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Species functional traits and abundance as drivers of multiplex ecological networks: first empirical quantification of inter-layer edge weights

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Many vertebrate species act as both plant pollinators and seed-dispersers, thus interconnecting these processes, particularly on islands. Ecological multilayer networks are a powerful tool to explore interdependencies between processes; however, quantifying the links between species engaging in different types of interactions (i.e. inter-layer edges) remains a great challenge. Here, we empirically measured inter-layer edge weights by quantifying the role of individually marked birds as both pollinators and seed-dispersers of Galápagos plant species over an entire year. Although most species (80%) engaged in both functions, we show that only a small proportion of individuals actually linked the two processes, highlighting the need to further consider intra-specific variability in individuals' functional roles. Furthermore, we found a high variation among species in linking both processes, i.e. some species contribute more than others to the modular organization of the multilayer network. Small and abundant species are particularly important for the cohesion of pollinator seed-dispersal networks, demonstrating the interplay between species traits and neutral processes structuring natural communities.

1. Background

Most species are involved in several types of biotic interactions. Given the intrinsic difficulty in understanding such a complexity, ecologists have traditionally studied these multiple interactions as discrete activities, particularly when implementing a network approach (e.g. herbivory, pollination, seed-dispersal networks, plant-mycorrhizal interactions) [1,2]. Nevertheless, these simplifications contrast with the way that interactions are really structured [3–7]. The outcomes of one type of interaction may directly or indirectly influence another type. As examples, plant–herbivore interactions can induce changes in flower availability affecting the network of pollination interactions [8–10], and changes in host–parasite interactions inevitably affect those between parasites and their parasitoids [11]. Hence, studying multiple interactions together seems crucial to predict system diversity and stability [12–14]. With the recent implementation of a multilayer network approach [4,7,15], and taking advantage of theoretical developments and new analytical tools derived from other research areas, ecologists have started to incorporate the interdependencies between ecological processes into the analysis of network structure [16].

An ecological multilayer network (EMN) can be composed of two or more layers representing different types of biotic interactions (i.e. multiplex EMN)

and/or different moments in time and space [4,15–17]. In these networks, links can connect nodes (e.g. species) within the same layer (i.e. intra-layer edges) or across layers (i.e. inter-layer edges). However, what makes EMN differ from monolayer networks is the incorporation of inter-layer edges, which provide information on the processes operating between layers and their role in the community structure [18]. Measuring intra-layer edge weights in a common currency and non-uniform inter-layer edge weights in the same currency as for intra-layer edge weights is critical for the realism of EMN, but represents an important challenge. This is particularly so in multiplex EMN, because data from different sampling methods, and at diverse taxonomic levels, need to be integrated and standardized. For this reason, most studies use unweighted inter-layer edges, assuming that all nodes link layers with the same weight [4,15,19,20]. By contrast, weighted inter-layer edges (i.e. non-uniform links between layers) effectively describe the assumed dependence of layers on each other, identifying the species that play a determinant role in linking different processes, and thus add substantial realism to the EMN [18]. For example, in spatial EMN not all animals move between forest patches (i.e. layers) with the same frequency, and therefore they do not have the same importance in functionally bridging such patches. Previous studies that used inter-layer edges either (i) used a uniform value for non-sampled edges [15]; (ii) inferred non-uniform weights from abundance data sampled in the field [4,17]; or (iii) used simulated non-uniform weights, not measured in the field [21].

Here, for the first time, we empirically estimated inter-layer edge weights, in the same currency as intra-layer edge weights in a multiplex EMN, by quantifying the role of each individual bird in two key ecological processes: pollination and seed-dispersal. On continents, pollination and seed-dispersal services tend to be provided by different animal guilds [20,22]; on islands, however, vertebrates often play an important role in both mutualisms [23–26]. In the Galápagos, land bird species are particularly involved in these two processes, with the potential to act as double mutualists of some plant species (i.e. the same bird species acts as pollinator and seed-disperser of the same plant species) [27]. Therefore, we decided to explore the overall structure and cohesion of pollination and seed-dispersal, two intertwined processes that have rarely been considered together [1,2,20,28]. Specifically, we explored how the strength of intra- and inter-layer connectivity affects the overall structure of the multiplex EMN. Secondly, we explored two key drivers of species importance as functional couplers between pollination and seed-dispersal services, namely, morphological traits between co-occurring species that match for carrying out an interaction, and abundances that determine species co-occurrence and the potential for species to interact [29–32]. Hence, we assessed how species traits and abundances are related to their overall importance in the multiplex EMN.

2. Material and methods

(a) Study sites and data collection: functional traits and interactions

The Galápagos are volcanic islands forming an archipelago at the Equator, ca 960 km west of South America. The climate is marked by a cold and dry season (June–December) and a hot and wet

season (January–May). The surface of the islands is mostly covered by two habitats: dry lowland and permanently humid highland [33].

We collected data from March 2010 to February 2011 on two Galápagos Islands, San Cristóbal and Santa Cruz, at four sites (two on each island). Two to four monthly visits were made per site, with a similar sampling effort (36 days in total per site), encompassing both seasons and both habitats (see [34] for details). At each site, we captured birds with mist nets operated for five consecutive hours after sunrise on each sampling day. All captured birds were individually marked with numbered metal rings, to prevent resampling the same individual on the same day, and characterized according to: (i) species identity, (ii) wing length, (iii) length of the third primary feather, (iv) tarsus length, (v) gape width, (vi) bill length and (vii) body mass. All data were collected according to standardized protocols [35]. These data were collected because they relate to the functional traits. For instance, wing length relates to bird mobility, flight and foraging mode [36]; gape width and bill length govern access to fruits and floral resources [37,38]; and body mass influences nutritional requirements [39].

Captured birds were individually placed in ringing bags for up to 30 min in order to produce a dropping. In the laboratory, intact seeds were extracted and identified to species level or morphospecies under a stereomicroscope, by comparison with a reference collection [40]. Additionally, birds were individually sampled for pollen attached to the throat and forehead by swabbing a cube (approx. 3 mm³) of fuchsine-stained glycerine jelly on their beak and peri-mandibular feathers. The gelatine cube was then placed on a microscope slide, melted and covered with a slip [26]. The entire slide area was inspected under a light microscope to count and identify all pollen grains to species level using a pollen reference collection [41]. In a few pollen-dense samples with grains almost homogeneously distributed (5%), ca 40% of the slide was inspected and pollen counts were extrapolated to obtain a total slide count. Evidence of bird flower visitation was considered if more than 10 pollen grains of a given species were detected in the sample. This threshold was set to reduce any erroneous inferences about visitation caused by pollen contamination [42,43]. All samples were identified with the unique individual ring number of the bird that produced them. Each captured individual was considered a sampling unit (8% of all ringed birds were recaptured, mean = 1.33 ± 0.68 captures per individual, range = 1–4).

(b) Multilayer network analysis

For each island, we assembled a diagonally coupled multiplex network formed by (i) two sets of ‘physical nodes’ representing bird and plant species, (ii) two layers representing the two types of interactions (α = pollination, β = seed-dispersal), (iii) four sets of ‘state nodes’ that correspond to the presence of each physical node in a given layer (i.e. pollinator or frugivore for bird species and pollen or seed for plant species) and (iv) two sets of species-level weighted edges: intra-layer edges that connect bird and plant species inside each layer (flower i - pollinator j in layer α or seed i - frugivore j in layer β), and inter-layer edges that connect bird species to their counterpart in the other layer (pollinator j in layer α - frugivore j in layer β). In the pollination layer, the weight of an intra-layer edge between flowering species i and pollinator species j at layer α is $w_{ij\alpha} = p_{ij}^{\alpha}/b_j^{\alpha}$, where $w_{ij\alpha}$ denotes an intra-layer edge weight in the layer α , p_{ij}^{α} is the number of individuals of bird species j on which pollen grains of the species i was detected, and b_j^{α} is the number of birds of species j at layer α . In the seed-dispersal layer, the weight of an intra-layer edge between seed species i and disperser species j at layer β is $w_{ij\beta} = p_{ij}^{\beta}/b_j^{\beta}$, where $w_{ij\beta}$ denotes an intra-layer edge weight in the layer β , p_{ij}^{β} is the number of individuals of bird species j on which seeds of the species i were detected, and b_j^{β} is the number of birds of species

j at layer β . The weight of an inter-layer edge that connects bird species j at layer α to bird species j at layer β is $w_{j\alpha\beta} = p_j^{\alpha\beta}/b_j^{\alpha\beta}$, where $w_{j\alpha\beta}$ denotes an inter-layer edge weight, $p_j^{\alpha\beta}$ is the number of individuals of bird species j on which both pollen grains and seeds of any plant (i.e. pollen and seeds could be of the same or different species) were detected, and $b_j^{\alpha\beta}$ is the number of captured individual birds of species j . Both intra- and inter-layer edge weights take values between 0 and 1. For example, a species can be in both layers but has an inter-layer edge weight of 0 if no individual has been detected as using both resources during the course of a year, whereas an inter-layer edge of 0.5 means that half of the total captured individual birds of a species were found to disperse both pollen and seeds during the course of a year. Inter-layer edges encode the bird functional role across processes and represent the extent to which each species mediates the effect of pollination on seed-dispersal and vice versa. The number of individuals dispersing pollen grains and seeds is considered a more realistic measure of the function they play in the ecosystem rather than the number of pollen grains and seeds found. This is because the viability of many pollen grains and seeds is likely to be density dependent, due to high levels of competition during recruitment [44,45].

We used capture rates (i.e. the number of bird captured) as a proxy of bird relative abundance; the sampling effort was the same for all studied species (length of mist nets used) and recaptured birds were excluded from the analysis. Estimating relative abundance using mist-net capture rates can be problematic since equally abundant species can vary in the probability of being captured [46]. However, for highly related forest birds of the similar size, like those in the Galápagos, capture frequencies can be directly used as a proxy of relative abundance [47], as more abundant species have a higher probability of being captured in the nets whereas rare species have a low capture probability [48,49]. To test whether our estimates of bird species abundances influenced their edge weights, we performed Spearman correlation between bird species abundances and their intra-layer edge weights in pollination, intra-layer edge weights in seed-dispersal and inter-layer edge weights. We carried out another Spearman correlation test between the number of times an individual bird was captured (in different days) and the number of times this individual carried pollen, seeds and both, to test if individuals captured more times were more likely to act as pollinators, seed-dispersers and pollinator-dispersers.

To understand community structure in coupled pollination and seed-dispersal processes, we calculated multilayer modularity, which measures the extent to which pollination and seed-dispersal interactions are organized into groups of strongly interacting species (i.e. modules) [15,50]. Modularity was maximized with a generalized Louvain algorithm implemented in MATLAB [51] and adapted for bipartite networks [4,15]. We used the default single-layer resolution, i.e. the importance given to the null model compared to the empirical data ($\gamma = 1$). We also calculated the mean number of modules and adjustability (i.e. module switching) of birds and plants as the proportion of species in a given group that appear in different modules. The modular structure of the observed EMN was tested by comparing it to the structure of networks built with three complementary null models (run 1000 times each) from the ‘vegan’ package in R, using code provided in Jutla *et al.* [51] modified by Pilosof *et al.* [4] to account for the bipartite nature of the multilayer network [15]. These were (i) an ‘intra-layer null model’ with the ‘r00_both’ algorithm, which maintains the large matrix total (i.e. the number of links), while redistributing the individual interactions independently for each layer [52], to assess whether the structure within each interaction layer influences the overall structure of the EMN [4]; (ii) an ‘inter-layer null model 1’ with the ‘r00_samp’ algorithm that changes the order of the ‘labels’ of the bird species in each matrix [52], to assess if the structure

of the EMN is dependent on the identity of the species connecting the two layers (i.e. nodal null model) [4,15,53]; and (iii) an ‘inter-layer null model 2’ with the ‘r00_both’ algorithm that reshuffles both the ‘labels’ of the bird species and the individual interactions [15,52]. The inter-layer null model 2 is better comparable to the intra-layer null model (both used the same algorithm) and was used to check if the selection of the shuffling algorithm influences modularity.

For each null model, we tested the hypothesis that the most modular configuration of the observed network is more modular than the most modular configuration of the shuffled networks. Significance was estimated as the proportion of the 1000 shuffled networks with lower maximized modularity than that of the observed network. We compared our results with shuffled networks to the values obtained for the observed networks using a one-sample t test [4].

(c) Effects of functional traits on network roles

We performed a principal component analysis (PCA) to condense all bird species traits (see section ‘a’ above) to obtain a small number of uncorrelated variables (i.e. principal components), using the ‘prcomp’ function in R ‘stats’ package.

To identify central bird species that are important within each layer but also for the EMN structure, the multilayer versatility of each species was calculated by implementing the PageRank algorithm in MuxViz 2.0 [15,54]. This metric describes the overall importance of a node based on a random walk between nodes within and across layers [55]. Versatility analyses need unimodal projections of two-mode networks as inputs. Thus, one of the sets of species (birds) was selected and two bird species were linked if they were connected to the same plant species (i.e. they pollinate or disperse the same plant species), using Newman’s method adapted for weighted networks with the R package ‘tnet’ [56,57]. We thus created an extended-edge list composed of intra-layer edges that represent an interaction between two bird species in the same layer (at layer α , bird species j and bird species k pollinate the same plant species i ; at layer β , bird species j and bird species k disperse the same plant species i), and inter-layer edges that represent an interaction of the same bird species across layers (pollinator j in layer α - frugivore j in layer β). In the pollination layer, intra-layer edge weights of the one-mode projection were quantified as $w_{jk\alpha} = \sum_i^{\alpha} w_{jki}/N_i - 1$, where $w_{jk\alpha}$ is the weight between bird species j and bird species k in the layer α , w_{jki} is the number of individual birds of species j that pollinate the plant species i and N_i is the number of bird species connected to the plant species i . In the seed-dispersal layer, intra-layer edge weights of the one-mode projection were quantified as $w_{jk\beta} = \sum_i^{\beta} w_{jki}/N_i - 1$, where $w_{jk\beta}$ is the weight between bird species j and bird species k in the layer β , w_{jki} is the number of individual birds of species j that disperse the plant species i and N_i is the number of bird species connected to the plant species i . Intra-layer edge weights were calculated in both directions, i.e. w_{jk} can be different to w_{kj} , and the sum is for all plant species shared by bird species j and k . Finally, inter-layer edge weights of the one-mode projection were quantified as $w_{j\alpha\beta} = \sum_i^{\alpha\beta} w_{jki}/N_i - 1$, where $w_{j\alpha\beta}$ is the weight of bird species j across layers, w_{jki} is the number of individual birds of species j that pollinate and disperse the plant species i and N_i is the number of bird species connected to the plant species i in both layers [58]. Intra- and inter-layer edge weights of the one-mode projection range from 0 to 1.

Finally, the influence of functional traits and abundances on multilayer versatility was assessed with a generalized linear mixed model (GLMM), adjusting data to a gamma distribution of errors with the R package ‘lme4’ [59]. We included the average bird species scores of the first and second principal components (PC1 and PC2) and bird species abundances as fixed effects.

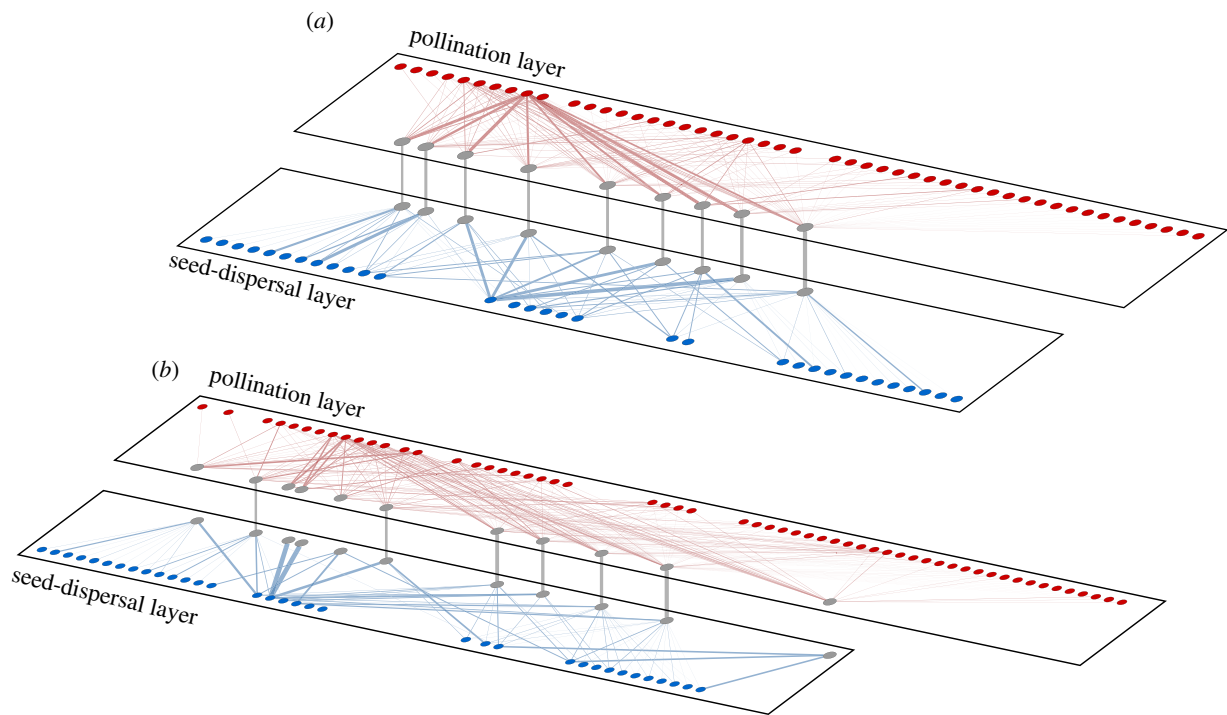


Figure 1. Multilayer networks studied on the islands of San Cristóbal (a) and Santa Cruz (b). Each layer corresponds to a different type of interaction (red, pollination; blue, seed-dispersal). Bird species are represented as grey nodes in both layers, while pollinated plants are red nodes in the pollination layer and dispersed plants are blue nodes in the seed-dispersal layer. Width of intra-layer edges are proportional to the number of individual sampled from each species bearing pollen grains or seeds, respectively. Inter-layer edges appear in grey and connect bird species which have individuals acting as both pollinators and seed-dispersers. (Online version in colour.)

To account for the variation in the availability of flowers and seeds between islands and for random variation among sites within each island, the model included ‘site nested within island’ as a random effect.

3. Results

(a) Pollination-dispersal networks

Dropping and pollen samples were collected from a total of 1921 individuals (16 species), of which 14% (276) contained more than 10 pollen grains, 36% (685) contained intact seeds and 7% (128) contained both pollen grains and seeds (electronic supplementary material, table S1 and figure S1). Overall, 9361 intact seeds from 46 plant species and three morphospecies were retrieved from the droppings of 13 bird species. Nearly half a million pollen grains from 78 plant species and three morphospecies were identified on the foreheads of 14 bird species (figure 1).

Overall, 80% of the bird species acted as both seed-dispersers and pollinators, however, only 7% of the individuals were actually observed engaging in both types of interactions during the entire year, i.e. effectively coupling the two processes (figure 1). Individuals of six bird species (small and medium ground-finches, *Geospiza fuliginosa* and *G. fortis*, woodpecker finch *Camarhynchus pallidus*, small tree-finch *C. parvulus*, Galápagos flycatcher *Myiarchus magnirostris* and yellow warbler *Setophaga petechia*) pollinated and dispersed the same plant species (*Bursera graveolens*, *Mentzelia aspera*, *Opuntia echios*, *Psidium guajava*, and *Rubus niveus*), thus acting as double mutualists.

Neither intra-layer edge weights (in the pollination and seed-dispersal) nor inter-layer edge weights correlated with species abundance ($r_s = -0.07$; $p = 0.779$; $r_s = 0.01$; $p = 0.951$;

$r_s = 0.25$; $p = 0.294$, respectively). Moreover, individuals captured more often were not more important as pollinators, seeds-dispersers or pollination-dispersal couplers ($r_s = 0.11$; $p = 0.069$; $r_s = 0.16$; $p = 0.161$; $r_s = 0.07$; $p = 0.940$, respectively).

(b) Modular structure of the multiplex network

Observed modularity was not significantly different than that predicted by the intra-layer null model, so reshuffling interactions within each process had no effect on the structure of the EMN (San Cristóbal: $Q_{\text{obs}} = 0.64$, $Q_{\text{null}} = 0.65$, $t = 12.24$, $p = 0.229$; Santa Cruz: $Q_{\text{obs}} = 0.60$, $Q_{\text{null}} = 0.59$, $t = 13.05$, $p = 0.497$). However, the structure of the EMN was influenced by the identity of the bird species connecting layers, with modularity being significantly lower than that predicted by the inter-layer null model 1 (San Cristóbal: $Q_{\text{obs}} = 0.44$, $Q_{\text{null}} = 0.48$, $t = -25.7$, $p < 0.001$; Santa Cruz: $Q_{\text{obs}} = 0.48$, $Q_{\text{null}} = 0.50$, $t = -17.4$, $p < 0.001$; figure 2). The outcome of inter-layer null model 2 (electronic supplementary material, Note 1) revealed a pattern similar to that of inter-layer null model 1. Therefore, our modularity analysis does not seem to be influenced by the selection of the reshuffling algorithm. The EMN was partitioned into a mean of 3.16 and 3.97 modules, and the inter-layer null model 1 consistently predicted fewer modules than observed ($t = -18.99$, $p < 0.001$; $t = -15.82$, $p < 0.001$, for San Cristóbal and Santa Cruz, respectively). Plants had a higher constancy and lower adjustability regarding their module affiliation with only nine out of the 77 plant species (6.7%) on San Cristóbal, and eight out of the 88 plant species (7.3%) on Santa Cruz remaining in the same module across the two types of interactions. By contrast, birds showed interactions with a different set of species in each layer, thus frequently changing their module affiliation (San Cristóbal: mean = 58.4%; Santa Cruz: mean = 53.3%). Adjustability was

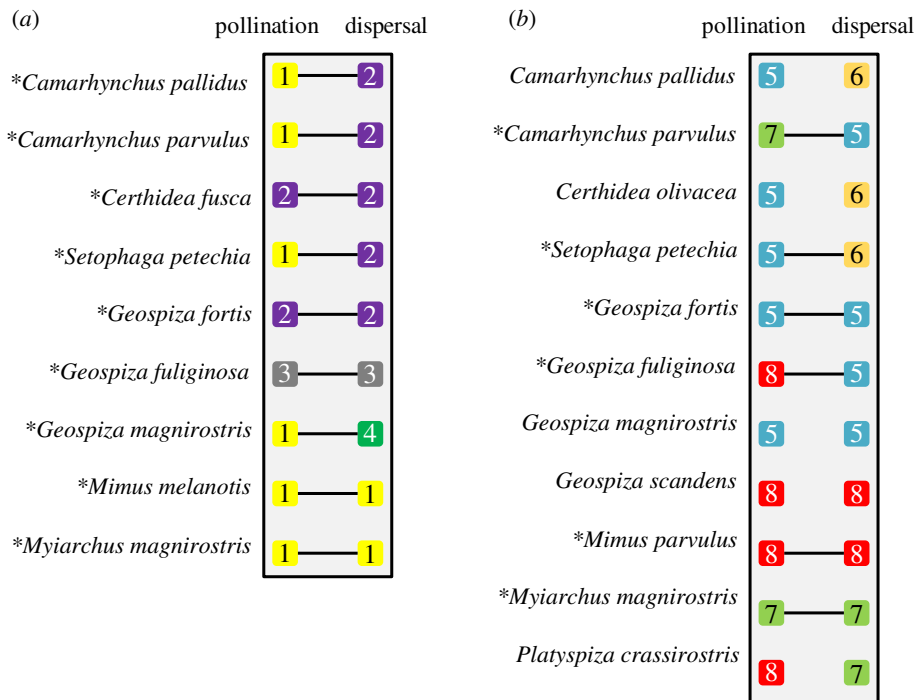


Figure 2. Module affiliation of bird species in the multiplex network according to the run with the highest maximized modularity. For each island (San Cristóbal, *a*; Santa Cruz, *b*), bird species with the same colour belong to the same interaction module. * Species that link pollination and seed-dispersal networks (i.e. bird species with individuals dispersing both pollen and seeds). Colours are not related between islands. (Online version in colour.)

Table 1. Total variance explained by each of the two principal components (PC1, PC2), and proportion of variance of each trait explained by the PC. The main trait contributing to each PC is highlighted in italics.

	PC1	PC2
standard deviation	2.26	0.67
% variance	85.27	7.61
cumulative %	85.27	92.88
trait		
wing length	<i>40.03</i>	15.96
third primary feather length	22.28	<i>16.61</i>
tarsus length	3.09	0.53
gape width	0.53	0.77
bill length	2.26	0.19
body mass	31.80	<i>65.93</i>

higher than predicted by the null models for both bird and plant species (all $p < 0.001$).

(c) Association between species traits, abundances and multilayer versatility

The PCA showed two components accounting for 92% of the total variance: PC1 accounted for 85% of the variance and was mainly explained by wing length, whereas PC2 accounted for 7% of the variance and was mostly explained by body mass (table 1).

Multilayer versatility revealed that the small ground-finch (*G. fuliginosa*) is disproportionately important, followed by Galápagos flycatcher (*M. magnirostris*) and yellow warbler (*S. petechia*) (see in figure 3 the ranking of bird species

according to their multilayer versatility and monolayer pollination and seed-dispersal networks). The importance of *G. fuliginosa* derives mainly from playing the most central role in the EMN structure because it shares plant partners with many other bird species.

Results from the GLMM showed that multilayer versatility was negatively associated with bird size (PC1) and positively associated with bird abundance (figure 4), indicating that small and abundant bird species tended to be more important connecting pollination and seed-dispersal networks. The variance accounted by bird size alone was 63%, while the variance accounted by species abundance was 25% [60].

4. Discussion

Estimating inter-layer edge weights (i.e. the strength with which each species connects different ecosystem functions) is not trivial, and there is still a lack of empirical data for most systems to accurately quantify them. In this study, we were able to use the same currency for intra- as inter-layer edge weights, which is necessary to explore and analyse the overall structure and cohesion of the pollination and seed-dispersal networks. These interconnected processes have rarely been considered together, and we use here two recently developed and highly informative descriptors of the multiplex network structure: multilayer modularity and versatility. We further explore the role of species traits and abundance as the drivers of species importance for bridging both processes.

(a) Interconnectivity of pollination-dispersal networks

Our results show that pollination seed-dispersal networks in the Galápagos are strongly interconnected by birds, given that 80% of all species (and 100% of species in one of the study islands) act as both pollen and seed-dispersers. This

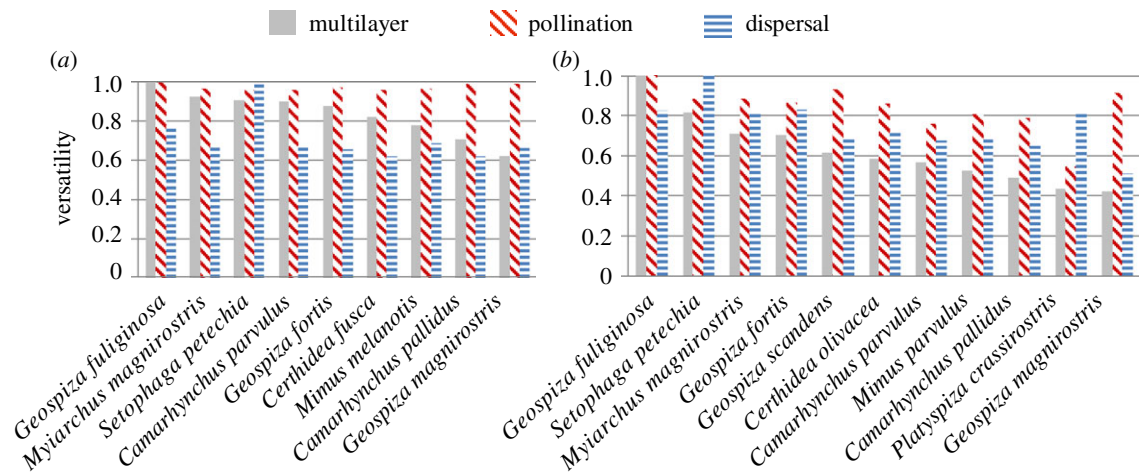


Figure 3. Versatility of bird species in the multiplex network and monolayer pollination and seed-dispersal networks on the islands of San Cristóbal (a) and Santa Cruz (b). (Online version in colour.)

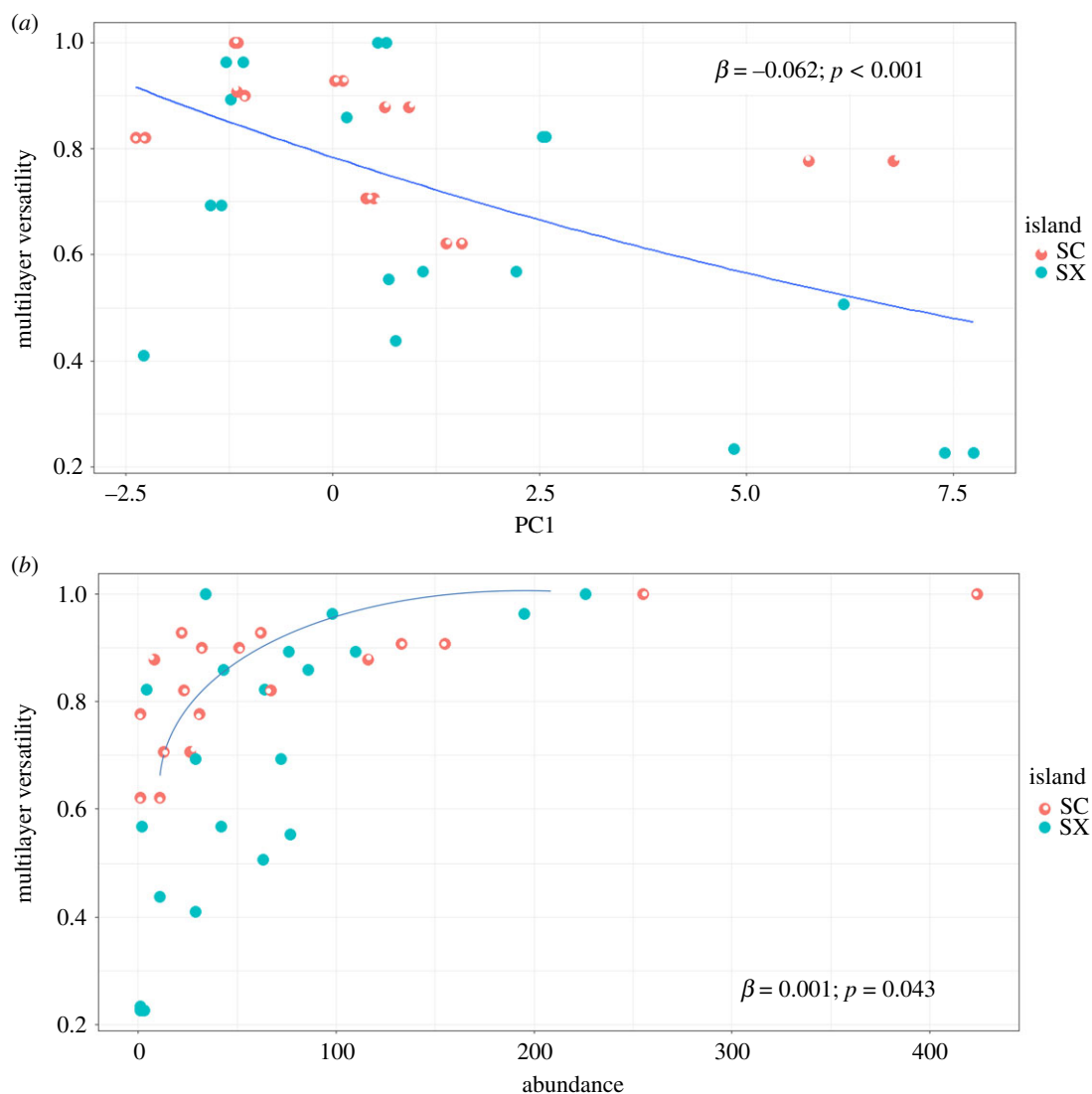


Figure 4. Relationships between species versatility, principal component 1 (PC1) and abundance in the multiplex network; GLMMs accounting for random variation among sites and islands. Slope estimates (β) and p values obtained for each variable are shown. We applied a logarithmic transformation of the scale (functions 'scale_y_log10' and 'scale_x_log10') to the PC1 plot, and of the coordinate system (function 'coord_trans') to the abundance plot. (Online version in colour.)

high network interconnectivity is attributed to the birds' response to the scarcity of their typical food (mostly insects), the abundance of floral resources and reduced predation risk, by massively widening their trophic niches towards flowers

and fruits [27,61]. Such 'interaction release' [61] is evident in both mutualisms. For example, the Galápagos flycatcher, a typical insectivorous bird, is a key seed-disperser of at least 13 plant species, and the small ground-finch, a typical

granivorous bird, visits the flowers of at least 34 plant species, being an effective pollinator of at least some of them [61,62]. Although most species engaged in both functions, only a small proportion of individuals effectively linked the two processes, stressing the need to further consider inter-individual variability when exploring species functional roles.

We estimated inter-layer edge weight by sampling the role of the same individual identified with a unique bird ring number during an entire year. An EMN can assume a uniform inter-layer edge weight for all species engaging in two layers or otherwise quantify the participation of each species across layers. The latter provides a much better reflection of real-world interactions [18,63]. We thus independently estimated empirical inter-layer edge weights for all species connecting the two processes, incorporating this information to evaluate the EMN structure. Our results show a wide variation among species in linking both processes, i.e. species contribute differently to the modular organization of the multilayer network. By contrast, the pattern of plant–bird interactions within each process does not seem to affect the overall modular structure. This is probably because plant–bird interactions in our system are largely opportunistic, and not the result of highly specialized interactions. Hence, our findings indicate that the identity of the species bridging the two processes has a stronger influence than the interactions established on each separate layer.

The opportunistic behaviour of Galápagos birds may also explain their high adjustability. This means that most bird species select a group of plants to explore for nectar resources and a different group as a fruit resource, taking advantage of all resources they can accede to a given time. This in turn could be due to differences in species traits that determine the possible types of interactions [64]. For instance, some plant species (e.g. *Waltheria ovata* and *Cryptocarpus pyriformis*) produce abundant flowers, which attract many bird species for pollen but produce dry fruits that are poorly attractive to dispersers [65]. Rainfall and cloud cover play an essential role in determining Galápagos plant growth and reproduction, and thus flower and fruit availability [66]. It might explain why some species are adjustable on one island but not on the other. The capacity of species to adjust their trophic interactions to specific contexts is probably crucial for species persistence in isolated and rapidly changing environments such as oceanic islands, promoting at the same time a greater connectivity across different processes [54].

(b) The role of niche and neutral processes in interconnected networks

The small ground-finch was the most important species to the cohesiveness of the multiplex network, by connecting the two stages of the reproductive cycle of plants, and thus it probably enhances the stability of plant communities [67]. Small ground-finches are known for incorporating a high proportion of small, soft seeds into their diets [68], and they also show a strong interaction release towards flower consumption [61]. Their importance as pollinators and seed-dispersers seems to be captured by multilayer analyses better than by monolayer networks (figure 3). This information is ecologically important because species with greater versatility can propagate the effect of disturbances through different processes. For instance, in intertwined mutualistic–antagonistic networks, such species are considered as ‘dual keystones’, i.e. having a double role in bottom-up and top-down processes in communities [14,69]. In

mutualistic EMN, central bird species may contribute more to maintaining part of the floral diversity by reinforcing key stages of plant life cycles, especially those acting as double mutualists (i.e. more pollination leading to more dispersal and vice versa) [25,27].

Body size and species abundance were two independent drivers of the importance of species in connecting pollination and seed-dispersal, indicating that both niche and neutral processes explain the structure of EMN. Mello *et al.* [20] previously assessed the role of animals in articulating two mutualistic networks, but they could not consider the influence of body size due to the small number of double interactions in that study. From monolayer networks, it is known that a trait that is critical for one type of interaction might be irrelevant for another type. For instance, bill length is a determinant in plant–pollinator interactions, but not particularly relevant in plant–frugivore interactions [70]. By contrast, a trait may be important to both kinds of interactions but differ in the magnitude or direction of its effect. For example, having a wide gape allows a bird to eat fruits of a broad range of sizes [71,72], but it can restrict its access to flower resources protected by tight corollas. However, when the two functional roles are tackled together (this study), the trait-based approach positions species differently according to their overall importance within the wider EMN. Therefore, labelling species as either pollinators or seed-dispersers is a clear oversimplification of their potential dual ecological role.

Body size strongly determines species’ energetic requirements. In highly variable environments such as the Galápagos, large birds are more strongly constrained by years of low food availability, for example, due to prolonged droughts [68]. Therefore, their functional role as mutualists is likely to be less stable than that of smaller birds might more easily cope with periods of food shortage due to their lower energetic requirements and potential to explore alternative food sources (e.g. insects). This effect is probably more evident in insular ecosystems, particularly on oceanic islands, characterized by low species diversity and functional redundancy [73].

The positive effect of species abundance on the cohesion of the EMN is consistent with other studies documenting how abundance drives generalization in both pollination and seed-dispersal monolayer networks [74,75]. Our work adds to such studies by quantifying the relative contribution of species abundance to the interconnectivity pattern of a multiplex EMN. As predicted by the neutral theory of biodiversity [76], in EMN of generalized free-living animals and plants, abundance is a key driver of interaction probability and consequently of species roles as connectors between processes. Networks depicting higher interaction specificity between animals and plants should however be less influenced by local abundance [31]. The positive effect of species abundance on the cohesion of the EMN might seem to contradict the non-significant effect that abundance has on edge weights for either pollination or seed-dispersal monolayer networks. However, the contribution of a species to network versatility is not simply the result of interaction weight with other species but also of how links are distributed [54], both across partner species within each layer and between the layers in which a species is present. For instance, an abundant species with low edge weight may have a high versatility if it distributes its interactions across species in different layers (e.g. *G. fortis*), whereas a rare species may have a high edge weight but a low versatility if most of its

interactions occur with a few species in only one layer (e.g. *G. magnirostris*) (figure 3; electronic supplementary material, figure S1).

For less abundant bird species or those with a low number of captures, our edge weights could be underestimated. However, an increase in the sampling effort (the number of nets multiplied by the number of hours) per month was not reflected in the capture of more birds (electronic supplementary material, table S1 and figure S2). The effect of abundance found in the GLMM seems not to be affected by sampling effort, since even considering *G. fuliginosa* as an outlier, multilayer versatility was still significantly associated with species abundances (electronic supplementary material, figure S3).

The interconnectivity pattern in real multiplex mutualistic networks appears to be explained by a combination of biological and neutral processes. Body size affected the overall importance of a species as a functional inter-layer connector. Given that species size is also related to its extinction risk, biased detection of inter-layer connectors might affect ecosystem functions in yet unpredictable ways. Even at the intra-specific level, we argue that identification of the key traits for bridging different types of interaction holds great potential to further understand the

strength of the evolutionary processes structuring the architecture of real-world networks, which are formed by hundreds of species interacting in multiple ways.

Data accessibility. Data are available at <https://doi.org/10.6084/m9.figshare.9644990.v2>.

Authors' contributions. A.T., R.H. and M.N. conceived the study; R.H. collected the data; R.H. and A.T. prepared the datasets; S.H.P. performed the statistical analyses; S.T. assisted with multilayer network analyses; C.T. and S.H.P. prepared figures; S.H.P. led the writing with significant contributions from all authors.

Competing interests. We declare we have no competing interests.

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