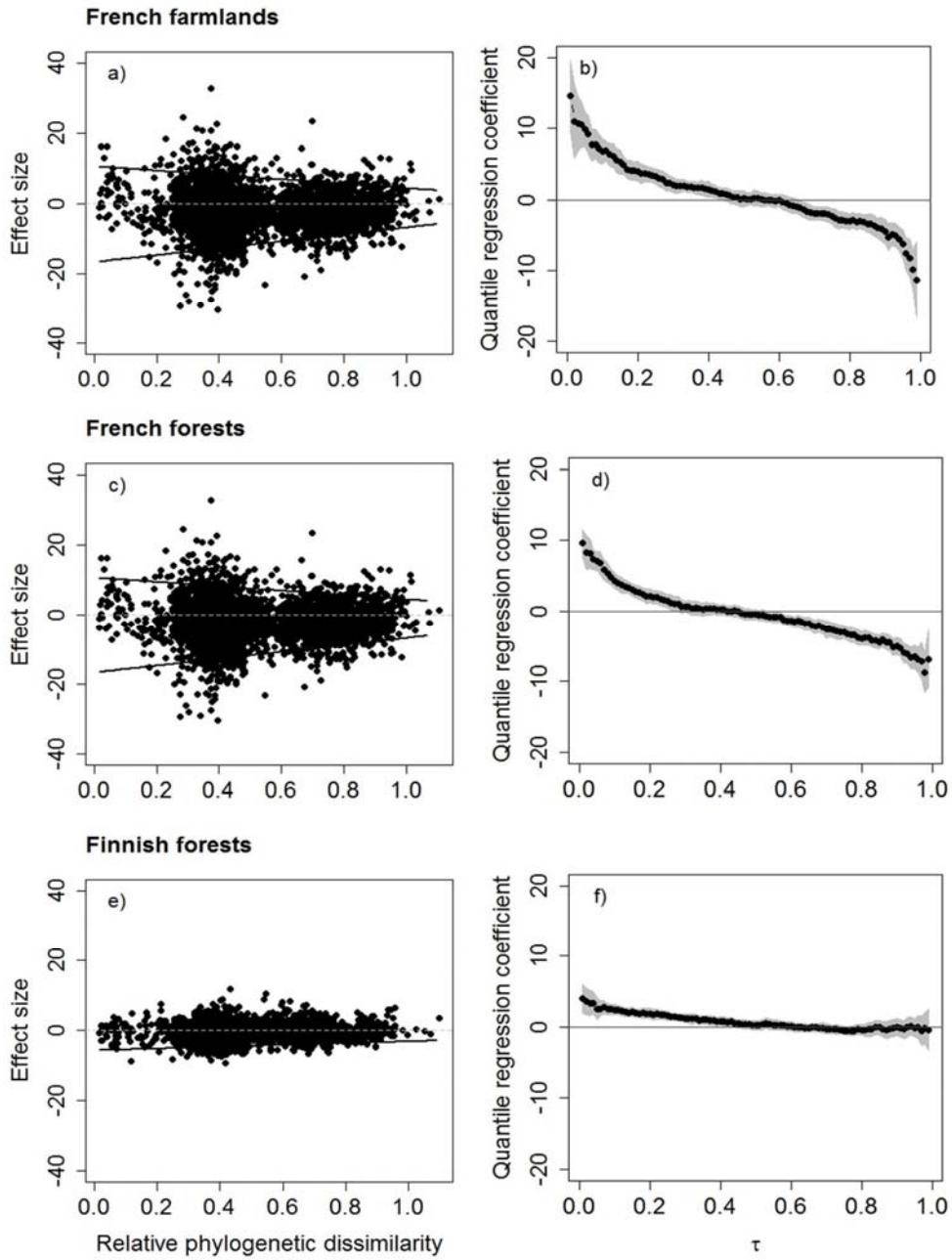
630   relationship.

631

Fig.1

632

633

French farmlands

French forests

Finnish forests

634

635   Fig. 2

French farmlands
a)
b)

French forests
c)
d)

Finnish forests
e)
f)

Relative phylogenetic dissimilarity

636

637

638   Fig. 3