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Unexpected Links between Communities of a Freshwater–Cropland Mediterranean Metanetwork

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Abstract: Cropland ecosystem functioning may be affected by human perturbations transmitted from adjacent ecosystems, such as freshwater systems. However, our limited knowledge of the ecological interactions within cropland–freshwater networks hinders projecting the consequences of anthropogenic pressures. We reviewed the information from freshwater and cropland communities in the Mediterranean zone of Chile and constructed an ecological metanetwork for characterizing the structure and projecting responses of this system facing environmental pressures. We performed a semi-qualitative analysis to identify the nodes that strongly influence other network components and (or) could significantly affect the transmission of effects within the system. Our analyses show that omnivore fish, amphibians, annual pollinated crops, and deciduous orchards are the most important groups. Although we expected that amphibious predators were the most important groups in transmitting perturbations between ecosystems, we also found groups of plants and pollinators performing this function. We stress that the fate of crop systems facing environmental disturbances should be assessed in a broader context rather than as an isolated system.

Keywords: Mediterranean-type ecosystem; qualitative network model; agriculture; food web



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1. Introduction

The necessary advances in the sustainable management of crop ecosystems are hampered by our incomplete knowledge of the collective functioning of ecological interactions. Interactions between species modulate biodiversity and shape services critical for crop production, such as biological pest control and pollination. These services are currently seriously threatened by climate change, habitat loss, pollution, biological invasions, and other anthropogenic pressures [1,2], imposing troubling uncertainties on food production.

An intrinsic feature of complex systems, and ecosystems as a class of them, is the intricate interconnectedness among their elements. This characteristic implies that matter, energy, information, and the changes produced in their components may spread through the system and cross human-defined limits. In this vein, anthropogenic disturbances that could even be local in their immediate impact are likely to be transmitted across ecosystem boundaries via the web of ecological interactions [3–6], affecting ecosystem functioning and provision of services, well beyond the initially affected system components. This is where a metaecological approach may help understand and manage environmental change's consequences at multiple spatial scales [7].

Metanetworks are defined as a set of spatially distributed local networks connected by species dispersal and influenced by colonization and extinction dynamics [8]. Here,

we consider that local networks are not only linked by species dispersal but also by life-cycle movements and foraging. Through metanetworks, mobile species may mediate indirect interactions between species in separated networks, facilitating the propagation of perturbations [9]. In agricultural landscapes, freshwater and cropland ecosystems are connected by the flow of organic and inorganic matter, including detritus, dissolved nutrients, and pollutants, and by the flow of organisms across their borders. For instance, during dispersal, winged adult stages of aquatic insects visit croplands [10–15], where they may interact with terrestrial animal and (or) plant species [16–20].

Freshwater food webs have been described since the late nineteenth century. Currently, many of them are considered to be highly resolved [21]. In contrast, ecological interaction networks that include crop plant species, describing trophic and non-trophic interactions, are scarce [22,23]. Some studies provide evidence of the potential influence of freshwater systems on crop species (e.g., [24,25]). However, we still know little about the structure and dynamics of freshwater–cropland ecological metanetworks (but see [26]). This lack of knowledge hinders our understanding of the functioning of this kind of metasystems, limiting our ability to anticipate the effects of anthropogenic pressures on biodiversity and food production.

In this study, we aimed to review the available information concerning the ecological interactions between the main living groups inhabiting a metasystem that includes freshwaters and croplands within a Mediterranean zone. Mediterranean-type ecosystems (MTEs) are distributed across continents and are ecologically valuable due to their unique biodiversity. In addition, these ecosystems are seriously threatened by the interaction between ongoing climate changes and the pressures driven by the growth of the agriculture industry [27–29].

By using the gathered data, we built a qualitative model representing the freshwater–cropland metasystem. This model is intended to be a simplified synthesis of the ecological interaction network operating in the study system and serves to explore questions regarding the structure and functioning of Mediterranean freshwater–cropland systems: (i) What are the main structural properties of the study metasystem? (ii) Which are the elements (i.e., living groups) with higher potential to influence other components of the network? (iii) Does the structural relevance of the network elements hold across different scales of influence? (iv) Which are the elements that may act as stepping stones for the transmission of ecological disturbances between freshwater and cropland subnetworks?

To address these questions, we combine standard tools of network analysis to compute centrality values of the network elements [30] with semi-qualitative techniques based on perturbation analysis of the community matrix near equilibrium [31–37]. Our study advances our understanding of the potential cross-influences between linked ecosystems while contributing to the knowledge about Mediterranean agroecosystems.

2. Materials and Methods

2.1. Study Area

In the present study, we reviewed the information from freshwater and cropland communities belonging to the Chilean MTE and constructed an ecological metanetwork for characterizing the structure and projecting responses of this specific kind of system facing environmental pressures.

MTEs are present in California, the Mediterranean Basin, South Africa, Australia, and Chile. These regions are between 32° and 40° of northern and southern hemispheres and are located on the west or south side of continents [38]. MTEs contain the richest extra-tropical flora of the world [39,40], supporting 20% of the known vascular plant diversity over only 2% of the land area of the Earth [41]. On the other hand, rivers and streams belonging to these ecosystems are considered ecologically unique owing to their seasonal sequence of biotic and abiotic regulation driven by the Mediterranean climate [42]. However, terrestrial and freshwater biodiversity is under threat in MTEs around the world [43–45]. All of this has led to consider those ecosystems as a conservation priority [46], categorizing them as

biodiversity hotspots [47]. MTEs are threatened by similar disturbances derived mainly from agriculture, livestock, industrial activities, and human growth [45].

Chilean MTE is not an exception to this trend since increases in human population densities and the development of agriculture exert severe pressures on both land use and water resources [27,28] (Figures S1 and S2). This zone has presented a continuous forest loss during the last 40 years, mainly attributed to the conversion of native forests to shrublands and exotic tree plantations [48]. On the other hand, Mediterranean Chile is the area with the largest number of exotic species, accumulating 50% of the exotic species of the country [49], potentially contributing jointly with other drivers to the loss of biodiversity in this zone.

2.2. Literature Review

We performed a bibliographic review of the ecological interactions within a freshwater–cropland metasystem from the Chilean Mediterranean zone. In the first step, we used Clarivate WoS and Scholar Google to search for papers relating to freshwater and cropland species belonging to Chile’s MTEs. When the information from this source was scarce, in the second step, we used books, studies published by government and non-government organizations, and research and review papers recommended by experts. The specific information sources used for each biological group are detailed in Supplementary S1 and Supplementary References [50–98].

2.3. Model Construction

To address our first question, once the information was gathered, we proceeded to build the qualitative model. First, we aggregated the biological entities into groups considering their ecological function, taxonomy, or trophic level (Step 1). The outputs of this procedure are the nodes of the network. Then, we defined the links between the network nodes (Step 2). Since each node may be composed of multiple groups of biological entities, the link estimation was made for each pair of nodes considering the ecological interactions between the groups that comprise each interacting node. In this process, we discarded all the links with scarce supporting evidence for an interaction. The output of this procedure is an undirected network. Afterward, we transformed the undirected edges into signed directed edges, considering the trophic and non-trophic relationships between each pair of nodes (Step 3). The output of this procedure is a signed directed network and its associated community matrix, which is the input of the posterior quantitative analysis. All the steps depicted above are explained in depth in Supplementary S2 [99–108].

We organized the system by defining four levels of resolution (Figure 1): the Functional Unit (defined here as a group that may be either a functional group, a taxonomic group, a trophic group, or a guild); the “aggregate” (a group of related Functional Units); the community within a specific ecosystem; and the metanetwork. Transmission of perturbations and cascading effects between ecosystems have been studied by modeling the local community or ecosystem, considering species’ populations or other ecosystem compartments as the system’s basic elements (e.g., [109–111]). Here, we use the Functional Unit (FU) as the basic unit to assess the extent of the effects of potential perturbations at intra-aggregate, intra-ecosystem, and inter-ecosystem scales.

Table 1. Description of model nodes.

Node Label	Functional Unit	Aggregate
1	Carnivore birds	Aquatic birds
2	Omnivore birds (AP)	Aquatic birds
3	Omnivore birds (TP)	Aquatic birds
4	Carnivore fish	Fish
5	Detritivore fish	Fish
6	Omnivore fish (FM)	Fish
7	Omnivore fish	Fish
8	Collector	Aquatic invertebrates

Table 1. Cont.

Node Label	Functional Unit	Aggregate
9	Collector/grazer	Aquatic invertebrates
10	Collector/grazer/predator	Aquatic invertebrates
11	Collector/predator	Aquatic invertebrates
12	Collector/shredder	Aquatic invertebrates
13	Filter	Aquatic invertebrates
14	Filter/collector/predator	Aquatic invertebrates
15	Grazer	Aquatic invertebrates
16	Predator	Aquatic invertebrates
17	Shredder	Aquatic invertebrates
18	High-profile	Diatoms
19	Motile	Diatoms
20	Planktic	Diatoms
21	Planktic/High-Profile	Diatoms
22	Helophyte	Macrophytes
23	Hydrophyte	Macrophytes
24	Hydrophyte/helophyte	Macrophytes
25	Amphibian	Ecosystems-linking
26	Birds (FCI)	Ecosystems-linking
27	Odonata	Ecosystems-linking
28	Carnivore birds	Cropland birds
29	Omnivore birds (C)	Cropland birds
30	Omnivore birds (I)	Cropland birds
31	Acari	Pests' natural enemies
32	Araneae	Pests' natural enemies
33	Coleoptera	Pests' natural enemies
34	Diptera	Pests' natural enemies
35	Diptera (PNE/P)	Pests' natural enemies/Pollinators
36	Hemiptera	Pests' natural enemies
37	Hymenoptera	Pests' natural enemies
38	Mantodea	Pests' natural enemies
39	Neuroptera	Pests' natural enemies
40	Orthoptera	Pests' natural enemies
41	Thysanoptera	Pests' natural enemies
42	Acariformes	Pests
43	Aphididae	Pests
44	Coleoptera	Pests
45	Collembola	Pests
46	Curculionidae	Pests
47	Diptera	Pests
48	Gastropoda	Pests
49	Hemiptera	Pests
50	Hymenoptera	Pests
51	Lepidoptera	Pests
52	Noctuidae	Pests
53	Orthoptera	Pests
54	Thysanoptera	Pests
55	Apini	Pollinators
56	Bombini	Pollinators
57	Diptera	Pollinators
58	Hymenoptera	Pollinators
59	Annual, non-pollinated	Crops
60	Annual, pollinated	Crops
61	Deciduous orchard	Crops
62	Perennial orchard	Crops
63	Vegetable	Crops

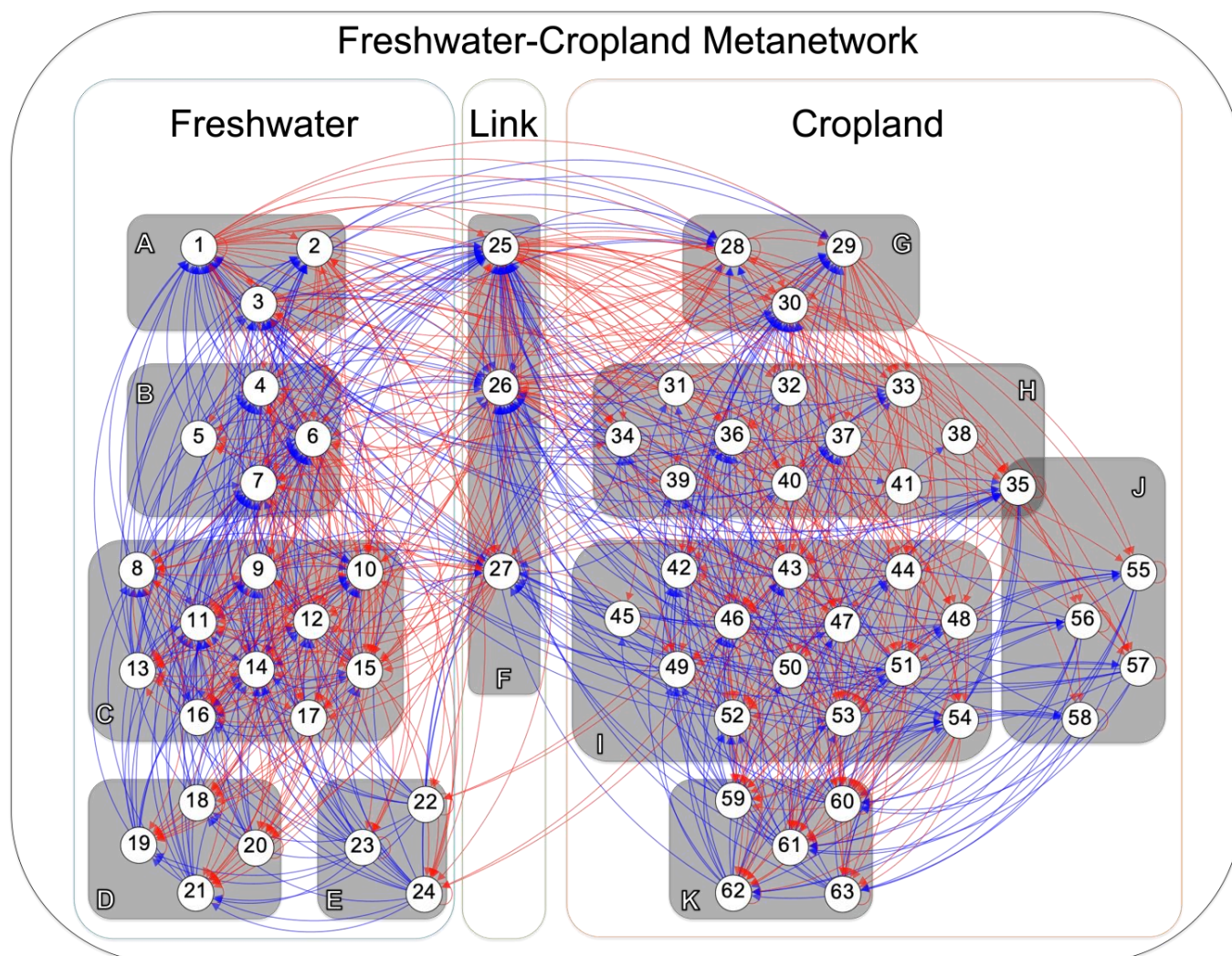


Figure 1. Signed directed graph of the ecological interactions metanetwork composed of the freshwater community, systems-linking module, and the cropland community. Nodes are grouped into the following aggregates: aquatic birds (A), fish (B), aquatic invertebrates (C), diatoms (D), macrophytes (E), ecosystems-linking species (F), cropland birds (G), pests' natural enemies (H), pests (I), pollinators (J), and crops (K). Blue and red arrows represent positive and negative direct effects, respectively. See Table 1 for a description of nodes' labels.

2.4. Node-Level Measures

For addressing the second and third questions, we analyzed the influence of each (source) node on the other (target) nodes considering our three defined scales of influence: intra-aggregate, intra-ecosystem, and inter-ecosystem.

To obtain the effects of every node on every other node of the network, we performed an assessment of the system response to potential external press perturbations. A press perturbation is a sustained shift in a parameter or factor influencing a population's rate of birth, death, or migration. This sustained change may result from internal or external processes (or forces) such as those caused by natural selection, the environment, or an experiment. In contrast, a pulse perturbation is an acute, short-term alteration of species numbers within a community, after which the system is studied as it relaxes back to its previous equilibrium state [31].

In the present study, we developed a model considering potential anthropogenic perturbations, considered to act from the system's environment via exerting pressures on the system's elements. To this end, we calculated the net-effect matrix $N = -M^{-1}$ [31,34,35,112].

The cells of this matrix, n_{ij} , indicate the projection of the sign and magnitude of the change in the equilibrium abundance of every node i of the network, generated by a press perturbation on a source node j . Each off-diagonal element of M was randomly varied between 1/2 and 2 (using a uniform distribution), maintaining the original signs of effects [37,113]. Self-effect terms on the diagonal of the community matrix were fixed at a value of -4 to fulfill the requirement of local system stability [32,35,112], assessed by the Lyapunov criterion. It is important to note that our system is defined for a specific equilibrium; thus, if the system were defined for a different equilibrium, the sign structure of the metanetwork may differ. The described procedure was iterated 1500 times, giving a set of 1500 matrices N containing the net effects between network nodes. Lastly, for each element n_{ij} of the N matrix, we calculated the mean and standard deviation (SD) over the 1500 values formerly estimated. We considered a mean value as “determined” if its error (mean \pm SD) does not contain zero and “undetermined” otherwise. In this way, we obtained a mean net-effect matrix \bar{N} , in which each cell \bar{n}_{ij} is the mean value previously estimated. Elements of the \bar{N} matrix with undetermined values were set to zero.

The intra-aggregate influence of each node x_j was obtained by averaging the terms \bar{n}_{ij} from \bar{N} over all rows $i \in A_j$ corresponding to nodes in the aggregate A_j , which x_j belongs to. For the intra-ecosystem influences, the net effect of each node x_j was calculated by averaging the terms \bar{n}_{ij} over all rows/nodes that belong to other aggregates in the same ecosystem that hosts the source node. The inter-ecosystem influence of x_j was estimated by averaging the terms \bar{n}_{ij} over all rows/nodes belonging to the adjacent ecosystem.

The magnitude of the influence values previously estimated indicates the relevance of each FU at different scales of influence. For categorizing the FUs according to their relevance, first, we scaled the influence values by the maximum of the absolute values within each scale of influence. High relevance influences show scaled absolute values between 2/3 and 1, whereas middle and low relevance influences show scaled absolute values between 1/3 and 2/3 and 0 and 1/3, respectively.

To address our fourth question, we analyzed the importance of each network node for the transmission of effects between freshwater and cropland ecosystems. Thus, we focused on the submatrix \hat{N} of \bar{N} that contains the responses in one (target) ecosystem to perturbations exerted on the adjacent (source) ecosystem. Submatrix \hat{N} contains elements \hat{n}_{ij} , where i are the indices of all nodes that belong to the target ecosystem, and j are the indices of all nodes that belong to the source ecosystem. Thus, the importance Y_i of node x_i for the transmission of net effects from a source to a target ecosystem was evaluated as $Y_i = C - T_i$, where C is the average over all \hat{n}_{ij} elements of \hat{N} obtained from the full network, and T_i is the same metric but obtained from the network (M) from which the node x_i was removed. For better comparison, the values of Y_i were standardized to z-scores. To account for alteration in strength, regardless of the sign of net effects across ecosystems, we repeated the same procedure but considering the absolute values of the entries of the submatrix \hat{N} . A positive z-score means that the presence of node x_i exerts a positive influence on the mean response of the target ecosystem. That is, the node x_i increases the magnitude of a positive mean response or it decreases the magnitude of a negative mean response. A negative z-score has the opposite interpretation.

Using Spearman and Kendall rank correlations, we compared the node importance in propagating impacts over the network with the standard centrality measures for directed graphs. Node importance in spreading impacts included estimates of the influence of each node at different scales (intra-aggregate, intra-ecosystem, and inter-ecosystem) and measures of the relevance of each node in the transmission of effects from the freshwater to the cropland ecosystem and vice versa. On the other hand, centrality measures included in-degree, out-degree, total degree, in-closeness, out-closeness, betweenness, PageRank, hub, and authority. Topological centrality measures inform about the structural importance of nodes in a network and have been found to be good predictors of node influence for the maintenance of global network properties ([114–116] but see also [117]). Therefore, we expect that more connected groups (i.e., with higher centrality values) will show higher

importance in linking the ecosystems and (or) influencing other nodes, regardless of the scale of influence.

We estimated the directed connectance C (excluding self-effects) for the entire network and the freshwater and cropland networks. We used the equation $C = L/S(S - 1)$ to calculate the connectance, where L is the number of links, and S is the number of nodes. In each case, we calculated the connectance considering only the positive or the negative links. Also, we estimated the mean and maximum trophic level of the entire metanetwork using the R package "NetIndices". On the other hand, diet overlap was assessed using Bray–Curtis dissimilarity analysis from the "vegan" package of R. The routines were coded in R project 3.3.3.

3. Results

3.1. Network Model Structure

From our review of Chilean freshwater and cropland ecosystems, we found 36 families of macrophytes, 12 orders of diatoms, 54 families of aquatic invertebrates, 12 families of fish, 37 species of freshwater birds, 45 crop species, 8 groups of pollinators, 60 groups of pests, 48 families of pests' natural enemies, and 31 species of croplands' visiting birds. For the aggregate that serves as a link between freshwater and cropland ecosystems, we found seven species of birds, four species of amphibians, and the order Odonata. Order richness was higher in the freshwater network, followed by the cropland and ecosystem-linking networks, with 64, 41, and 6 orders, respectively. The Supplementary Materials contains specific details about all these groups and their interactions (Tables S1–S14).

The obtained qualitative network model is composed of 63 nodes (FUs). The cropland ecosystem has 36 FUs, composed of 3 FUs for cropland birds, 10 FUs for natural enemies of pest species, 13 FUs for pests, 4 FUs for pollinators, 1 FU for pests' natural enemies/pollinators, and 5 FUs for crops. On the other hand, the freshwater ecosystem has 24 FUs, composed of 3 FUs for freshwater birds, 4 FUs for fish, 10 FUs for aquatic invertebrates, 4 FUs for diatoms, and 3 FUs for macrophytes. Three FUs were classified in the ecosystems-linking aggregate. The number of directed edges between nodes is 876 (Figure 1, Figure S4 and S5; Table 1 and Table S15).

Considering only the positive links, the connectance values are 0.11, 0.27, and 0.12 for the entire metanetwork, the freshwater, and cropland networks, respectively. On the other hand, the connectance values considering the negative links are 0.10, 0.25, and 0.09 for the entire metanetwork, the freshwater and cropland networks, respectively. The mean trophic levels for the entire metanetwork, freshwater, and cropland networks were 2.16, 1.87, and 2.27, respectively. The maximum trophic level for the freshwater network was 3.27, while for the cropland network, it was 3.67, obtained in both cases for carnivore birds. Considering the zero values, the mean diet overlap values for the entire metanetwork, freshwater, and cropland networks were 8%, 16%, and 12%, respectively (Table S16). On the other hand, excluding the zero values, the mean diet overlap values for the entire metanetwork, freshwater, and cropland networks were 43%, 53%, and 53%, respectively.

3.2. Influences of Nodes within the Network

At the intra-aggregate scale, the most important FUs were omnivore fish (FM), carnivore fish, annual non-pollinated crops, omnivore birds (cropland), and planktic/high-profile diatoms. Of the rest of the nodes of the network, 15 of them had middle relevance, and 40 had low relevance (Figure 2 and Table S17). All the FUs had a negative influence on their own aggregate except pollinators, dipterans-PNE/P, pests' natural enemies of the order Mantodea, and pests of the order Collembola. On the other hand, carnivore birds (cropland) and omnivore fish have null influence on their own aggregates.

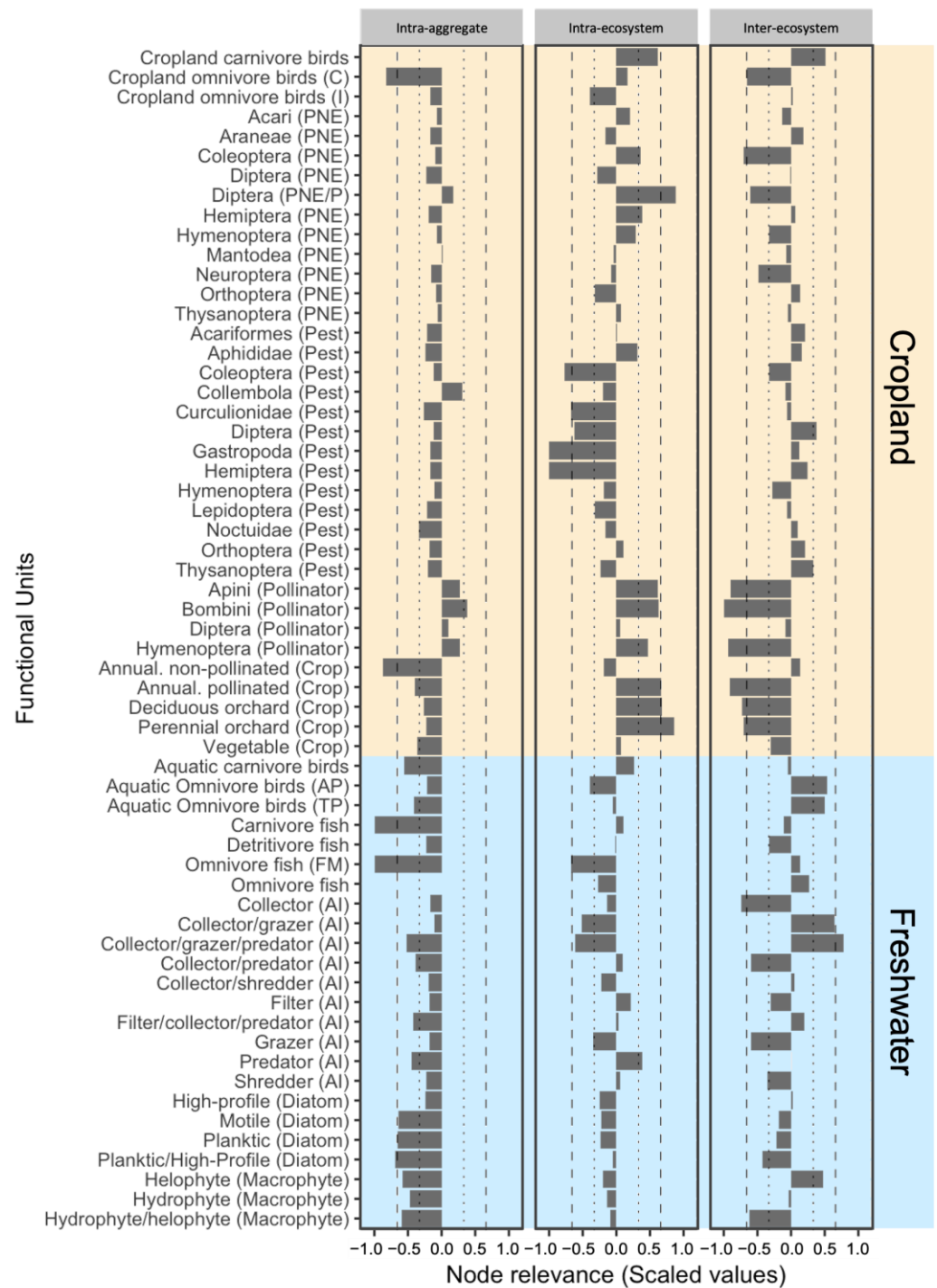


Figure 2. Relevance of Functional Units (nodes) at intra-aggregate, intra-ecosystem, and inter-ecosystem scales. Each bar represents the level of relevance of each node. A positive press perturbation on each node may produce a mean increase (positive value) or decrease (negative value) in the equilibrium abundance of the rest of the nodes at different scales. A negative press perturbation would yield the same effects but with the opposite sign. The presented data were obtained by scaling the influence values by the maximum of the absolute values within each scale of influence. Values between the dotted lines are considered of low relevance (between scaled absolute values 0 and 1/3), values between the dotted line and the dashed lines are considered of middle relevance (between scaled absolute values 1/3 and 2/3), and values outside the dashed lines are considered of high relevance (between scaled absolute values 2/3 and 1).

The most important FUs at the intra-ecosystem scale were gastropod pests, hemipteran pests, dipterans-PNE/P, perennial orchards, coleopteran pests, Curculionidae pests, deciduous orchards, omnivores-FM fish and annual pollinated crops. From the rest of the FUs, 13 were classified as of middle relevance and 38 as of low relevance (Figure 2 and Table S17). Almost half of the FUs had a positive influence on other FUs from aggregates of their own ecosystem. From the most important FUs at this scale, both fish and pests had a negative influence, while dipterans and crops had a positive influence.

At the inter-ecosystem scale, the most relevant FUs were hymenopteran pollinators, pollinators from the tribes Apini and Bombini, annual pollinated crops, aquatic invertebrates classified as collectors and collectors/grazers/predators, deciduous and perennial orchards, coleopteran natural enemies, and omnivore birds (cropland). The rest of the network is divided into 15 FUs of middle relevance and 35 FUs of low relevance (Figure 2 and Table S17). Most of the FUs had a negative influence on their adjacent ecosystem (58% of the network). All the most important FUs at this scale had a negative influence, except collector/grazer/predator invertebrates.

Most of the measures of node importance were weakly correlated with estimated centrality measures (Spearman $\rho < 0.4$, Table S18). Kendall correlation coefficients showed a very weak association between variables in most cases ($\tau < 0.2$, Table S19).

3.3. Transmission of Effects between Ecosystems

The most relevant FUs in the transmission of perturbations between cropland and freshwater ecosystems were carnivore birds (cropland), annual pollinated crops, amphibians, Apini pollinators (Hymenoptera), and deciduous orchards (Figure 3). The presence of amphibians in the network generated a negative influence on the responses of both freshwater and cropland ecosystems. When carnivore birds (cropland) and Apini pollinators (Hymenoptera) were present, they produced a positive influence on the responses of the cropland ecosystem. On the other hand, responses of freshwater ecosystems were influenced negatively by the presence of annual pollinated crops and deciduous orchards.

Considering the effects on the strength of responses regardless of their sign (absolute values), the most important FUs were omnivores-TP birds (freshwater), omnivores-C birds (cropland), omnivores-FM fish, carnivore birds (freshwater), macrophytes (hydrophyte/helophyte), deciduous orchards, amphibians, and annual pollinated crops (Figure 4). The presence of omnivores-FM fish produced a negative influence on the strength of responses of both freshwater and cropland ecosystems. The strength of responses of the cropland ecosystem was influenced positively by the presence of omnivores-TP birds (freshwater), omnivores-C birds (cropland), carnivore birds (freshwater), and amphibians. In a similar way, when carnivore birds (freshwater), macrophytes (hydrophyte/helophyte), deciduous orchards, and annual pollinated crops were present, they generated a positive influence on the responses of the freshwater ecosystem.

Most of the important FUs in the transmission of effects belong to higher or lower trophic levels but not intermediate ones. In general, measures of the importance of nodes for the transmission of effects between ecosystems were weakly correlated to estimated centrality measures (Spearman $\rho < 0.4$, Table S18). Only 8 out of 36 correlations were classified as moderate. These correlations were between the importance of nodes in the transmission of effects from freshwater to cropland and: (i) the in-degree centrality (Spearman $\rho = 0.52$); (ii) the out-degree centrality (Spearman $\rho = 0.52$); (iii) the total-degree centrality (Spearman $\rho = 0.53$); (iv) the in-closeness centrality (Spearman $\rho = 0.43$); (v) the out-closeness centrality (Spearman $\rho = 0.4$); (vi) the PageRank centrality (Spearman $\rho = 0.46$); (vii) the hubs centrality (Spearman $\rho = 0.6$); (viii) the authorities centrality (Spearman $\rho = 0.58$). On the other hand, in most cases, Kendall correlation coefficients showed a very weak association between variables ($\tau < 0.2$, Table S19).

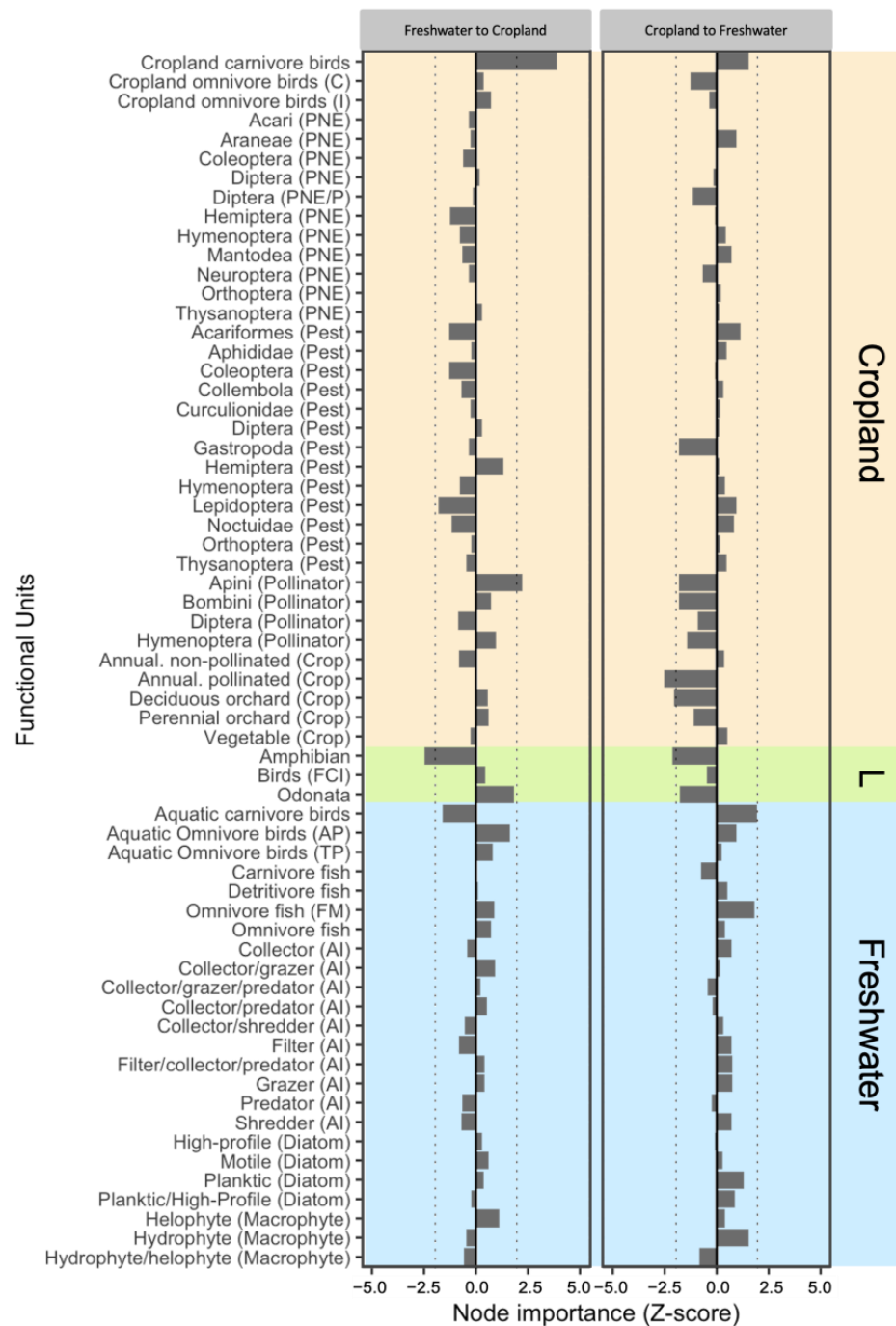


Figure 3. Importance of nodes in the transmission of effects between ecosystems. Each bar represents the effect of the presence of each node on the responses to perturbations. The left graph depicts the results for the transmission of effects from the freshwater ecosystem to the cropland ecosystem, while the right graph shows the results for transmissions in the opposite direction. Different background colors denote the location of nodes within the network. The “L” stands for Link. The dotted lines indicate 95% confidence limits.

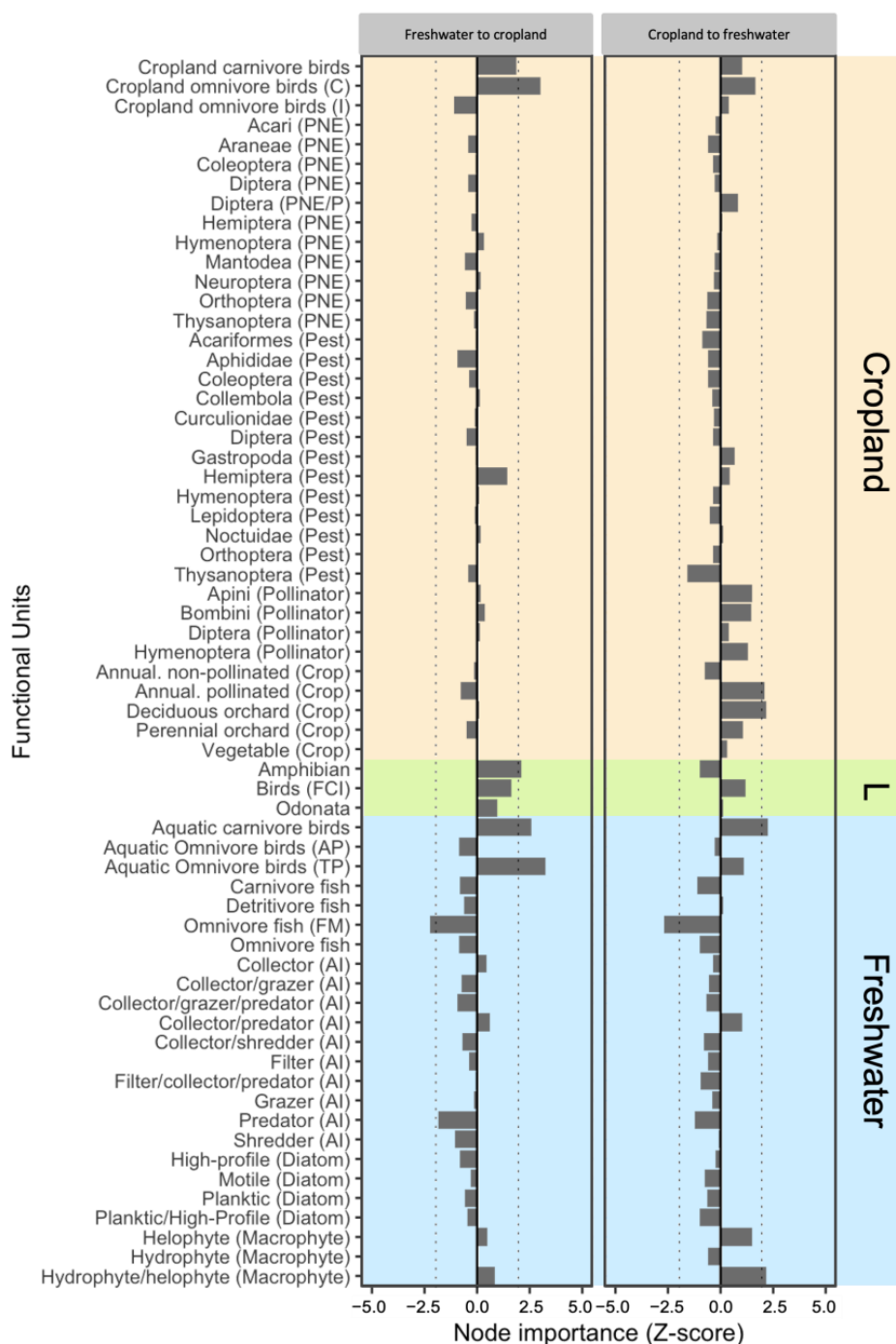


Figure 4. Importance of nodes in the transmission of effects between ecosystems. Each bar represents the effect of each node’s presence on the strength of the responses to perturbations. We estimated each node’s importance considering the absolute values of the net effects to account for alteration in the strength of effects, regardless of their sign. Codes as for Figure 3.

4. Discussion

Using a qualitative model of communities embedded in a Mediterranean freshwater–cropland metanetwork, we were able to identify the most relevant nodes in the transmission of perturbation’s effects within the system.

We specifically found that omnivore fish (FM) have major influences at the intra-aggregate and intra-ecosystem scales. In contrast, deciduous and perennial orchards and annual pollinated crops mainly influence other nodes at the intra-ecosystem and inter-

ecosystem scales. Also, we found that omnivore birds (cropland) have main influences at the intra-aggregate and inter-ecosystem scales. On the other hand, we observed that the most relevant ecosystems-linking FUs are amphibians, omnivore fish (FM), aquatic carnivore birds, annual pollinated crops, and deciduous orchards. Finally, we found that standard centrality measures are not good predictors of node importance in propagating impacts within the network.

We identified 10 different FUs having an essential role in the transmission of perturbation's effects between ecosystems. However, these results are not entirely in agreement with our expectations since (i) not all the FUs initially proposed as ecosystems-linking were confirmed as significantly relevant, and (ii) not all of the FUs identified as important were amphibious predators. We thought that amphibians (anurans), odonates, and birds FCI (listed as freshwater and cropland inhabitants) would be important in the transmission of effects between freshwater and cropland ecosystems, but only the first was significantly relevant. On the other hand, six out of ten relevant FUs are composed of predators that prey on a mixture of freshwater and terrestrial prey items. Surprisingly, we identified four ecosystem-linking nodes that are not predators: Apini, annual crops (pollinated), deciduous orchards, and macrophytes (hydrophyte/helophyte). To our knowledge, no previous studies have assessed the importance of nodes in the transmission of effects between freshwater and cropland networks. Notwithstanding, some theoretical evidence from agroecosystems may serve for comparison with our findings. Pocock et al. [22] showed that pollinators were not strongly linked to other nodes. Pollinator robustness to plant extinction was weakly associated with the robustness of the other components of this ecosystem. On the other hand, they found that crop species tended to have low importance as triggers of cascading effects within the network compared to other plant species. This evidence is not in line with our results; however, the results of Pocock et al. [22] are not entirely comparable to ours since, in their model, pollinator species interact uniquely with plant species. Unfortunately, their study did not include macrophytes.

Another interesting finding is that almost all relevant ecosystems-linking FUs belong to higher or lower trophic levels of both freshwater and cropland communities. As we expected, mobile amphibious top predators, such as birds, mammals, reptiles, amphibians, and insects, have a key role in connecting aquatic and land ecosystems [74]. Also, it has been reported that generalist top predator populations can be affected by alterations in the fluxes of prey resources coming from an adjacent ecosystem [118–121]. This generates notable changes in population abundance and interaction strengths within their local ecosystem. On the other hand, ecosystem components at basal levels may also be relevant in linking freshwater and land systems. For example, terrestrial leaf litter and particulate organic matter may get into the base of aquatic systems, generating alterations in their trophic dynamics [122–125]. Also, adult aquatic insect carcasses may enrich terrestrial systems with nutrients, indirectly affecting plants, herbivores, and their predators [126–129]. However, our network model represents energy fluxes among living beings; hence, it lacks nodes representing non-living components at the system base. Consequently, we cannot compare our findings directly to the evidence presented above.

We also find a weak-to-moderate relationship between the topological importance of nodes and the nodes' importance based on the net effect matrix. This means that nodes showing higher centrality values are not the same nodes that play a relevant role in propagating impacts. A similar result was found by Puche et al. [37] in a shallow macrophyte-dominated freshwater system. They estimated centrality measures and node effectiveness, defined as the average capacity of a node to affect the others when being disturbed. Although they did not explicitly relate centrality measures and effectiveness, our analysis performed with their data shows very weak and non-significant correlations (Spearman $\rho < 0.1$, $p > 0.6$). A weak association between these two kinds of nodes' importance measures was not expected, suggesting that the results from the calculation of net effects cannot be anticipated by classical node centrality measures. Exploring the relationship between these structural and functional measures may enhance our knowledge

of how the system's topology and dynamics evolve, helping to understand the emergent behavior [130].

Empirical evidence shows that changes in the abundance or presence of some species can generate indirect effects on other species inhabiting an adjacent ecosystem [17,131]. These indirect paths may also serve to propagate the effects of anthropogenic pressures across ecosystems [3–6]. In our study, we identified the FUs that strongly influence other network components and (or) could significantly affect the transmission of effects within the system. In this vein, the most noticeable FUs were omnivore fish (FM), amphibians, annual pollinated crops, and deciduous orchards. Some of these FUs are composed of threatened species, invasive species, or crop species that may trigger ecological cascades within the metanetwork. Threatened species may likely initiate ecological cascades since they have traits that make them more susceptible to population decline and extinction [132,133]. Invasive species may compete with or predate on native species (e.g., [134,135]), alter their habitat (e.g., [136]), spread diseases (e.g., [137]), change the structure and function of their ecosystems [138], and consequentially affect the provision of ecosystem services [139]. The presence or changes in abundance of invasive species may diminish or increase their impacts, affecting other species linked to them and generating indirect effects along the food web [140,141]. On the other hand, the variation in the diversity of crops and the proportion of some crop species in the landscape may trigger cascades of indirect effects on other components of the system [142,143]. In the Mediterranean zone of Chile, omnivore fish (FM) species have been classified as invasive and threatened. Specifically, Vila and Habit [81] categorized all the fish from the Atherinopsidae family as vulnerable (*Basilichthys microlepidotus*, *Odontesthes mauleanum*, *Odontesthes brevianalis*) and all the species from the family Cyprinidae as introduced (*Carassius carassius*, *Cyprinus carpio*, *Ctenopharyngodon idella*, *Tinca tinca*). Other introduced fish species that may be present in the zone belong to the families Acipenseridae, Ictaluridae, and Anablepidae. Regarding amphibians of the Chilean MTE, one species of the family Calyptocephalellidae is classified as vulnerable (*Calyptocephalella gayi*; [144]), and one introduced species of the family Pipidae (*Xenopus laevis*; [49]). Another vulnerable species that could be considered is *Rhinella arunco* [144]; however, the species of Bufonidae were excluded from our study due to the lack of data about their diets. Considering the entire metanetwork, we can observe that some aggregates accumulate more alien species than others. Specifically, we found that the aggregates with the most introduced species are pests, fish, natural enemies, and macrophytes, with 27, 19, 13, and 13 species, respectively ([49,81,145]; Table S20). However, only fish and macrophytes seem important in transmitting effects between ecosystems (Table S21). Regarding deciduous orchards and annual pollinated crops, it has been reported that these plant species use 20.6% and 6.2% of all harvested areas of Chile, respectively. On the other hand, deciduous orchards present the lowest variability in the between-year rate of area change within 2000–2020 [146], while annual pollinated crops show the highest variability. The latter means that drastic changes in the size of the harvested area of annual pollinated crops are more likely than for the other crops, which may foster the generation of cascades of effects despite their low proportion in the landscape.

Concerning the countries and zones with MTEs around the world (for a list of considered countries and zones, see Table S22), there are 47 threatened species of omnivore fish (FM) (Cyprinidae) and four threatened species of amphibians (Calyptocephalellidae and Pipidae) [147]. In the case of crops, deciduous orchards and annual pollinated plants use an average of 11.3% and 4.9% of all harvested areas of Mediterranean countries, respectively. On the other hand, the variability on the between-year rate of area change in deciduous orchards in Mediterranean zones is the lowest among all the crops, while annual pollinated crops present the second highest variability [146].

Despite the insights generated by our analysis, we identify limitations in our research. First, it is known that the projections obtained through the inverse of the negative community matrix are sensitive to interaction strength uncertainty [33,148]. In particular, Novak et al. [148] found that the proportion of correct predictions decreases drastically at

error factors greater than 1.5, especially for networks with more than 50 components and connectance values over 0.1. However, semi-quantitative and fully quantitative models suffer from similar limitations related to parameter uncertainty. Therefore, although our results show central tendencies based on many randomized networks, they should be interpreted cautiously, considering the large associated dispersion. The empirical estimation of interaction strengths is the best way to deal with this issue, but this task is difficult and resource-demanding.

Second, in this study, we measured the dynamic importance of nodes using the net effect matrix obtained from the inverse of the negative community matrix. This method allows for predicting species' responses to press perturbations, assuming that the system is at or near an equilibrium state. However, this assumption may not be entirely realistic since some ecosystems exhibit non-equilibrium dynamics [149], generating time-variable cross-ecosystem subsidies [150]. The pulsating nature of cross-ecosystem fluxes is a relevant feature that may determine the dynamics of the whole metasystem [109]. Therefore, more theoretical advances are needed to address non-equilibrium dynamics in a qualitative modeling setting. As argued by Ramos-Jiliberto and Jiliberto Herrera [113], a promising approach is to apply the theory of "entire bounded solutions" developed in the field of non-autonomous dynamical systems [151] as a generalization of the equilibrium assumption. Nevertheless, Dambacher and Ramos-Jiliberto [152] reported successful cases in which they compared the predictions made using qualitative modeling with empirical results from lake systems that are not strictly under equilibrium. This suggests that our results may yield at least a reasonable approximation of the dynamics of natural systems.

Third, some groups of biological entities that may be important were not considered in our study. Our model did not include bats, rodents, and weeds since we did not find enough information about them. These groups may play a relevant role in cropland ecosystems, affecting the crops negatively or causing cascading effects within the system [22,153,154].

Fourth, we did not include non-living variables in our network model, such as nutrients and detritus, due to the scarcity of empirical research addressing these ecosystem components, particularly in the Chilean Mediterranean zone. Including these variables qualitatively would blur our analysis. Therefore, we decided to keep them out of the model, although nutrient recycling may exert relevant effects on ecosystem functioning [155–157]. As new data become available, we will be better positioned to expand our model by including the non-living variables of our study system.

Finally, we did not consider the presence of other components within the landscape, such as natural and semi-natural habitats, which may affect the abundance and interactions of species from cropland and freshwater communities [158–162]. For instance, riparian vegetation may have a positive influence on pollinators [163], act as a barrier or a corridor for aquatic insect species during dispersal [10,164], but also may serve as energy source for freshwater food webs in the form of leaf-litter [165] and terrestrial invertebrates [166]. Since our model is not spatially explicit, it does not consider the influence of landscape composition and configuration on the metanetwork. However, in future studies, the influence of a landscape component could be modeled using a semi-qualitative approach, adding a variable (node) representing the landscape component and its effects (links) on each Functional Unit.

5. Conclusions

This article presented a qualitative model of a freshwater–cropland metanetwork from the Mediterranean zone of Chile. We used this network to identify groups of biological entities relevant to the transmission of perturbations among the system.

This network model represents the first step in characterizing this type of metasystems within MTEs worldwide. Global change is affecting zones with Mediterranean climates in a similar fashion; therefore, a complete understanding of the structure and function of these systems will allow us to predict the effects of human perturbations in a better and more generalized way within MTEs.

We observed that transmission of perturbations is mainly performed by a small but diverse set of FUs, including vertebrates, invertebrates, and plants, both from freshwater and cropland systems. Nowadays, most of these FUs are not considered especially relevant; however, they could serve as indicators of ecosystem integrity in the future.

We found weak-to-moderate relationships between standard centrality measures and the measures of node importance based on the net effect matrix. This issue should be thoroughly analyzed in subsequent studies to identify a method for integrating the results of these two types of measures.

The present work offers an approach for studying the potential entanglement between services provided by species belonging to different ecosystems. An increase in our knowledge about this type of metasystems will improve the management of freshwater and cropland ecosystems, considered within an integrated whole.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15091011/s1>, Supplementary S1: Information sources; Supplementary References: Pests and their natural enemies; Supplementary S2: Steps of the model construction process; R Code; Figure S1: Map showing the different land uses within the study area; Figure S2: Map showing the agricultural land and the water bodies within the study area; Figure S3: Heat map for the estimated Net Effect Matrix; Figure S4: Signed directed graph of the ecological interactions metanetwork composed of the freshwater community, systems-linking module, and the cropland community (higher resolution); Figure S5: Signed directed graph showing the direct interactions between the aggregates; Table S1: List of macrophytes, diatoms, aquatic invertebrates, fish, and birds found in the Chilean Mediterranean freshwater ecosystem; Table S2: List of crops, pollinators, pests, pests' natural enemies, and birds found in the Chilean Mediterranean cropland ecosystem; Table S3: List of birds, amphibians, and insects found in the ecosystem-linking aggregate within a freshwater–cropland metanetwork from Mediterranean Chile; Table S4: Interactions between macrophytes and diatoms; Table S5: Interactions between aquatic invertebrates and their resources; Table S6: Interactions between fish and their prey; Table S7: Interactions between freshwater inhabitant birds and their prey; Table S8: Interactions between crops and pollinators; Table S9: Interactions between crops and pests; Table S10: Interactions between invertebrate natural enemies and pests; Table S11: Interactions between cropland inhabitant birds and their prey; Table S12: Interactions between ecosystem-linking birds and their prey; Table S13: Interactions between ecosystem-linking amphibians and their prey; Table S14: Interactions between ecosystem-linking odonotans and their prey; Table S15: Community matrix for the freshwater–cropland metanetwork from Mediterranean Chile; Table S16: Diet overlap values estimated for the Functional Units of the freshwater network, the cropland network and the entire metanetwork; Table S17: Relevance of Functional Units at intra-aggregate, inter-ecosystem, and inter-ecosystem scales; Table S18: Spearman's rank correlation coefficient for relationship between standard centrality measures and node importance measures estimated in this study; Table S19: Kendall's rank correlation coefficient for relationship between standard centrality measures and node importance measures estimated in this study; Table S20: List of introduced species for each aggregate of the freshwater–cropland metanetwork; Table S21: Number of introduced species and the importance of each aggregate in the transmission of effects between ecosystems; Table S22: Countries and regions with MTEs considered in our analysis.

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