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1 Linking species interactions with phylogenetic and functional distance in European bird assemblages
2 at broad spatial scales

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4

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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 al.*,
60 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 al.*, 1990; Thomson *et al.*, 2003; Seppänen & Forsman, 2007; Loukola *et al.*, 2013; Kivelä *et al.*, 2014).
 74
 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
 79 Although biotic interactions, and particularly competition, have a long history in the study of
 80 community patterns their importance is often neglected at broad spatial scales where speciation,
 81 extinction and geographic dispersal are expected to be the main driving processes (Gaston &
 82 Blackburn, 2000). Recently, Araújo and Rozenfeld (2014) modelled spatial consequences of all types
 83 of species interactions (continuum from positive to negative) and concluded that, in particular,
 84 positive species interactions can be manifested from local to larger scales. Indeed, a few empirical
 85 studies have revealed both aggregated and segregated distribution patterns among ecologically
 86 similar species, likely resulting from both competitive and positive interactions, independent of
 87 habitat characteristics, at broad spatial scales (Gotelli *et al.*, 2010; Ricklefs, 2012).
 88
 89 The strength of species associations may depend on functional and phylogenetic similarity of species
 90 involved. Both heterospecific information use and the limiting similarity principle predict that
 91 species associations are most intense, but in opposite directions, among functionally similar species
 92 (Fig. 1). Heterospecific information use predicts positive associations between species that use
 93 similar resources, i.e. are functionally similar, because the information value decreases with
 94 increasing ecological distance (Seppänen *et al.*, 2007), while limiting similarity predicts mutual
 95 avoidance between similar species due to costs of competition (MacArthur & Levins, 1967).
 96 However, it is likely that both competition and heterospecific information use are context
 97 dependent and the net outcome of an association between similar species depends on the costs of
 98 competition and benefits of information use (Mönkkönen *et al.*, 1999; Seppänen *et al.*, 2007).
 Therefore, associations between functionally similar species may be strong, either positive or
 negative and the strength of the association may decrease with decreased species similarity. The

likelihood of finding such a relationship depends, however, on the traits considered (Trisos *et al.*, 2014). Using phylogenetic information can be a relevant approach to avoid a priori trait selection. Similar patterns are indeed also likely for phylogenetic distance providing that trait conservatism renders closely related species also ecologically more similar (Mouquet *et al.*, 2012). In this case, phylogenetically closely related species should also show both the strongest positive and negative associations, and phylogenetically distant species should show neutral associations. So far, however, empirical tests of this hypothesis have yielded mixed results (Violle *et al.*, 2011; Godoy *et al.*, 2014).

Earlier research on general mechanisms of community assembly commonly separated the effects of competitive interactions from environmental forcing causing positive covariation among species abundances and provided support for environmental variation rather than competition driving the variation in species abundances (Houlahan *et al.*, 2007; Mutshinda *et al.*, 2009; Ricklefs, 2012). However, some of the positive covariation may be due to positive interactions between species, over and above habitat filtering and productivity. Moreover, even if environmental forcing generally prevails over competitive interactions, negative interactions may not be trivial. Thus both negative and positive interactions can leave a signature on community assembly that affects both historical and ecological distribution patterns. In this article, we study (i) whether there are positive or negative associations among bird species in local communities, independently of habitat characteristics, and consequent community patterns at large geographical scales, and (ii) whether these positive or negative associations are related to functional similarity and/or phylogenetic distance of the species. We predict that functional dissimilarity/phylogenetic distance and the strength of the associations form a ‘funnel plot’ where the strongest associations, either positive or negative, are between functionally similar or phylogenetically close species whereas the associations grow weaker with increasing dissimilarity/distance (Fig. 1). We use comprehensive bird census data from French forests and farmlands as well as Finnish forests, and analyze the three datasets separately to test for consistency of results across habitat types and geographic areas. Using these three datasets separately offers a possibility to test the same question on the same group of species

originating from quite different kinds of landscapes and climatic conditions. Consistent patterns would imply generality and call for further scrutiny of underlying mechanisms.

Material and methods

Data

Data were extracted from two independent datasets from France and Finland. They are very well suited for the study because together they cover a wide extent (with a relatively small grain size) and consequently also a wide spectrum of climatic and environmental conditions, and they are both of high quality gathered over multiple years and multiple sites. The French Breeding Bird Survey is a large-scale, multi-year and multi-plot monitoring program of the French avifauna. The program followed a standardized protocol from 2001 to 2012 (Jiguet *et al.*, 2012) where 2x2 km sampling plots are randomly selected within 10-km radius areas, which ensures a representative sampling of existing habitats. In each plot, 10 point count stations were evenly distributed. At each station, the observer recorded all birds heard and seen during 5 minutes, in two sessions during the breeding season. For each species in each point count station and each year, the maximum number of individuals recorded during the two sessions is retained as a proxy for the local abundance of that species in that plot and year.

In Finland, point counts have been conducted as part of the national common bird monitoring scheme between 1984 and 2011 (Laaksonen & Lehtikoinen, 2013). Each census route included 20 point count stations located in the habitat that is uniform within 50-m radius of the station. The habitat of each point was classified into 17 different habitat categories. Stations within a route were at least 250 m apart in forested habitats and 350 m apart in open habitats to avoid pseudo-replication. Due to very short and synchronized breeding season of boreal birds, a route was censused only once per season. At each station, an observer counted, for 5 mins, all the observed land birds during late spring – early summer (May 20 – June 20 in south-central Finland, May 30 -

June 30 in northern Finland). In both monitoring projects, surveys were conducted early in the morning (typically between sunrise and 10 am), which is when the birds were most active, and only on days with good weather conditions (no rain or heavy wind).

Data handling

Original French data included plots sampled for at least two years, i.e. 1,914 plots and 19,140 point count stations. Finnish data included 286 routes and 5,760 stations. From these data we first created three independent data sets by selecting the point count stations situated in forests or in farmlands only (French farmlands, French forests, Finnish forests; Finnish farmland data were too small for the analysis). The aim was to remove most of the variation in bird abundances resulting from habitat structures (habitat filtering). Indeed, one of the obvious sources of species segregation or aggregation is the main habitat type in which a given plot is monitored. A negative association between farmland birds and forest birds would be interpreted as a signal of competition although those two groups simply do not co-occur. The three datasets contain about 2,900–9,000 point count stations but a rather narrow range of habitats (Table 1). We analyzed the three datasets separately to test for the consistency of results across habitat types and geographic areas.

We excluded all waterbirds and birds of prey since point count census at the local point count station level provides reliable information on species abundances only for land birds with relatively small home ranges. We also excluded very rare species that were present in less than 2% of the point count stations. After filtering, our data included 43,000-206,000 observations for 76-83 species (Table 1), for which we calculated average abundance values across years per point count station. The same species occurred in multiple data sets: the number of shared species was 67 in French forest and farmland data, 51 in French and Finnish forest data, and 45 in French farmland and Finnish forest data.

The matrix of pairwise functional distances was produced from 22 functional traits (Appendix S1 in Supporting Information) using methods described in Devictor *et al.* (2010). These traits encompassed life-history traits and feeding habits (Petchey *et al.*, 2007) and were identified as being important in determining the response of bird species to environmental change and in determining the contribution of bird species to ecosystem functions (Sekericioglu, 2006). From these traits, we calculated the Gower distance to represent pairwise trait distances estimated from the species trait matrix (Legendre & Legendre, 1998). As we aim to remove habitat-induced distances between species we calculated a separate matrix for each set of species (French farmlands, French forests, Finnish forests). Gower distance accounts for both continuous and qualitative traits (Mouchet *et al.*, 2008) and were measured with the function ‘daisy’ of the R package ‘cluster’ (Maechler *et al.*, 2016). All pairwise distances were standardized by dividing original distance values with the range of values.

We extracted pair-wise phylogenetic distances directly from a dated molecular phylogenetic tree assembled by Thuiller *et al.* (2011) and then used ultrametric distances from this tree representing relative phylogenetic distances among species using the function ‘cl_ultrametric’ in the R package ‘clue’ (Hornik, 2005). Phylogenetic information was not available for 7 species in Finnish forest dataset, and thus we performed analyses of phylogenetic distance on 69 species.

Statistical analyses

We adopt the pairwise approach to analyze species effects on each other’s abundance, i.e., consider a species pair as the fundamental unit in interactions. The procedure has advantages over the matrix method i.e. where a target of interest is the whole community i.e. presence-absence matrix that has been used since the beginning of the studies of co-occurrence patterns (Diamond, 1975; Connor *et al.*, 2013). Most communities contain many potential species pairs each of which may exhibit positive, negative or random associations. Therefore, single metrics that summarizes an entire 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

effectively controls for fine scale habitat filtering. Fifth, we entered community size (summed abundances of all species, excluding species_i and species_j) as a fixed effect controlling for the possibility that species abundances may covary with total community size because of independent responses to productivity. Finally, we added the abundance of species_j as a fixed effect. We log-transformed ($\log(n+1)$) all abundances prior to analyses and saved pairwise regression coefficients for further analyses. Estimating pairwise associations using Poisson distribution yielded too many convergence problems and was not feasible due to a very high number of models. Note that using Poisson distribution should not change the general conclusions derived from our framework based on log-transformed abundances (Ives, 2015).

To infer whether the observed associations differ from what could be observed on the basis of randomly distributed individuals we used a null model approach. First, we defined a regional species pool as all observed species and their abundances, separately for each habitat in each biogeographical zone. Next, we randomly sampled the observed number of individuals from the regional species pool while preserving the abundance of each species and observed total abundance in each point count station. In other words, we kept the size of the regional habitat-specific species pools and the size of the local communities fixed, and within these constraints we randomized the composition of local communities at point count stations (see Crist *et al.*, 2003, for a similar approach). This type of randomization makes a plausible assumption that species habitat associations, their relative abundances in regional pools and local community size are real ecological properties worth retaining while relaxing deterministic pairwise associations. Then we fitted the linear mixed-effect model described above for the randomized datasets. We repeated this procedure 1000 times and calculated the standardized effect size as the difference between observed pairwise regression coefficient and mean expected coefficient, divided by the standard deviation. Thus, the effect size measures the direction (positive or negative) and strength of species interactions in the datasets, independent from what one expects by chance and sampling artefacts.

Because the effect sizes within species pairs (effect of species_i on species_j, and *vice versa*) were strongly correlated (Spearman's $\rho = 0.943$, $n = 3,403$, $P < 0.001$; Spearman's $\rho = 0.956$, $n = 2,926$, $P < 0.001$; Spearman's $\rho = 0.960$, $n = 2,850$, $P < 0.001$; in French farmlands, French forest, and Finnish forests, respectively) we used the mean of the effect sizes of each species pair (ES_{mean}) as an observation unit in the analysis. Given that these observations are not independent (every species is represented in multiple species pairs) we used bootstrap method to calculate standard errors (Koenker, 2013).

We considered pairwise species effect sizes “strong” when absolute effect size values were >2 (i.e. observed association deviated more than two standard deviations from the expected) and “weak” when effect size values were <2 . We predicted a relationship between the magnitude of the effect sizes, both positive and negative, and functional dissimilarity/phylogenetic distance. The magnitude should decrease with increasing dissimilarity/distance. To test this, we used quantile regression (Cade & Noon, 2003) for all quantiles from 1 to 99% quantiles (τ ranges from 0.01 to 0.99) at intervals of 1%. We predicted that the regression between effect size and dissimilarity/distance would result in a negative coefficient in the upper ($>50\%$) quantiles (reflecting smaller positive effect sizes with increasing dissimilarity/distance) and a positive coefficient in the lower ($<50\%$) quantiles (reflecting smaller negative effect sizes with increasing dissimilarity/distance). If these predictions are verified, the shape of the relationship should be a ‘funnel plot’ with higher numbers of positive and negative associations for lower values of functional dissimilarity or phylogenetic distance (Fig. 1). To infer whether this is truly the case we plotted the coefficient of each of the quantile regression as a function of the quantile (τ) in question, and expect to see a negative relationship. As we do not have a specific hypothesis about the overall relationship in the data we do not concentrate on the general tendency, i.e. 50% quantile, but on upper vs lower quantiles. We performed linear mixed-effect models with package ‘lme4’ (Bates *et al.*, 2014) and quantile regression with ‘quantreg’ (Koenker, 2013) in R Version 3.0.3 (R Development Core Team, 2014), and the iterations for the null model approach with Taito supercluster provided by CSC - IT Center for Science Ltd

(<https://research.csc.fi/research-home>). The R script for calculating the effect sizes is provided as Appendix S3. Other analyses we performed with IBM SPSS Statistics 22.0 (IBM, Armonk, New York, USA).

Results

We observed both positive and negative regression coefficients among species pairs tested in all three datasets. The means of the observed coefficients were positive (0.02) and the distribution of coefficients were highly similar in the three datasets (see Appendix S4). Likewise, the effect sizes (ES_{mean}) were centered close to zero. A large proportion of pairwise species effect sizes can be considered strong as absolute effect size values larger than two (i.e. observed association deviated more than two standard deviations from the expected) constituted 83, 63 and 41% of all pairwise effect sizes in French farmland ($n=6,806$), French forest ($n=5,852$) and Finnish forest dataset ($n=5,700$), respectively. In all three datasets, strong negative associations were approximately twice as common as strong positive associations: 57 vs 26% in French farmland, 39 vs 23% in French forest, and 27 vs 15% in Finnish forest data. Thus, birds are not distributed randomly with respect to each other in local communities, when controlling for habitat filtering and productivity, and we found asymmetry between positive and negative associations with prevalence of the latter.

The relationship between functional dissimilarity and the mean of the effect sizes for species pairs (ES_{mean}) showed differences among the three datasets. In French farmlands there was no relationship in the lower quantiles but a negative relationship in the upper quantiles whereas in French forests there was only a trend in both lower and upper quantiles (Fig. 2a,b). By contrast, in Finnish forests there was a positive relationship in the lower quantiles and a negative relationship in the upper quantiles (Fig. 2c). Thus, in French farmlands the level of aggregation increased with decreasing functional similarity, in Finnish forests both the level of segregation and aggregations increased with decreasing functional similarity, while in French forests there were no relationships.

Phylogenetic distance and ES_{mean} showed significant relationships in both ends of the quantile spectrum in French farmlands and forests (Fig. 3a,b). Thus, both aggregated and segregated distributions of species abundances increased as a function of decreasing phylogenetic distance. In Finnish forests, there was a positive relationship between phylogenetic distance and ES_{mean} in the lower quantiles but no relationship in the upper quantiles (Fig. 3c).

Discussion

Bird species showed both spatial aggregation and segregation in their abundances, independently of habitat structures. Even though overall mean effect sizes of species associations in the local communities were centered on zero, we found the majority of species were relatively strongly associated with each other. This highlights the importance of both negative and positive biotic interactions in affecting community assembly. Our study using natural communities across a wide geographic area yielded results that are consistent with the results of the local manipulative experiments: negative associations are common but also positive associations frequently occur (Bertness & Callaway, 1994; Gurevitch *et al.*, 2000; Forsman *et al.*, 2002; Martorell & Freckleton, 2014; but see Gotelli & Ulrich, 2010). Moreover, our results suggest that high functional and phylogenetic similarities can be important determinants increasing the probability of both negative and positive associations. Also, we found that in bird communities strong negative associations were twice as common as strong positive associations. This is in line with empirical results of Gotelli *et al.* (2010) who showed strong predominance of spatially segregated over aggregated distributions within foraging and congeneric guilds in Danish avifauna.

Species abundance is affected by a multitude of factors, such as habitat, productivity and geographical position. Our pairwise approach controlled for the effects of habitat, first, by restricting the analysis only to a limited set of habitat classes (Table 1) and, second, by entering habitat class as a factor in the model. Moreover, we entered biogeographic zone, sampling site, and second order

trend surface in abundances to control for the effects of geographic factors such as species geographic distributions and climate related variation. Finally, we controlled for the community size, i.e. species independent responses to productivity. Yet our analysis revealed strong signals of positive abundance associations. Thus, species abundances were probably affected also by positive biotic interactions between species, and these interactions were strong enough to show up as aggregated distributions. The recurrent finding that species abundances in natural communities tend to covary positively rather than negatively has commonly been attributed to environmental forcing (Houlahan *et al.*, 2007; Mutshinda *et al.*, 2009; Ricklefs, 2012). Our results suggest that a proportion of this positive covariation is likely due to positive interactions. Therefore, dominance of positive covariation over compensatory dynamics in community dynamics does not necessarily imply low frequency of species interactions. Future studies testing assembly theories should therefore refrain from using strictly dichotomist approaches such as compensatory dynamics versus environmental forcing, but also consider the possibility of positive interactions and underlying processes such as conspecific or heterospecific information use.

In all three datasets, closer species pairs with respect to phylogenetic distances are those showing stronger segregation in their abundances. Neutral associations, however, were found throughout the phylogenetic distance spectrum. Thus, a part of phylogenetically close bird species indeed seem to compete more strongly than distantly related species which plausibly leads to avoidance of such species in habitat selection. In Finnish forest bird assemblages, but not in the two French datasets, the signal of spatial segregation increased also with increasing functional similarity. In concordance with the prediction of heterospecific information use (Seppänen *et al.*, 2007), the signal of spatial aggregations was stronger for pairs consisting of similar species and grew weaker with increasing dissimilarity. However, whether the pattern was detected for phylogenetic distance, functional dissimilarity or both showed variation among datasets: in French forests aggregation was related to phylogenetic distance, in Finnish forests to functional dissimilarity, and in French farmlands to both.

In summary, segregated abundances were related to phylogenetic distance in all of the three cases, to functional dissimilarity in only one, whereas aggregated abundances were related both to phylogenetic distance and functional dissimilarity in two cases. Thus, the phylogenetic signal in segregated abundances was stronger than that of functional (ecological) similarity. This suggests that the traits we used for functional dissimilarity might not be those that actually affect species competitive environment but more relevant in terms of heterospecific information use, whereas phylogenetic signal encompass traits of direct relevance in both respects. This result also raises the issue of trait selection in trait-based analysis. It is likely that a part of the results is dependent on the particular combination of trait used. A finer examination of pairwise associations i.e. whether segregated versus aggregated associations are influenced by a specific combination of traits, whether there is any specific trait enhancing coexistence or whether aggregations are phylogenetically clustered, would be an interesting extension of our approach.

Another reason why species pairs consisting of phylogenetically closely related species showed strong segregation in their abundances could result from allopatric speciation. Phylogenetic overdispersion, which is often attributed to negative biotic interactions, may instead be consistent with a neutral model of allopatric speciation (Pigot & Etienne, 2015). If allospecies rarely co-occurred in the bird assemblages we studied, and differ somewhat in their functional traits, one could see a pattern where phylogenetic distance is more directly driving negative abundance associations than functional similarity. Allopatric speciation does not, however, provide an explanation for phylogenetic and functional patterning of positive abundance associations. It is possible, and even probable, that for some species pairs the costs of competition and benefits of information use adds up to show as a neutral association. Hence, it is important to bear in mind that small effect sizes in our study do not necessarily indicate no or weak interactions.

Our approach where we simultaneously addressed both negative and positive interactions, and provided support for both, may help to understand why earlier work has found mixed results concerning the role of phylogenetic and ecological distance in species interactions (Violle *et al.*,

2011; Godoy *et al.*, 2014). Our results support a common expectation in the community assembly literature that due to competition, close relatives and functionally similar species should show segregated patterns in abundance (Webb *et al.*, 2002). But more interestingly, our results suggest that close relatives and functionally similar species also may also aggregate, which is reflected as positive associations among species' abundances. The likely mechanism is the use of social information (Seppänen *et al.*, 2007) and/or facilitative interactions among species (Bruno *et al.*, 2003). It is evident that both clustering and overdispersion of co-occurring species within communities may occur simultaneously. Our results challenge the implicit assumption pertinent to community phylogenetics that assembly through positive associations decreases with increasing assembly by competition (see Gerhold *et al.*, 2015). Thus, the relative balance of positive and negative interactions in community assembly cannot be quantified by a single parameter of phylogenetic (or functional) dispersion.

We acknowledge the fact that only experimental set-ups can truly prove the strength and the sign of the interaction between a species pair. It is clear that the data used here do not capture all the small scale habitat characteristics which may affect species aggregation and segregation patterns. Indeed, a detailed data of environmental conditions might attenuate the coefficients we found. On the other hand, it has been shown that even when modeling forest bird species distributions with a very detailed forest structure data the density of a bird species remains a significant predictor of the density of a close relative (Kosicki *et al.*, 2015).

Social information use and subsequent aggregated distribution in local communities result in variation in local species diversity at a given site that deviates from diversity predicted by environmental factors only, creating both hot and cold spots of species diversity in the landscape (Seppänen *et al.*, 2007). Interspecific competition resulting in segregated distribution may also create similar deviations from predictions. Our results suggest that such diversity anomalies should carry phylogenetic/functional signal. Species' interactions may render a proportion of suitable habitat patches unoccupied by the species also because dispersal among patches in the landscape

may be affected by the presence of close relatives and/or functionally similar species. Consequently, colonization and extinction in fragmented landscapes is no longer a sole function of landscape patterns and species dispersal abilities but hinges also on other species' ability to persist in fragmented landscapes. Given that interspecific social information use is widespread (Seppänen *et al.*, 2007), from the point of view of species' conservation, it is important to keep in mind that the effect of close relatives and ecologically similar species may also be positive.

Predicting species responses to various global changes has become crucial due to the ongoing biodiversity crisis. Our results accompany earlier literature (e.g. Araújo & Rozenfeld, 2014) suggesting that a failure to incorporate species interactions may account for the mixed results of earlier species distribution modeling efforts that ignore interactions.

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Supporting Information

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

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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

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.

Fig.1

634

635 Fig. 2

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637

638 Fig. 3