Species traits and community structure can drive large-scale spatial propagation of effects in ecosystems

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Abstract

Species can directly and indirectly affect others across communities and habitats, yet the spatial scale over which such effects spread remains unclear. This uncertainty arises in part because the species traits and landscape structures allowing indirect effects to propagate may differ across scales. Here, we introduce a topological network metric, communicability, to explore how indirect effects propagate across space in simulated metacommunities and in a large-scale plant-frugivore network across the territory of Aotearoa New Zealand. We show that generalist birds and plants spread indirect effects efficiently at the local scale, whereas a widespread distribution further allowed species to propagate effects across the landscape. Habitat composition, rather than arrangement, was the most important landscape factor in our study, generating several hotspots of effect propagation around forested areas. Overall, our results indicate that generalist and widespread species, two characteristics associated with species invasions, are the most likely to propagate large-scale ecological impacts.

Introduction

Every species influences its surroundings to different degrees, including its biotic and abiotic context. For example, predators or mutualists directly influence the demography of their interaction partners through consumption or facilitation, or the population dynamics of non-partner species through one or more shared partners (i.e. indirect effects (Pires *et al.*, 2020)). Quantifying how these effects propagate across space is crucial for understanding the rate and extent to which disturbance propagates in ecological systems and the relative importance of different species and habitats in connecting communities and ecosystems (Hackett *et al.*, 2019).

Measuring the spatial propagation of ecological effects across communities is challenging, as they may involve many direct and indirect pathways, which are exceedingly difficult to track simultaneously in natural systems. Therefore, our understanding of indirect effects in natural systems comes mostly from studies where such indirect effects are linear and non-spatial, or from small, experimentally manipulable communities. This began with work on trophic cascades, whereby the biomass of a primary resource is indirectly affected by a top predator, via changes in the biomass

of an intermediate consumer (Ripple *et al.*, 2016). Later studies used dynamical simulations of networks (Montoya *et al.*, 2009) or experimental species removals from communities to demonstrate that the population (Wootton, 2002) and evolutionary (Cosmo *et al.*, 2023) impacts of indirect effects can be at least as important as those of direct effects. Additional studies combined network analysis with experimental manipulations of host-parasitoid systems to demonstrate indirect effects among hosts via shared parasitoids (Morris *et al.*, 2004; Tack *et al.*, 2011).

Studies of indirect effects in ecological systems have mostly focused on local communities, often assumed to be spatially homogeneous and ignoring cross-habitat connections. Yet, populations and communities are open systems in which fluxes of individuals and nutrients are key for their dynamics (Gounand *et al.*, 2018; Gravel *et al.*, 2016). Consequently, theory has shown that indirect effects can vary markedly across space depending on whether species disperse across patches, forage, or both (García-Callejas *et al.*, 2019). In addition, indirect effects can also occur across habitat boundaries, between e.g. aquatic and terrestrial habitats (Knight *et al.*, 2005) or native forest and plantations (Frost *et al.*, 2016). Despite this potential for spatial propoagation of indirect effects, the role of different spatial configurations or different species in driving indirect effects has not yet been tested.

We hypothesise that species' propensity to spatially propagate indirect effects likely depends on their traits. First, species' traits can predict their tendency to interact with others (Bartomeus *et al.*, 2016). Second, although species' tendency to connect with others within a habitat can vary independently of their role in connecting across habitats (Hackett *et al.*, 2019), traits such as trophic generalism (within a habitat) can determine a species' propensity to spill over from one habitat to another (Frost *et al.*, 2015). Thus, we hypothesize that the traits that predict species' tendency to propagate indirect effects can differ across spatial scales. Moreover, because species traits can determine the environments they inhabit, traits may influence the impact of landscape configuration on dispersal among populations (Duflot *et al.*, 2014; Thierry *et al.*, 2022), and therefore on the propagation of effects. Likewise, native and exotic species tend to have markedly different network roles (Aizen *et al.*, 2008), and varying abilities to indirectly influence each other (Allen *et al.*, 2020, 2021). Therefore, we hypothesise that species provenance may be a

relevant trait for understanding their contribution to propagation of indirect effects.

Combined, these evidences and hypotheses suggest that the spatial propagation of indirect effects may i) be non-trivial to predict, ii) potentially spread between populations that do not interact directly, iii) be related to species-level traits, and iv) cross habitat boundaries, with implications for spatial conservation and restoration actions. Yet, despite their importance, we lack a general understanding of what factors determine the strength or probability of spatially-propagating indirect effects. In particular, we lack a conceptual ground from which to build theory and models, quantitative metrics that capture how effects propagate across ecological systems, and large-scale spatial data with which to test and refine hypotheses.

Here we study the propagation of direct and indirect effects across space in ecological systems. We intentionally refer to the propagation of *effects*, as that term encompasses any potential process propagating between any two nodes in a network. In ecological terms, these effects will generally be reflected in variations in population abundances or vital rates which arise through a species interaction. We first introduce a new metric from network theory to quantify propagation across direct and indirect paths between species. This metric, *communicability*, estimates the propagation of effects between any two nodes in a network only from information about its structure (Estrada & Hatano, 2008), potentially bypassing the need to quantify the population dynamics of the interacting nodes (i.e. species). Then, we explore the role of landscape-level configuration and species-level properties in driving the propagation of effects across space, using simulated landscapes. Lastly, we scale up our findings by analyzing how effects are propagated in a large-scale ecological system: the network of plants and bird frugivores across the territory of Aotearoa New Zealand. We overcome data limitations by generating a data-informed country-scale network of species interactions. Through this approach, we evaluate which traits (provenance, morphological- and/or interaction-traits) are related to the observed capacity of species to link ecological communities in space by propagating effects across scales, and which landscape properties promote or hinder the propagation of effects across the territory.

Methods

Propagation of effects in ecological communities: communicability

By conceptualizing ecological communities as networks, whereby species (or populations) are nodes that are connected through links representing ecological interactions, we can analyze how community structure relates to the propagation of ecological effects. The topological structure of a network provides information on how effects on a given node can spread through the rest of the network (Wang *et al.*, 2017). Any two nodes in a network can be linked through a multitude of paths, including the shortest path(s) between them and all non-shortest paths (Fig. 1). In nodes that are not directly connected, the flow of effects is commonly analysed through their shortest path, i.e. the path that connects both nodes via the smallest number of steps. This is the case, for example, in analyses of trophic cascades along linear chains (Estes *et al.*, 1998; Ford & Goheen, 2015). The length of shortest paths is captured in network metrics such as betweenness and closeness centrality. However, recent studies have emphasized the importance of indirect, non-shortest paths, in connecting nodes across different types of networks (Akbarzadeh & Estrada, 2018; García-Callejas *et al.*, 2019). The combined flow across all possible paths is quantified by the *communicability* between the two nodes (Estrada & Hatano, 2008; Estrada *et al.*, 2012). In this metric, shorter paths have larger contributions to the flow between nodes than longer ones. In particular, as defined in Estrada & Hatano (2008), if p_{ij}^{s} is the number of shortest paths between the nodes i and j having length s, and W_{ij}^{k} is the number of walks connecting i and j of length $k^{ij} > s$, the communicability between nodes i and j is defined as

$$G_{ij} = \frac{1}{s!} p_{ij} + \sum_{k>s} \frac{1}{k!} W_{ij}^{k} \tag{1}$$

This definition implies that as the length k of the paths increases, these will have an exponentially decreasing effect on the overall communicability between i and j. The formulation also allows differentiation of the effect of shortest paths and paths of arbitrary length on the metric. Further, for obtaining its aggregated value, it can be reformulated in terms of powers of the interaction matrix $\mathbf{A}$, as

$$G_{ij} = \sum_{k=0}^{\infty} \frac{(\mathbf{A}^k)_{ij}}{k!} = (e^{\mathbf{A}})_{ij} \tag{2}$$

Importantly, these expressions are valid for binary matrices (Estrada & Hatano, 2008) and for positive weighted matrices (Estrada *et al.*, 2012). The communicability metric at the network level is the average of the pairwise values. For a square matrix $\mathbf{A}$ with S nodes:

$$G(\mathbf{A}) = \frac{\sum_{i \neq j} G_{ij}}{S(S-1)} \tag{3}$$

Note that we use the notation G_{ij} to define the communicability between the pair of nodes (i, j), and $G(\mathbf{A})$ for the network-level metric computed on the matrix $\mathbf{A}$. This metric should be standardized in order to allow meaningful comparisons across systems. For doing so, here we extend the normalization scheme that Bertagnolli *et al.* (2021) developed for the information flow of a network through its shortest paths. In particular, we first denote $SP(i, j)$ as a weighted and possibly directed shortest path from node i to j in a weighted matrix w. The total weight (or flow) alongside $SP(i, j)$ is then $\phi_{i,j} = \sum_{n,m \in SP(i,j)} w_{nm}$. The matrix $\Phi = (\phi_{ij})$ represents an artificial connectivity matrix made of shortcuts, where total weights along shortest paths are wired in one topological step (see Fig. 1 of Bertagnolli *et al.* (2021) for an example). Given an interaction matrix $\mathbf{A}$ we can define a maximally connected matrix $\Phi_{\mathbf{A}}$, and the normalized communicability metric is simply

$$\overline{G}(\mathbf{A}) = \frac{G(\mathbf{A})}{G(\Phi_{\mathbf{A}})} \tag{4}$$

Communicability in simulated metacommunities

In the Supplementary Section "Communicability in small metacommunities" we provide a worked example for obtaining and evaluating network-level communicability, and its behaviour across different metacommunity structures. Furthermore, because communicability is a structural metric, it does not account for the dynamics of the system - e.g. whether variations in abundance across species modify indirect effects in the system, or whether negative and positive indirect effects

potentially cancel each other out. Therefore, we tested the correspondence of our communicability metric with a dynamical approach to quantify net effects between species based on estimating population dynamics (Supplementary Section "Structural and dynamical propagation").

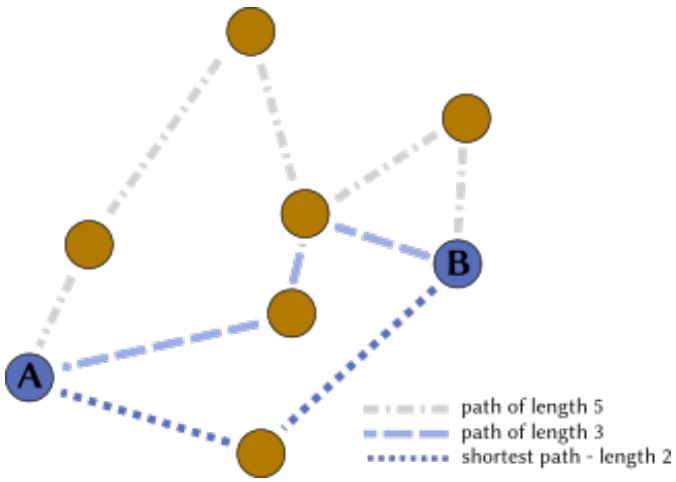

Fig. 1: Shortest path and two examples of non-shortest paths between two nodes A and B in a network. Communicability G_{AB} approximates the effects that propagate from A to B, accounting for every path connecting them. The shortest path has the strongest influence on the metric, and every other indirect path has a contribution to communicability that decays exponentially with its path length, i.e. the number of links that are crossed. Here we draw binary links for simplicity, but the metric can also be obtained for positive-weighted networks.

To test how species traits and landscape structure influence the propagation of effects in a controlled setting, we simulated gridded landscapes populated by virtual species, with varying levels of three key parameters: the spatial distribution of species, the distribution of interactions between species, and their dispersal abilities. The first step was to generate the virtual landscapes, which we model as meta-communities in a multi-layer network framework. Within the multi-layer network, nodes are species and there are two types of links: interactions within a grid cell and dispersal among grid cells (with dispersal links connecting spatially separated populations of the same species).

We created grids of 100 cells (10×10) and imputed a randomly generated value in the interval [0,1] to each cell, representing a single environmental dimension. To test the influence of landscape configuration, we generated landscapes with varying levels of spatial autocorrelation $c \in [0.1, 0.9]$ in their environmental dimension (Fig. S1), analogous to a habitat fragmentation gradient. In parallel to creating these gridded landscapes, we generated regional pools of 30 species, where

each species was randomly assigned three uncorrelated values. First, a numeric value $n \in [0, 1]$ representing its optimum in the landscape environmental dimension defined above. Second, another numerical value to each species representing its dispersal potential. The dispersal potential for each species was sampled from an exponential distribution, whose rate parameter $d \in [0.1, 0.9]$ is the control parameter of the gradient in dispersal abilities (Fig. S2). Third, a measure of the species' degree (i.e. its number of interaction partners or links) in the network of interactions among the 30 species. Specifically, we obtained species' degrees by sampling from poisson distributions with means in the interval $\lambda \in [3, 15]$. The metawebs of species interactions (the networks of all potential interactions between the species present in the meta-community) were thus built from these species degree sequences by assigning links randomly among species (Fig. S3).

For each simulated lanscape, we finally placed the virtual species in grid cells according to their environmental optimum, whereby species i, with environmental optimum e_i, would be present in all cells with values $e_i \pm 0.2$. Two species were linked (i.e. interacted) in a cell if they did so in the metaweb, such that each cell in the landscape had a local interaction network that was a subset of the metaweb. Finally, the dispersal links between occurrences of a given species in different cells were imputed according to its dispersal potential: if a population of a species was present in a cell that was within the dispersal range of another population of that same species in another cell, a dispersal link was established between both populations. For simplicity, we did not include spatial links connecting different species in our networks. In our simulated landscapes, interaction and dispersal links are both binary, so communicability is equally affected by dispersal and interaction links. Thus, each simulated landscape resulted from a combination of 1) spatial autocorrelation in an environmental dimension (c), which influenced the distribution of the virtual species, 2) connectivity of the corresponding metaweb (λ), and 3) distribution of dispersal distances (d).

Note that this approach is static, i.e. we do not model occupancy dynamics, but rather each virtual landscape represents a single snapshot of a metacommunity given by these three control parameters. We generated a gradient of 5 values for each of these parameters, for a total of $5^3 = 125$ combinations. For each of these combinations we generated 10 landscape replicates, for a total of 1250 simulated landscapes. Lastly, for each of these, we obtained the species-level aggregated

communicability G_{i*} (Eq. 2), which informs about the contribution of species i in propagating effects across the landscape, and the normalised landscape-level communicability $\overline{G}$ (Eq. 4).

We assessed how landscape-level communicability $\overline{G}$ was influenced by the three control parameters of our simulated landscapes, namely 1) landscape configuration (i.e. spatial autocorrelation of the environmental dimension), 2) metaweb structure summarised via species degree and its corresponding distribution, which implies overall metaweb connectance (Poisot & Gravel, 2014), and 3) dispersal capacity in the species pool. Likewise, at the species level, we evaluated the relationship between species' communicability G_{i*} and three species-level properties: 1) prevalence (the number of occuppied cells in the simulated landscape), 2) generality (degree in the metaweb), and 3) dispersal distance. Since these results are obtained from *in silico* observations, we analysed them qualitatively rather than performing statistical tests on the simulation outputs (White *et al.*, 2014).

Scaling up with plant-frugivore interactions

We used a national metaweb of plant-frugivore interactions to project a whole-country spatial interaction and dispersal network, across a grid of the two main islands of Aotearoa New Zealand (in a similar approach to the simulated landscapes). We then used this spatial multi-layer network to evaluate how species' potential to indirectly affect others (measured as communicability) is influenced by spatial context. Specifically, we asked which characteristics of species and parts of the territory contributed the most to spatial communicability, and why? Aotearoa New Zealand represents an ideal setting for such a study, because it encompasses 1) both highly fragmented landscapes and large natural areas, and 2) a large variety of habitats and climate types. For building the spatial multi-layer network, we used interactions between 102 plant species and their 22 bird frugivores for the two main islands of Aotearoa New Zealand, originally obtained by Peralta *et al.* (2020) from the literature and from direct observations. To complement these interaction data, we obtained the spatial distribution of each plant and bird species by combining different sources of observational data, complemented by estimating potential co-occurrences from observed data and environmental covariates. In parallel, we obtained relevant traits for bird species from

Peralta *et al.* (2020), from the AVONET database (Tobias *et al.*, 2022) and body sizes from the study by Lislevand *et al.* (2007). Morphological traits for plant species were also obtained from Peralta *et al.* (2020).

Species distributions: observations and modelled occurrences

In order to obtain a baseline spatial distribution of each plant and bird species, we compiled observations from two diferent sources and modelled the expected occurrence of each species according to environmental, spatial, and biotic covariates. Specifically, we first compiled plant and bird observations from systematic samples of Aotearoa New Zealand biodiversity. We gathered plant observations from datasets contained in the New Zealand National Vegetation Survey Databank (`https://nvs.landcareresearch.co.nz`, Wiser *et al.* (2001)). For bird species, we gathered observations from the New Zealand Department of Conservation 'Tier 1' monitoring program (Allen *et al.*, 2013). The details of these sampling schemes are available in the references, but summarising, these datasets represent systematic observations of plant/bird individuals that we filtered to presence/absence data across the grid of the territory. However, the spatial extent covered by these datasets is limited, in most cases, to land owned by public organisations. We therefore developed a modelling approach to project their distribution over the whole study area. In particular, we expanded the joint species distribution model of Hierarchical Modelling of Species Communities (HMSC, Ovaskainen & Abrego (2020); Ovaskainen *et al.* (2017)), implemented through the R-package Hmsc-R (Tikhonov *et al.*, 2020b) with a nearest-neighbor Gaussian process for spatial data (Tikhonov *et al.*, 2020a) (see Supplementary Section "Observed and predicted occurrences" for details). From this model, we obtained the expected occurrences of every plant and bird species in the studied area, and we used those as proxies of the real distribution of bird and plant species in the rest of the analyses (see Figs. S11-14 for examples of observed and predicted occurrences). Note that these expected occurrences account for fine-scale environmental variation (e.g. land-use, elevation) within a species' range.

Empirical multi-layer network

We combined the metaweb of empirically-observed interactions between plants and birds with the spatial occurrences derived from our model to generate spatially explicit local networks of plants and frugivores, connected via dispersal. For doing so, we divided the studied area into a grid of square cells of 10x10 km, resulting in 3030 grid cells. This resolution represents a balance between computational tractability and a reasonable spatial extent for local interactions, considering the mobility of bird species. The local network at any given cell was built from the modelled occurrences of bird and plant species in that cell, and co-occurring bird and plant species were deemed to interact if they did so in the regional metaweb. This approach assumes that any species which are known to interact do so at some time in every location in which they co-occur. While we acknowledge that potential interactions are not always realised (Jordano, 2016), adding noise to the realisation of interactions would not change the qualitative direction of our results, but rather would simply add variance. Conversely, it is also unlikely that all interactions between all species have been observed and recorded in the literature, so our metaweb of potential interactions is likely to be conservative; however, approaches to infer interactions (e.g., based on species traits) also carry uncertainty (Bartomeus *et al.*, 2016).

In a last step, local networks in each cell were connected by dispersing bird populations to form a multilayer network, whereby interactions within cells are intra-layer links and dispersal among cells generates inter-layer links. First, we estimated bird dispersal kernels from empirically-derived traits, in particular their Hand-Wing Index (a trait strongly correlated with dispersal distance in birds, Sheard *et al.* (2020)). We assumed a negative exponential dispersal decay with distance of the form:

$$f_{ij}^{s} = e^{-\frac{1}{HWI_s} * d_{ij}} \tag{5}$$

where f_{ij}^{s} is the dispersal rate between cells i and j for species s, HWI_s is the hand-wing index of species s and d_{ij} is the distance between cells i and j. Two populations of a bird species (in nearby cells) were connected with a strength between [0,1] determined by their dispersal kernel and the distance between the two cells. By linking local communities in this way, we assume,

for simplicity, that dispersal by birds is most important for fruiting species, and its dynamics are much faster, than dispersal of plant propagules by other means, so we ignore dispersal by plants.

Communicability calculation

For obtaining the overall communicability of this national multilayer network, which we can later decompose per species or grid cell, we need a full metacommunity structure in matrix form, i.e. a supra-adjacency matrix (Gravel *et al.*, 2016). The supra-adjacency matrix of the whole Aotearoa New Zealand multi-layer network is of size $(3030 \times 124)^2$ (i.e. 3030 cells multiplied by 124 species on each dimension of the square matrix), which renders it unfeasible to analyze as a whole. Therefore, we calculated the communicability of the species in the studied area through a moving-window approach. We selected each of the 3030 cells sequentially and calculated the communicability G_{i*} of local populations in that cell and a surrounding buffer of 30km, which represents a neighbourhood of 29 cells. This distance is the maximum distance computationally feasible to calculate for our study area, and a preliminary test showed that the communicability rank of species did not vary significantly at increasing distances, i.e. the most important species are preserved (Figs. S4 and S5). This means that the spatial contributions to communicability are concentrated in a relatively close neighborhood of the focal area of the populations, which is consistent with the life history and movement patterns of the species considered here.

From this calculation, we obtained a normalised communicability per local population of each species in each cell. The average of these local communicability values of populations across cells is what we term "average population communicability". In addition, we obtained the overall communicability of every species in the studied area, as the sum of their local communicability values - we denote this as "aggregate species communicability". Finally, the aggregated communicability of a given cell is the sum of the communicabilities of the local populations within that cell.

Statistical analyses

We analysed whether the communicability of a given species was related to its provenance (native vs. exotic), its network degree, and morphological traits (body mass for birds; fruit diameter and

maximum mean vegetative height for plants). We selected these variables because they are ecologically meaningful, relatively easy to obtain compared with other traits, and were not correlated among them in either birds or plants (Figs. S15 and S16). In particular, we did not include bird gape size, despite including fruit diameter, because it is highly correlated with body mass (Fig. S14), and our focus is not in predicting interactions through trait matching, but rather analysing the importance of general, overarching traits. In addition, we did not include dispersal ability, quantified via the Hand-Wing Index, to avoid circularity, because that trait was used to link populations in our spatial network in the first place. We repeated these analyses for the average population communicability and the aggregate species communicability, to understand potential differences between local and regional drivers. For quantifying network degree, we considered at the local scale the average local degree of the species, across all cells in which the species appears (including local and dispersal links). For the regional scale, the degree metric is that of the species in the metaweb. At the regional level, we also considered species' prevalence (the number of cells with recorded presences) as a predictor. For these analyses, we used generalised linear models with a tweedie distribution and log link function, implemented in the glmmTMB package v1.1.7 (Brooks *et al.*, 2017). The tweedie distribution is a flexible distribution that can explicitly model zeros and positive continuous values.

We also tested whether the aggregated communicability of a given cell was related to landscape characteristics: percentage of forest cover, percentage of shrubland cover, and habitat diversity (measured as the Shannon index of the relative frequency of habitat types present in the cell). We obtained spatial habitat data for New Zealand from the IUCN habitat characterisation map by Jung *et al.* (2020). We modelled these relationships with a generalised additive model with a tweedie distribution and log link function, explicitly considering spatial autocorrelation via a smoothing term on the coordinates of cell centroids. We implemented this model in the mgcv package v1.9-0. (Wood, 2011). For this and the previous models, we scaled all numerical variables before fitting and checked model consistency with the DHARMa package v0.4.6 (Hartig, 2022).

Results

Communicability in simulated metacommunities

The communicability metric presented here shows a good agreement with dynamic estimates of net effects between species (as calculated in e.g. Montoya *et al.* (2009)), so we consider it a valid first approximation of the propagation of indirect effects between populations, in the absence of more detailed information (see the Supplementary Section "Structural and dynamical propagation" for details). Therefore, we analysed in simulated meta-communities the determinants of landscape communicability, representing the potential for indirect effects to be propagated among species in our simulated landscapes. Communicability was mainly influenced by the structure of the metaweb (Fig. 2): higher species mean degree (i.e. species being interaction generalists), with corresponding higher metaweb connectance, resulted in higher communicability in the simulated landscapes. There was a smaller but positive signal of increasing dispersal distance, and lastly, landscape configuration (autocorrelation of the environmental dimension) showed no effect on the communicability values. At the species level, communicability was only influenced by a species' prevalence (the number of presences in the landscape), with an average Spearman's correlation coefficient of 0.73 (Fig. 3). Species' generality (degree in the metaweb) and dispersal distance were mostly uncorrelated with their aggregated communicability. Together, these simulations indicate that a species' prevalence in the landscape has the greatest impact on its ability to indirectly affect others, whereas its generalism and dispersal ability are more important at the community scale (i.e. when many species change in these traits).

Aotearoa New Zealand plant-frugivore metanetwork

The metanetwork of plant-frugivore interactions in Aotearoa New Zealand, after filtering for those species with available trait data, is composed of 102 plant species and 22 bird species, of which 92 plants and 14 birds are native. It has a connectance of 0.44, and the most generalist species are the New Zealand bellbird (*Anthornis melanura*), the kererū (*Hemiphaga novaeseelandiae*), and the silvereye (*Zosterops lateralis*) with 57 interaction partners recorded for each species, while there

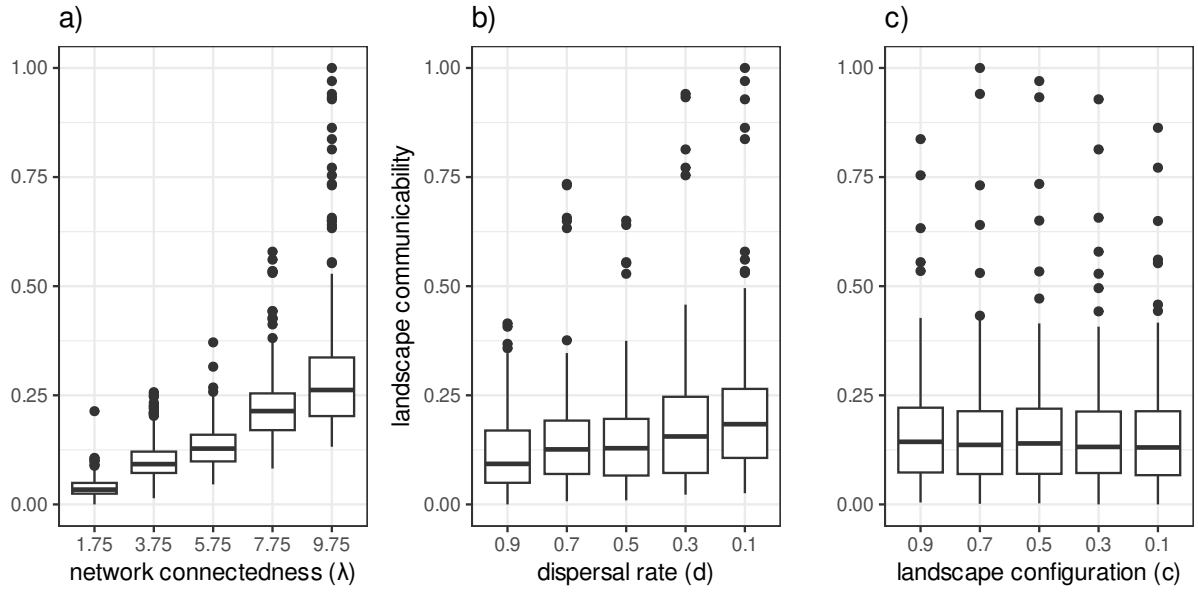

Fig. 2: Network-level communicability in simulated landscapes and its variation with three landscape-level factors: a) connectedness of species interactions (λ of the poisson distribution of links per species, i.e. degree, in the metanetwork); b) dispersal ability of species (rate parameter of an exponential distribution, with higher values indicating that species disperse greater distances); c) landscape configuration (spatial autocorrelation in the suitability of the environment for different species). In the boxplots, the horizontal black lines represent the median, the lower and upper hinges correspond to the 25th and 75th percentiles, and the vertical lines extend to the largest/smallest value up to 1.5 times the interquartile range (distance between 25th and 75th percentiles). N = 250 in each boxplot.

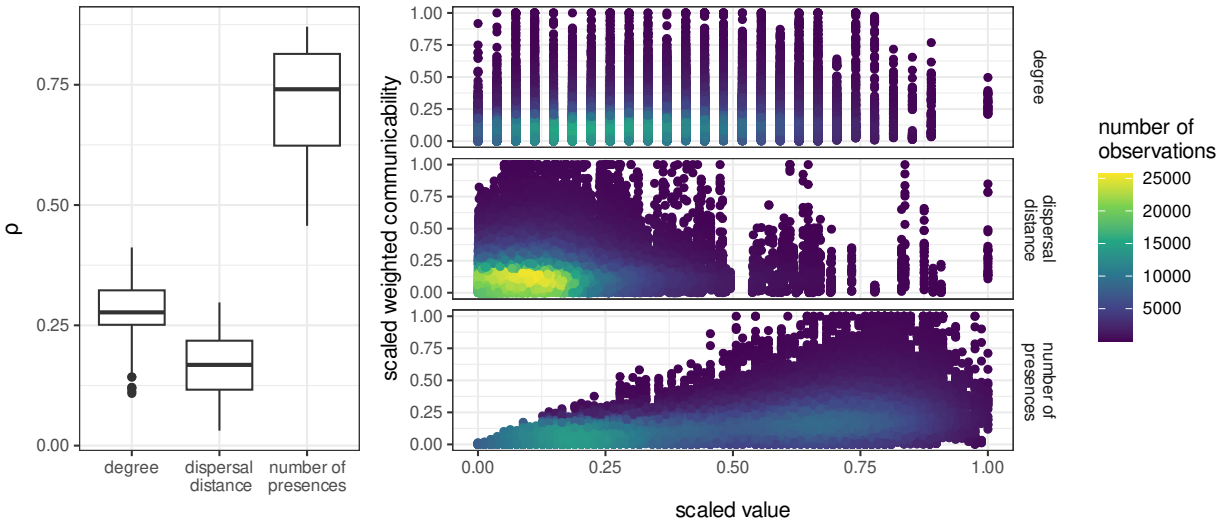

Fig. 3: Species-level communicability and its correlation with species traits. The left panel shows the distribution of Spearman's ρ correlation values between communicability and species' generality (degree), dispersal rate, and prevalence (the number of presences in the virtual landscape), respectively. The right panel shows how observations are distributed across these factors. N = 125 in boxplots of left panel, 34745 in each scatterplot of right panel.

are 27 plant species with only one recorded bird frugivore in the metaweb. The most prevalent species according to our distribution analysis are all bird species: the eurasian chaffinch (*Fringilla coelebs*, Fringillidae), the blackbird (*Turdus merula*, Turdidae), the silvereye (*Zosterops lateralis*, Zosteropidae), and the grey warbler (*Gerygone igata*, Acanthizidae), all present in more than two thirds of the territory ($>$ 2000 cells out of 3030).

Population and species-level communicability

The ranking of species according to their communicability varied depending on the spatial scale considered. Within local communities (panel A of Fig. 4), the kererū (*Hemiphaga novaeseelandiae*, a native bird from the Columbidae family) showed the highest average population-level communicability, followed by raukawa (*Raukaua edgerleyi*), a native plant from the Araliaceae family. However, the most important species when aggregating all local populations, i.e. at the scale of the whole study area (panel B of Fig. 4), were two bird species with widespread distributions in Aotearoa New Zealand: the silvereye and the blackbird. Silvereyes were self-introduced from Australia in the first half of the 19th century, so here we consider them a native species. Blackbirds,

on the other hand, are a worldwide distributed exotic species.

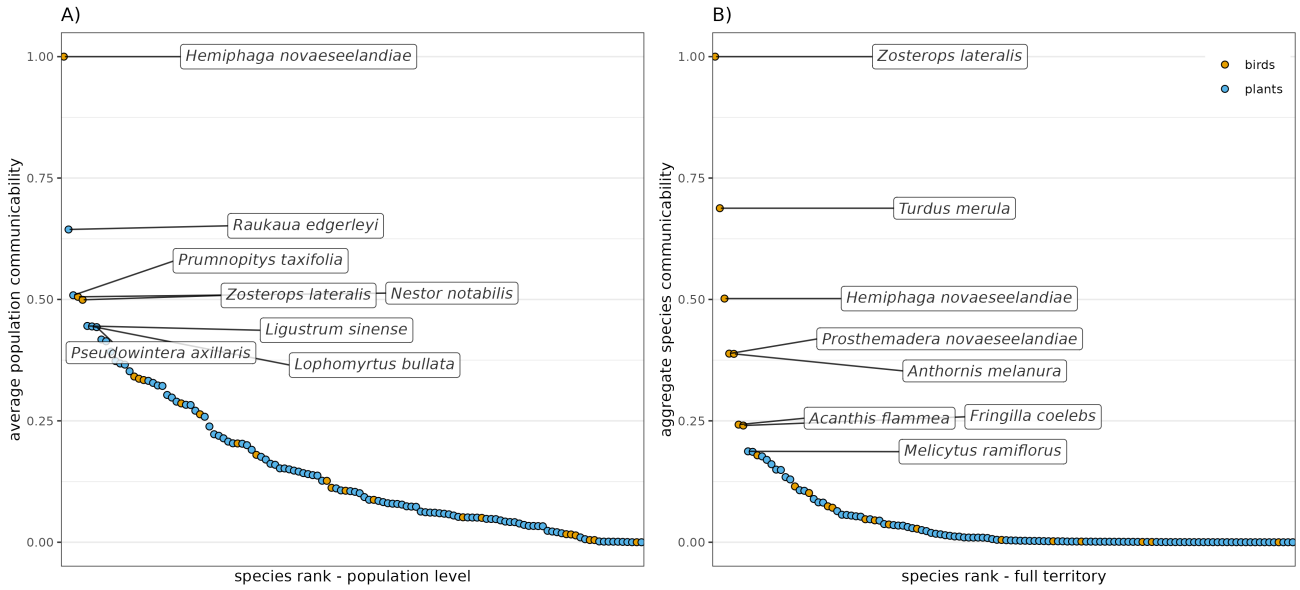

Fig. 4: Relative communicability values at the scale of local populations (panel A) and the whole study area (panel B). Communicability values are scaled in the range 0-1 in both cases.

These differences in ranking across scales emerged from the differing importance of traits across scales. Bird communicability within local communities was postively and significantly related to generality (network degree, Table 1), and also showed a non-significant tendency towards a positive relationship with body mass. At the regional level, it was likewise positively related to species degree in the metaweb, and also to prevalence (Table S1). The communicability of plant species, in turn, was significantly positively related at the population level to network degree and to fruit diameter (Table 2). At the regional level (Table S2), as with bird species, the highest positive effect on communicability was that of species prevalence followed by species degree, but native provenance also had a significant positive effect. Neither fruit diameter nor maximum average height had a significant effect at the regional level. In addition to examining the statistical significance of the models, we explored the partition of model variances between the different predictors. We did so because our study, while based on empirical data, has a variable sample size depending on the number of grid cells in which we discretise the studied area - in such cases, p-values can potentially be subject to high rates of type-I errors. The partitioning of the explained variance from each model confirmed the discussed trends: at the local level, the most important variable was always

the local population degree, both for birds (Table S4) and plants (Table S5). At the species level, species prevalence and degree in the metaweb were the variables explaining more variance for both groups (Tables S6 and S7).

Table 1: Coefficients of the generalised linear model relating population-level communicability with species traits, for bird species. Dispersion coefficient is 0.575.

	estimate	std.error	z	p.value
Intercept	-1.674	0.367	-4.559	< 0.001
status (Native)	-0.318	0.496	-0.642	0.521
degree	0.725	0.233	3.110	0.002
body mass (g)	0.384	0.216	1.780	0.075

Table 2: Coefficients of the generalised linear model relating population-level communicability with species traits, for plant species. Dispersion coefficient is 0.214.

	estimate	std.error	z	p.value
Intercept	-2.174	0.224	-9.708	< 0.001
status (Native)	0.015	0.236	0.064	0.949
degree	0.675	0.073	9.233	< 0.001
fruit diameter (mm)	0.111	0.055	2.001	0.045
max mean height (m)	0.045	0.069	0.651	0.515

The aggregated communicability of the plant and bird populations in each cell widely varied across the studied area (Fig. 5). In particular, most of the territory showed comparatively low values of communicability, and only a few spatial clusters displayed clearly larger values. These spatial clusters of high communicability were all in forested areas, and mostly surrounded by crop and/or pasture landscapes, as in the Whanganui National Park (the single cluster with highest communicability values, in the center-east of the North Island) or the Tararua Forest Park (southern border of the North Island).

Besides the visual inspection, communicability at the cell level was significantly and positively related to the percentage of forest and shrubland cover in the cell, and significantly but negatively related to the diversity of habitat types within the cell, measured as the Shannon index of the relative frequency of habitat types in the cell. These relationships had also a spatial signal, as there was a signficant spatial auto-correlation term in the analysis (Table 3). The influence of

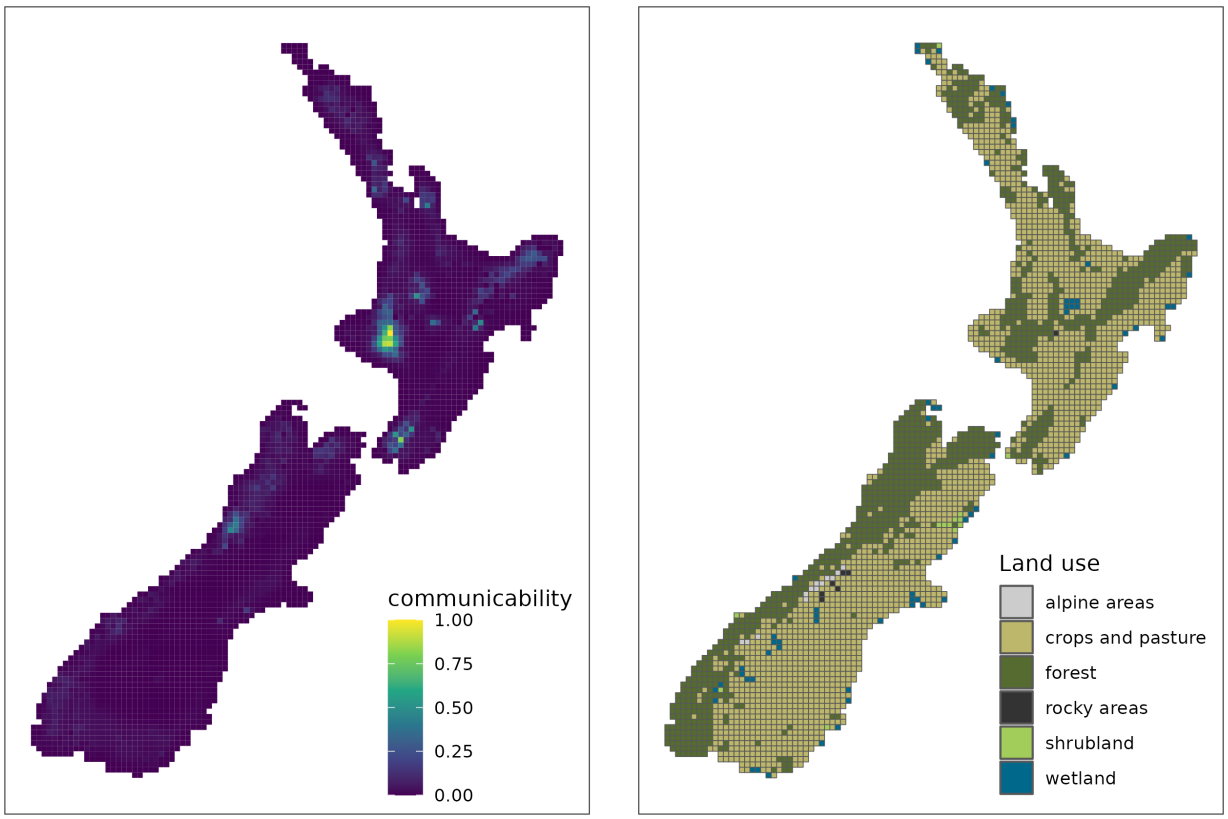

Fig. 5: The study area (North and South Islands of Aotearoa New Zealand) showing the division in grid cells. In the left panel, aggregated communicability per cell of 10 x 10km, calculated as the sum of the communicability of each species present in the cell. In the right panel, most prevalent land use category in each cell.

forest cover was likely mediated by changes in species richness, as percentage forest cover has a statistically significant positive correlation with the proportion of native bird species (Spearman's $\rho = 0.65$) and with overall bird richness ($\rho = 0.57$), as well as with the proportion of native plant species ($\rho = 0.44$) and overall plant richness ($\rho = 0.66$). Shrubland cover percentage and the diversity of habitat types showed weaker correlations among them and with other variables, always being < 0.5 (see Fig. S14 for all pairwise correlations). We further considered the effect of forest/shrubland cover in the neighbouring area of the focal cell, as well as the diversity of habitat types in that neighbouring area, but discarded these variables due to their high correlation with their cell-level counterparts. Nevertheless, the results of a model with neighbor-only landscape variables (Table S3) showed similar patterns as our main model.

Table 3: Coefficients of the generalised additive model relating the aggregated communicability values of each grid cell with landscape characteristics. The expressive degrees of freedom of the spatial smoothing term is 28.17, with an F-value of 43.21 and a p-value < 0.001.

	estimate	std.error	t	p.value
Intercept	12.657	0.02	623.008	< 0.001
forest cover (%)	1.009	0.025	39.651	< 0.001
shrubland cover (%)	0.407	0.026	15.733	< 0.001
habitat diversity	-0.198	0.026	-7.773	< 0.001

Discussion

Quantifying the biotic effects of species and their spatial signature are paramount to understanding and predicting spatial ecological dynamics within (Morris *et al.*, 2005) and across habitats (Frost *et al.*, 2016). The propagation of direct and indirect effects is also particularly relevant for understanding the effects of invasive species (Vagnon *et al.*, 2022), changing species distributions and disease spread in ecosystems (Tompkins *et al.*, 2011). Here we used tools from network theory and statistical physics to show that the spatial structure of biotic interactions and dispersal can be used to approximate the spread of direct and indirect effects. More importantly, we used these tools to demonstrate the scale-dependent role of different species, traits and landscape characteristics in this tapestry of direct and indirect interactions.

Focusing on the plant-frugivore network of Aotearoa New Zealand, we have identified key species and traits at the local (panel A of Fig. 4, Tables 1 and 2) and regional scales (panel B of Fig. 4, Tables S1 and S2) that disproportionaly connect the territory through direct and indirect biotic effects. We have further identified the relative importance of different areas in spreading or containing biotic effects (Fig. 5, Table 3). These results illustrated the importance of clear and measurable ecological mechanisms: morphological traits and/or regional prevalence for plants and birds, and land-use structure collectively shape the propagation of effects.

We have suggested that a species' potential to spread biotic effects across space can be conceptually related to different drivers. In particular, this capacity should be higher for species with (1) comparatively high dispersal ability, (2) a larger number of connections with other species (e.g. node degree), (3) higher abundance, or spatial prevalence across the landscape (assuming that local populations are connected to a certain extent in a metapopulation). Here we have shown that, indeed, bird and plant species that interact with many partners within local networks and across the country have the greatest potential to directly and indirectly affect others (i.e. highest communicability) in the Aotearoa New Zealand plant-frugivore network. Moreover species with a widespread distribution are most important for propagating effects at large scales. These insights are also in line with our theoretical expectations from simulated metacommunities. Other characteristics, such as species provenance or different morphological traits (bird body mass, plant fruit

diameter or maximum mean height) were not as clearly related to local or regional communicability. The ability of generalist, widely-distributed species to propagate effects at large scales is concerning given that many species are invading new territory to expand their range, and that these invasive species interact with many partners locally, in both their native and exotic ranges (Aizen *et al.*, 2008; Emer *et al.*, 2016), and globally (Fricke & Svenning, 2020).

Neither bird body mass nor plant maximum mean height were strongly correlated with species degree or prevalence, suggesting that in this system, body mass alone cannot explain species prevalence or degree of generalism/specialisation. The ecological processes and traits driving, in the first place, network roles and prevalence and, in turn, the capacity to propagate ecological effects across space are thus likely to vary across taxonomical groups and habitat types, but we hypothesise that will involve combinations of morphological and behavioural traits, in still unexplored "propagation syndromes" (Martins *et al.*, in preparation). Nevertheless, we have shown quantitatively that these easily-observed characteristics (species degree and prevalence) are a useful proxy of the importance of a species in effect propagation, which should be of importance in spatial conservation or in predictions of disease spread across taxa. Further refinements of this approach may incorporate population densities when this information is available: among the insights that this could provide, we hypothesise that expected higher population densities of large-bodied species in undisturbed habitats may better disentangle the relationships between body mass and species distributions across habitats. That would lead, in turn, to a better characterisation of the relationship between body mass and the capacity to propagate effects within and across habitats.

The analysis of communicability across space provides complementary insights to our species-level analyses. Areas with high forest and shrubland cover were comparatively more important for the propagation of ecological effects in space. In Aotearoa New Zealand, higher forest cover is associated with a higher diversity of both plants and birds, and with a higher frequency of native bird species (Fig. S17). This suggests that communicability is partly mediated by spatial patterns of diversity, and by the differential spatial distribution of native and exotic species in our system. In other ecosystem types, communicability may thus not be necessarily related to forest cover,

but to other spatial land-use configurations. The influence of the surrounding areas in our study system is qualitatively similar to that of the local community, showing that high forest/shrubland cover surrounding the focal habitat is beneficial to its diversity (Ruffell *et al.*, 2017) and to its communicability. This relationship is nevertheless likely to vary across ecosystem types. For example, we would expect a positive effect of landscape habitat diversity on spatial communicability in landscapes with a high diversity across different habitat types and many generalist species connecting them.

These insights must be understood as first approximations to the propagation of biotic effects across space, mediated by species interactions. The plant-frugivore network of Aotearoa New Zealand represents demographic effects on the species considered: we assumed that effective interactions have a positive effect on the populations of the species involved, and that this effect is propagated through the subsequent interactions in the network. Nevertheless, the approach presented here can be used to model other effects mediated by interactions, e.g. on phenotipic selection or on behavioral changes. The key assumption of the communicability metric we introduced is that the only driver behind the propagation of effects is the presence (or strength) of a link between a pair of species. We have shown that this is a reasonable assumption for relatively simplified ecological communities, where dynamical effects are not expected to vary widely in sign or strength across species. Another dimension that should be explored in further studies is the temporal one: variations in network topology across time or temporal delays in the propagation of effects can be potentially important modifiers of the standard communicability metric that we obtained. For example, in applied settings, a natural follow up would be to conduct specific observations and/or experiments about the spatiotemporal demographic effects of the species deemed as important in analyses of effect propagation, such as here the silvereye or, locally, the kererū.

The formulation of the communicability metric implies an exponentially decreasing contribution of longer, indirect paths between species. While this has desirable mathematical properties (see Estrada & Hatano (2008)), it does not reflect any specific ecological assumption or mechanism, and can be replaced by other formulations. Another interesting property of the communicability metric, when applied to a pair of nodes, is that it is straightforward to separate the contribution

from the shortest paths between them from that of longer, indirect propagation paths. Overall, we believe that communicability can be a useful addition to the toolbox of ecological network analysis, if its limitations are explicitely accounted for.

Conclusions

Understanding how biotic effects spread in ecological systems is a fundamental unresolved question in ecology. A mechanistic understanding of effect spread requires detailed, context-specific information on species demography, interactions, and spatial patterns, which can be overwhelmingly costly to obtain, even for moderately diverse ecological communities. We have shown that an approach based on the topology of pairwise interactions in a (meta)community allows a good approximation of such indirect effects between species at varying scales. Both numerical simulations and empirical results from a large-scale plant-frugivore network identified ubiquitous and generalist species as key agents for the propagation of indirect effects across space. Whether this insight holds across ecosystem types and taxa, the temporal scales of effect propagation, or indeed, how to independently measure such indirect effects in complex natural systems, are important questions that arise from our results and will help advance our understanding of the spatiotemporal patterns of biodiversity.

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