Inferring Functional Taxonomy from Network Structure

Alje van Dam[1], **Kayla R. Sale-Hale**[2,3*], **Surendra Hazarie**[4], **and Carla N. Rivera**[5]

[1]Copernicus Institute, Utrecht University, Utrecht, The Netherlands
[2]University of Arizona, Ecology & Evolutionary Biology, Tucson, 85721, United States
[3]University of Michigan, Ecology & Evolutionary Biology, Ann Arbor, 48109, United States
[4]University of Rochester, Physics, Rochester, United States
[5]Center of Applied Ecology and Sustainability (CAPES), Santiago, PC 6513677, Chile
*Correspondence to: kaylasale@icloud.com

ABSTRACT

The projection of bipartite graphs has proven to be a useful tool to infer similarity measures between nodes of either one of the node types, based on how many links they share with nodes of another type. In economics this has lead to the concept of the product space[1], which is a network that connects products based on their co-locations in different countries. The relatedness between products in this networks is thought to be representative of the 'capabilities' that are required to produce such products. Here we apply similar concepts to plant-pollinator networks and evaluate the results in light of natural history. By projecting plant-pollinator networks onto plant-plant and pollinator-pollinator networks, we aim to derive a measure of relatedness between plants based on the ecological traits that a pollinator must have to feed on it, and likewise a measure of relatedness between pollinators in terms of the traits they share, that allow them to feed on the same plants.

By running community detection algorithms on the projected networks we create a functional taxonomy based on these (unobserved) ecological traits, and compare this taxonomy to taxonomies based on observable traits. As opposed to evolutionary taxonomies, our inferred taxonomies can represent a 'partner space,' describing how plants see their pollinator community in terms of their capabilities and vice versa. Trait-based community detection formalizes the concept of 'pollination syndromes,' the idea that pollinators in a pollination network with similar traits prefer similar plants with similar traits (e.g. flies pollinators prefer white-flowered plants)[2].

We find that detected communities are well-aligned with pollination guilds formed from field observations of flower visitors but that most basic (empirically-recorded) plant traits are not predictive of the communities observed from the projected plant-pollinator networks, suggesting that other traits play a significant role in plant choice for pollinators.

This indicates the non-trivial nature of the communities identified by looking at plant-pollinator networks, reinforces criticisms of pollination syndromes, and may inspire future ecological research such as the identification of characteristic ecological traits that form these communities.

1 Introduction

Bipartite networks are ubiquitous and a useful representation of many systems, ranging from academia (scientific collaborations[3]) to ecological systems (mutualistic networks and host-parasitoid networks[4]) and economics (world trade country-product network[5]).

The one-mode projection of bipartite graphs has proven to be a useful tool to infer similarity measures between nodes of either one of the node types, based on how many links they share with nodes of another type[6]. An appealing example in economics is the concept of the product space[1], which uses world trade data to define a bipartite country-product network in which links indicate that a country is an exporter of a certain product. The product space is a one-mode projection of the country-product network that shows relatedness between products based on their co-locations in different countries.

Furthermore, the country-product network is found to be nested[5], meaning that the countries exporting the highest diversity of products (the countries with high degree in the bipartite network) are also the countries that export the products that are most rare (products with low degree), and rare products are only exported by highly diverse countries. The nested structure of the bipartite country-product network has led to development of algorithms that exploit this nested structure in order to infer the 'complexity' or 'fitness' of countries' economies and 'level of sophistication' of products[5 7]. These metrics have been shown to be predictive of the development of countries in terms of GDP[8].

In ecology, nestedness is a well known property of many bipartite networks[9], in particular plant-pollinator networks, where generalist pollinators tend to pollinate specialist plants and generalist plants are pollinated by specialist pollinators (i.e. specialists tend to interact with a proper subset of generalists' partners)[10]. The nested structure of ecological networks has been suggested to promote species coexistence by reducing competition and improving robustness to disturbance[9]. Therefore it seems natural to explore whether methods developed in the field of economic complexity can be useful in the field of ecology. One example of such application is the use of the economic Fitness-complexity algorithm[7] on bipartite networks of active (e.g. pollinators) and passive (e.g. plants) species. This application leads to measures of 'importance' of active species for the robustness of the network, enabling identification of 'keystone' species in the network[11].

Although Dominguez & Garcia (2015)[11] apply the Fitness-complexity algorithm[7] to plant-pollinator networks, they do not apply the underlying logic of the 'theory of capabilities' underlying it[5, 12]. Here we aim to explore further the analogy of this perspective in plant-pollinator networks, as well as key differences. In particular, we explore if we can find a useful categorization of plant and pollinator species in terms of their ecological 'traits' (which are unobserved) using community detection on the projected networks. For example, we aim to find communities of plants that are similar in terms of the trait requirements they pose on pollinators to be able to feed on them.

2 Economic 'capabilities' and ecological traits

Economic complexity is based on the idea of 'capabilities', which are non-tradeable inputs, such as certain infrastructure, regulations and specific labor skills[5]. Every product requires a specific set of capabilities to produce it, where more sophisticated products may require many more capabilities than simple ones. In order to produce a certain product, countries must have the capabilities it requires for production. Hence capabilities enable countries to make products, and products in turn require capabilities in order to be produced.

Products can then be considered related if they share many of these capability requirements, and their 'complexity' a measure of how many capabilities they have or require respectively. Similarly, countries are related in terms of the capabilities they possess and the number of capabilities they have is a measure of the complexity of their economies.

Although these capabilities are abstract and not measurable, one can infer information about them using the structure of the bipartite network. A country producing multiple products for example, must have all capabilities required for producing all its products. Hence products that often co-occur in the same countries are likely to have related capability requirements. The relatedness between products in terms of their capabilities can thus be inferred by inspecting their co-occurrences in countries. This is done by projecting the bipartite product-country network onto a product-product network, in which the links between the nodes represent their relatedness in terms of their capability requirements[1].

We pose that in the context of plant-pollinator networks, the underlying 'capabilities' in economic complexity can be interpreted as ecological traits. Suppose plant species have some set of traits that result in requirements for the species that are trying to feed on their floral rewards. Examples of this could be day/night blooming, corolla length, flower color, scents, etc. This thus sets the collection of traits a pollinator species must have in order to be able to feed from a specific plant species (e.g. nocturnally active, long beak, color and scent preference etc.).

Using this perspective, we can think of the nested structure of mutualistic networks as arising from the existence of these ecological traits. Pollinators with many traits are expected to be generalists, since they can feed on a larger variety of plants. For plants on the other hand, ecological traits pose restrictions to which pollinators are able to feed on them, so plants with many traits are expected to be specialists. In this light we might reinterpret the rankings found by Dominquez & Garcia (2015)[11] to give a ranking in terms of the 'number of ecological features' for either type of species. Plants with many requirements are specialist and therefore 'vulnerable' to not being pollinated. Pollinators with many traits on the other hand are generalist (therefore 'important' as they are responsible for the pollination of many plants, including specialist plants).

There is a long history of attempting to identify character suites (requirements and capabilities) in pollination interactions[2]. For example, in myophily, pollination by flies, plants tend to have flat or radial shaped flowers that bloom during the day, are white, yellow, or greenish in color, have a mild scent, and produce small amounts of easily accessed, highly concentrated nectar, whereas in ornithophily, pollination by birds, plants to have short- to medium-length tube flowers that are red or orange, scentless, with large amounts of concealed nectar of low concentration. There is clear empirical evidence for evolutionary convergence towards these suites of ecological traits (called "pollination syndromes") that attract or filter out different flower visitors. However, pollination syndromes are statistical in nature: plant traits are not perfectly predictive of flower visitor or pollinator identity and temporal and spatial variation can be further confounding. Some plants may even exhibit traits amenable to a wide range of pollinators, so that their pollination syndrome is best described as "generalism." Though ecological traits are both potentially constraints and innovations from evolutionary history, even species within a genus can exhibit different pollination syndromes. Additionally, selective forces from herbivores can shape flower morphology, potentially contradicting convergence towards a pollination syndrome[2]. We hope to avoid this messiness by inferring a functional taxonomy directly from the plant-pollinator network.

3 Inferring functional taxonomy

We can construct plant-plant and pollinator-pollinator networks by projecting plant-pollinator networks, where the weights of the links in the projected network give a measure of relatedness between species in terms of their ecological traits. In the pollinator-pollinator projection, two pollinators are related if they pollinate many of the same plants, implying they have similar ecological traits. When projecting on the plant layer, plants are then related if they are pollinated by a similar set of pollinators, implying they have similar restrictions for their pollination.

Finding community structure in the projected networks would then mean that these communities share a (set of) common ecological traits. These communities could thus potentially reveal a 'functional taxonomy' based on the mutualistic interactions between species, as opposed to morphological, genetic or other directly observable features. Note that some of these traits may be known from ecology (e.g. flower color, pollinator sensory ability) and are used in formation of pollination syndromes. In the current framework however the nature of these traits remains unknown and can be of any form (i.e. unobservable), as long as they represent a requirement for formation of a link in the bipartite network.

4 Methods

We consider a bipartite plant-pollinator network as given by the $N_a \times N_p$ adjacency matrix B, where N_p gives the number of plants and N_a the number of pollinators in the network. We thus have $B_{ap} = 1$ if pollinator species a feeds on plants species p. One can project the bipartite network to a one-mode network with adjacency matrix $A = B^T B$. This matrix has as entries $A_{pp'}$ the number of shared links to node of type p between two species p and p'. We then compute the similarity matrix as[13]

$$S_{pp'} = 2\frac{A_{pp'}}{A_{pp} + A_{p'p'}}.$$

The $S_{pp'}$ matrix is a symmetric matrix that denotes the similarities between species p and p' measured by how many connections to species of the other type they share. Note that if p and p' share *all* their links, then $A_{pp} = A_{p'p'} = A_{pp'}$ so $S_{pp'} = 1$. On the other hand, sharing no links implies $S_{pp'} = 0$. For intermediate cases, the similarity $S_{pp'}$ increases as the number of shared links $A_{pp'}$ is a larger fraction of the total number of links that p and p' have ($A_{pp} + A_{p'p'}$). This projection method has been used in the context of economic development to construct networks that represent similarity between countries and products[13].

We can perform community detection on the resultant similarity networks. In particular, we choose the leading eigenvector detection algorithm[14]. This particular method leverages the expected number of links predicted by the configuration model to detect stronger-than-expected connections. With this, any community structure that appears implies clusters that share ecological traits beyond what a random graph would suggest.

We then compare the identified communities with communities determined using ecological traits and natural history (e.g. pollination syndromes) and field observations. We discuss our results in terms of functional taxonomy, and explore whether inferred capabilities and requirements match with traits considered relevant by ecologists.

5 Data

Here, we investigate a 719 species plant-pollinator network (Kato 2000) as compiled on Web-of-Life[15]. This network was chosen because the author recorded ecological trait details for species. We use these traits to compare our inferred taxonomy with one formed using ecological knowledge. In this network, a link was recorded between a plant and insect species if the insect was observed to land on the plant's flower. In other words, as is typical in pollination studies, these networks are better described as "plant-insect visitor networks," because insects were not necessarily observed to interact with plants' reproductive organs or to successfully cross-fertilize plants. See the original paper for more methodological details[16]. For tractability, we only examine the plant-plant and plant-trait network projections.

Kato[16] reported an impressive pollination network collected from 1995-1999 across the eight main islands of the Amami Islands, Japan. The Amami islands are subtropical, with five main types of natural vegetation (lowland forest, mountain forest, mangrove forest, coastal scrub, and coastal meadow), all of which were sampled. Six-hundred nine (609) anthophilous insect pollinator species (mostly flies, bees, beetles, moths, and butterflies) were observed to visit 110 flowering plant species (from 9 orders plus one *Cycas* and one *Pinus* species). Approximately 1250 vascular plant species are known to inhabit the Amami Islands. Kato observed 164 plant species, but excluded those that were observed to receive less than eight visits. We used the following traits reported by Kato to analyze plant community assignments (Table 1, Fig. 1): growth habit, nativity, breeding system, flower color, flower symmetry, flower morphology, and months when blooming. Flower color and flowering season are non-exclusive traits, i.e. flowers of a given plant species may have been orange and white.

The observed insect pollinators were grouped into 16 taxonomic groups: hemipterans (an order of "true bugs" including aphids, leafhoppers, and cicadas), beetles, wasps, small bees, megachilid (a family of solitary bees, commonly called the

Table 1. Description of plant traits recorded by Kato 2000 and listed for each plant species in 2. Pollination guild and cluster as assigned in Kato 2000 (see main text).

MB	months when blooming: I, February; II: March; III: April; IV: May; V-VII: June; VIII-IX: July; X: August; XI: October; XII-XIII: December.
GH	growing habit: a, annual; 1, liana; p, perrennial; s, shrub; t, tree.
N	nativity: a, alien; c, cultivated; n, native.
BS	breeding system: d, dioecious; h, hermaphrodite; m, monoecious.
FC	flower color: b, blue; c, cream; g, green; o, orange; pk, pink; pl, purple; r, red; w, white; y, yellow.
FS	flower symmetry: a, actinomorphic; z, sygomorphic.
FM	flower morphology: a, apetalous; b, brush; c, cup/bell-shaped; f, funnelform; h, head; o, open regular; p, papilionaceous; r, rotate; t, tubular.
NV	number of flower visitors observed.
CL	cluster detected by an analysis of flower visitor spectra.

"leafcutter bees"), *Tetralonia* (a genus of bees[17]), *Amegilla* (a genus of solitary "digger" bees), *Colletes/Apis* (two genera of bees, commonly called the "plasterer" and "honeybees"), syrphid flies (a family of flies, commonly referred to as "flower" or "hoverflies"), calyptrate flies (a subsection of flies), small flies, butterflies, hawkmoths, moths, and others. Then the percentage of individual visits that came from each insect visitor taxonomic group was determined to define "flower-visitor spectrum" for each plant species. A cluster analysis using Ward's minimum variance method was performed on the flower-visitor spectrum of 81 of the plants, resulting in 14 clusters. In order to determine which insects of the flower-visitors were successful pollinators of each plant species, Kato applied field observations, including observations of flower visitor behavior, pollen attachment on the visitors' body, and floral morphology, to his cluster analysis in order to group plants into pollination guilds (see above). This resulted in 104 of the plant species classified into 13 pollination guilds (*Amegilla*, *Tetralonia*, *Xylocopa* (a genus of carpenter bees), *Colletes/Apis*, hawkmoth-, butterfly-, small bee-, calyptrate fly-, syrphid fly-, beetle-, small fly-, wasp-, and various insect- and wind-pollinated guilds. We compare Kato's pollination guilds to communities determined from our similarity analysis of the plant-insect-visitor network.

6 Results

We detected five communities in the plant-plant similarity projection of the Japanese plant-pollinator network (Fig. 1). Interestingly, they were well-aligned with the pollination guilds proposed by Kato 2000[16], but not with the 13 clusters found through Kato's initial analysis of insect visitors. Notice that we performed community analysis on 110 plant species, but Kato only assigned pollination guilds to 104 species.

The similarity analysis grouped *Colletes/Apis*-, wasp-, calyptrate fly-, and various insects-pollinated plants together (Community 0), butterfly- and *Tetralonia*-pollinated plants together (Community 1), hawkmoth- and megachilid- and *Amegilla*-pollinated plants together (Community 2), and syrphid fly-pollinated plants together (Community 3). Small-bee and small-fly pollination guilds were split between Communities 0 and 3. Community 4 contained a beetle-pollinated species and a species unlabeled by Kato. Three species, *Eurya japonica*, *Lasianthus japonicus*, and *Pinus luchuensis*, were disconnected nodes and are not shown. Species from Clusters 2, 3, 8, 9, 10, 12 were split among the communities we detected, and Clusters 4, 5, 6, 7, and 11 had only one or two species.

The communities we detected were generally characterized by the following traits: Community 0 contained species of mostly open regular morphologies. Community 1 contained mostly white, hermaphroditic flowers that were not apetalous. Community 2 contained trees, shrubs, and perennials with white, green or yellow flowers that were neither head-shaped nor funnelform. Community 3 contained shrubs and perennials with pink, purple, white, yellow, and cream flowers. Note however that ecological traits were not consistent within communities and did not consistently distinguish between communities. Additionally, the communities did not correspond to taxonomic families or orders (and thus to evolutionary history).

We analyzed the species that were assigned to different communities than the rest of their pollination guild and the sub-structure of the small-fly and small-bee pollination guilds. The traits of *Ilex integra* (calyptrate fly-pollinated), *Vaccinium wrightii* (*Xylocopa*-pollianted), and *Rubus grayanus* (*Tetralonia*-pollinated) are similar to other plant species in their pollination guild. *R. grayanus* and *V. wrightii* were observed to receive very few insect visits, but the other species received many (> 10 visits), so differences in community assignment were due purely to insect visitor identity.

Small-bee pollinated plants that were grouped into Community 3 were shrubs, perennials, and lianas with yellow, white, and pink flowers, whereas those grouped into Community 0 were trees, perennials, and lianas with a hermaphroditic breeding system and mostly open regular flowers of many colors (yellow, white, pink, purple, green, and cream). Analyzing the traits of

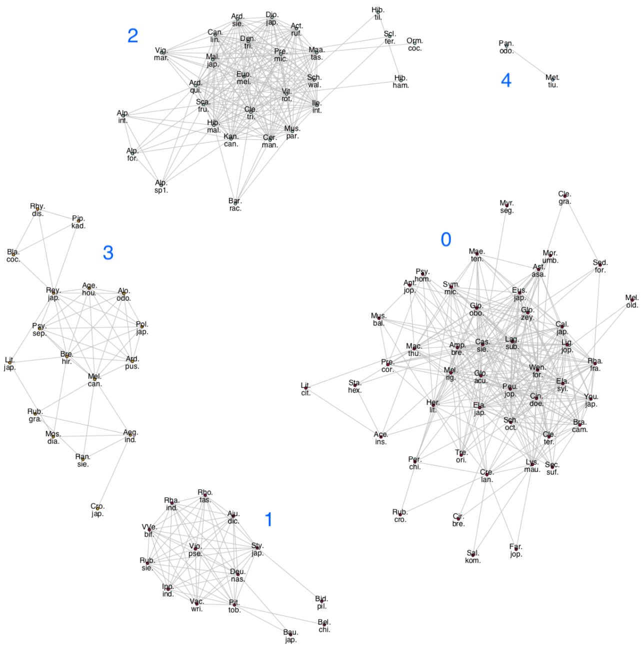

Figure 1. Plant similarity network for Japanese plant-pollinator network. Plant species names are abbreviated to the first three letters of the genus and epithet (e.g. *Schima wallichii* is abbreviated to Schi. wal.). See Table 2 for pollination guild and community assignments.

Deutzia naseana, the small-bee pollinated plant grouped into Community 1, suggests that it should be grouped with Community 3. Similarly, small-fly pollinated plants that were grouped into Community 3 were trees, perennials, and lianas of all breeding systems with cream and white flowers, whereas those grouped into Community 0 were trees, perennials, and shrubs with a hermaphroditic breeding system and white, cream, and pink open regular flowers.

Therefore, our community-detection technique recovered the large-scale structure of the pollination guilds labeled by Kato 2000[16], but the communities did not correspond to clear groupings of the plants' ecological traits nor to their taxonomy.

7 Discussion

Fascinatingly, the communities we detected align with pollination guilds inferred using ecological observations and natural history. Our communities are not partitioned around the recorded ecological traits, but do represent clusters made bringing inherent ecological knowledge and field observations to bear. This implies that the similarity network technique may indeed recover capabilities and requirements associated with successful pollination instead of just visitation. Since the plant-pollinator process is fully determined by the algorithm and the trait relevance is subject to human bias, it could be possible to use community detection to calibrate the resolution with which traits should be recorded. For example, daily flowering time (anthesis), presence of nectar guides (UV reflection), and concentration and volume of nectar produced by plants are traits considered relevant to pollination syndromes[2], but require more detailed observations than the traits included here. If there is a regime of detail where the manually constructed trait networks lead to similar community structure as the empirical pollination observations, then that could suggest a method of trait observation that has real network consequence.

Our approach is potentially ecologically informative in that it poses hypotheses about the inter-relatedness of pollination guilds. For example, our analysis suggests that plants thought to rely on butterfly or *Tetralonia* pollination have a similar set of insect visitors and thus a similar set of perceived capabilities to potential pollinators. Alternatively, there may be spatial or temporal differences in pollination behavior, with, for example, *Tetralonia* bees visiting flowers at dawn and butterflies visiting latter in the morning. Additionally, our analysis suggests a partition into two communities between between plants thought to be pollinated by small bees and flies.

Table 2. List of plant species used in our community analysis. Community assignments as depicted in Figure 1. Pollination guild and cluster as assigned in Kato 2000 (see main text). Traits and taxonomy from Kato 2000. Key in Table 1.

Community	Pollination	Taxonomy		Traits								
Assignment	Guild	Species Name	Family	MB	GH	N	BS	FC	FS	FM	NV	CL
0	?	*Aster asa-grayi*	Asteraceae	III	p	n	h	pl	a	h	5	
0	?	*Cirsium brevicaule*	Asteraceae	III-VI	p	n	h	w	a	h	3	
0	?	*Heritiera littoralis*	Sterculiaceae	V-VI	t	n	m	pl	a	o	55	C1
0	?	*Litsea citriodora*	Lauraceae	III	t	n	d	c	a	o	4	
0	?	*Morinda umbellata*	Rubiaceae	VI	t	n	h	g	a	o	1	
0	*Apis/Colletes*	*Brassica campestris*	Brassicaceae	III	a	c	h	y	a	r	11	C8
0	*Apis/Colletes*	*Crepidiastrum lanceolatum*	Asteraceae	XII-III	p	n	h	y	a	h	44	C6
0	*Apis/Colletes*	*Farfugium japonicum*	Asteraceae	XII	p	n	h	y	a	h	8	C1
0	*Apis/Colletes*	*Rubus croceacanthus*	Rosaceae	II	s	n	h	w	a	r	3	C6
0	beetle	*Stauntonia hexaphylla*	Lardizabalaceae	III-IV	l	n	h	w	a	o	7	C1
0	bird?	*Musa balbisiana*	Musaceae	VIII	p	n	m	pl	z	t	1	
0	calyptrate fly	*Antidesma japonicum*	Euphorbiaceae	V-VI	s	n	d	pk	a	a	17	C8
0	calyptrate fly	*Lysimachia mauritiana*	Primulaceae	III-IV	p	n	h	w	a	o	10	C12
0	calyptrate fly	*Schefflera octophylla*	Araliaceae	XII	t	n	h	g	a	o	40	C8
0	small bee	*Ampelopsis brevipedunculata var. glabrifolia*	Viraceae	VI-VIII	l	n	h	g	a	o	45	C3
0	small bee	*Callicarpa japonica var. luxurians*	Verbenaceae	VIII	t	n	h	pl	a	o	15	C12
0	small bee	*Castanopsis sieboldii subsp. leutchuensis*	Fagaceae	III-IV	t	n	h	y	a	a	238	C12
0	small bee	*Cinnamomum doederleinii*	Lauraceae	VI	t	n	h	c	a	o	22	C9
0	small bee	*Clematis grata var. ryukyuensis*	Ranunculaceae	X	l	n	h	w	a	o	1	
0	small bee	*Clematis terniflora*	Ranunculaceae	V-VI	l	n	h	w	a	o	16	C12
0	small bee	*Elaeocarpus japonicus*	Elaeocarpaceae	IV	t	n	h	w	a	o	67	C9
0	small bee	*Elaeocarpus sylvestris var. ellipticus*	Elaeocarpaceae	VI	t	n	h	pk	a	o	35	C1
0	small bee	*Lagerstroemia subcostata*	Lythraceae	VII-VIII	t	n	h	pk	a	r	67	C1
0	small bee	*Ligustrum japonicum*	Oleaceae	VI	t	n	h	w	a	t	16	C12
0	small bee	*Meliosma rigida*	Sabiaceae	IV	t	n	h	c	a	o	0	
0	small bee	*Peucedanum japonicum*	Apiaceae	III-V	p	n	h	w	a	o	66	C12
0	small bee	*Sedum formosanum*	Crassulaceae	VI	p	n	h	y	a	o	3	
0	small bee	*Symplocos microcalyx*	Symploacaceae	III-IV	t	n	h	w	a	o	56	C12
0	small bee	*Wendlandia formosana*	Rubiaceae	VI-VII	t	n	h	w	a	o	51	C1
0	small bee	*Youngia japonica*	Asteraceae	III	p	n	h	y	a	h	39	
0	small fly	*Machilus thunbergii*	Lauraceae	III	t	n	h	c	a	o	41	C9
0	small fly	*Maesa tenera*	Myrsinaceae	III-IV	s	n	h	w	a	o	29	C9
0	small fly	*Persicaria chinensis*	Polygonaceae	V-XII	p	n	h	pk	a	o	6	C12
0	various insects	*Acer insulae*	Aceraceae	III	t	n	d	g	a	o	12	C1
0	various insects	*Euscaphis japonica*	Staphyleaceae	IV	t	n	h	g	a	o	18	C12
0	various insects	*Glochidion acuminatum*	Euphorbiaceae	V-VI	t	n	m	g	a	a	101	C3

Community Assignment	Pollination Guild	Taxonomy		Traits								
		Species Name	Family	MB	GH	N	BS	FC	FS	FM	NV	CL
0	various insects	*Glochidion obovatum*	Euphorbiaceae	V-X	t	n	m	g	a	a	34	C1
0	various insects	*Glochidion zeylanicum*	Euphorbiaceae	V-VI	t	n	m	g	a	a	34	C1
0	various insects	*Premna corymbosa var. obtusifolia*	Verbenaceae	VI-VIII	s	n	h	c	z	o	8	C3
0	various insects	*Rhamnella franguloides var. inaequilatera*	Rhamnaceae	VI	t	n	h	g	a	o	21	C12
0	various insects	*Securinega suffruticosa var. amamiense*	Euphorbiaceae	V	s	n	d	y	a	a	6	
0	various insects	*Trema orientalis*	Ulmaceae	V-VI	t	n	d	g	a	a	16	C1
0	wasp	*Psychotria homalosperma*	Rubiaceae	VI-VIII	t	n	d	w	a	c	3	C4
0	wind	*Myrsine seguinii*	Myrsinaceae	II	t	n	d	g	a	o	1	
0	wind?	*Salsola komarovii*	Chenopodiaceae	XII	a	n	h	h	a	a	1	
1	?	*Bidens pilosa var. radiata*	Asteraceae	II-III	a	a	h	w	a	h	1	
1	butterfly	*Bauhinia japonica*	Caesarpinaceae	VI	l	n	h	c	a	r	1	C11
1	butterfly	*Belamcanda chinensis*	Iridaceae	V	p	n	h	o	a	f	1	C11
1	small bee	*Deutzia naseana*	Hydrangeaceae	III-IV	s	n	h	w	a	o	43	C3
1	*Tetralonia*	*Ajuga dictyocarpa*	Lamiaceae	III-IV	p	n	h	pk	z	t	4	C14
1	*Tetralonia*	*Ipomoea indica*	Convolvulaceae	III-XII	p	n	h	b	a	o	1	
1	*Tetralonia*	*Pittosporum tobira*	Pittosporaceae	III-IV	t	n	d	w	a	t	50	C12
1	*Tetralonia*	*Rhaphiolepis indica var. umbellata*	Rosaceae	IV	t	n	h	w	a	o	4	C14
1	*Tetralonia*	*Rhododendron tashiroi*	Ericaceae	III	t	n	h	pk	a	f	1	C14
1	*Tetralonia*	*Rubus sieboldii*	Rosaceae	III-IV	s	n	h	w	a	r	3	C14
1	*Tetralonia*	*Styrax japonica*	Styracaceae	II-IV	t	n	h	w	a	r	22	
1	*Tetralonia*	*Viola pseudo-japonica*	Violaceae	II-III	p	n	h	pl	z	t	1	C14
1	*Tetralonia*	*Wedelia biflora*	Asteraceae	III-XII	p	n	h	y	a	h	2	
1	*Xylocopa*	*Vaccinium wrightii*	Ericaceae	IV-V	t	n	h	w	a	c	2	C2
2	*Amegilla*	*Alpinia formosana*	Zingiberaceae	VI-VII	p	n	h	w/r	z	t	2	C10
2	*Amegilla*	*Alpinia intermedia*	Zingiberaceae	VI-VII	p	n	h	w/pk	z	t	3	C10
2	*Amegilla*	*Alpinia speciosa*	Zingiberaceae	V-VII	p	n	h	w/o	z	t	6	C10
2	*Amegilla*	*Scaevola frutescens*	Goodeniaceae	VI-VIII	s	n	h	w	z	t	10	C8
2	calyptrate fly	*Ilex integra*	Aquilfoliaceae	VI	t	n	d	g	a	o	35	C3
2	hawkmoth	*Barringtonia racemosa*	Lecythidaceae	XIII	t	n	h	w	a	b	1	C5
2	hawkmoth	*Cerbera manghas*	Apocynaceae	VI-X	t	n	h	w	a	t	4	C2
2	hawkmoth	*Clerodendrum trichotomum var. yakusimense*	Verbenaceae	VIII-X	t	n	h	w	z	t	41	C9
2	hawkmoth	*Musaenda parviflora*	Rubiaceae	V-VI	t	n	d	o/w	a	t	34	C12
2	megachilid	*Canavalia lineata*	Caesarpinaceae	VI-VII	p	n	h	pl	z	p	3	C13
2	megachilid	*Hibiscus hamabo*	Malvaceae	VI-VII	t	n	h	y	a	r	3	C13
2	megachilid	*Hibiscus tiliaceus*	Malvaceae	VI-XII	t	n	h	y	a	r	4	C13
2	megachilid	*Maackia tashiroi*	Fabaceae	VII	t	n	h	e	z	p	7	C13
2	megachilid	*Ormocarpum cochinchinens*	Fabaceae	VII	t	n	h	w/pl	z	p	1	C13
2	megachilid	*Vigna marina*	Fabaceae	VI-VII	p	n	h	y	z	p	6	C3
2	wind	*Scleria terrestris*	Cyperaceae	III	p	n	m	g	a	a	0	

Community	Pollination	Taxonomy		Traits								
Assignment	Guild	Species Name	Family	MB	GH	N	BS	FC	FS	FM	NV	CL
2	*Xylocopa*	*Actinidia rufa*	Actinidiaceae	V	t	n	m	w	a	r	1	
2	*Xylocopa*	*Ardisia quinquegona*	Myrsinaceae	V-VI	t	n	h	w	a	o	35	C12
2	*Xylocopa*	*Ardisia sieboldii*	Myrsinaceae	V-VI	t	n	h	w	a	o	57	C12
2	*Xylocopa*	*Dendropanax trifidus*	Araliaceae	VIII	t	n	h	g	a	o	17	C1
2	*Xylocopa*	*Diospyrus japonica*	Ebenaceae	VI	t	n	d	g	a	c	8	C2
2	*Xylocopa*	*Euodia meliifolia*	Rutaceae	X	t	n	d	w	a	o	25	C3
2	*Xylocopa*	*Hibiscus makinoi*	Malvaceae	X-XII	t	n	h	pk	a	r	11	C3
2	*Xylocopa*	*Kandelia candel*	Rhizophoraceae	VIII	t	n	h	w	a	r	18	C3
2	*Xylocopa*	*Mallotus japonicus*	Euphorbiaceae	V-VI	t	n	m	y	a	a	110	C8
2	*Xylocopa*	*Premna microphylla*	Verbenaceae	V,VIII	t	n	h	c	z	o	10	C3
2	*Xylocopa*	*Schima wallichii*	Theaceae	V-VI	t	n	h	w	a	r	78	
2	*Xylocopa*	*Vitex rotundifolia*	Verbenaceae	VI-X	s	n	h	pl	z	t	16	C3
3	?	*Aeginetia indica*	Orobanchaceae	X	p	n	h	pk	a	t	5	
3	?	*Ageratum houstonianum*	Asteraceae	X	a	a	h	pl	a	h	3	
3	*Amegilla*	*Melastoma candidum*	Melastomataceae	V-VII	s	n	h	pk	a	r	12	C10
3	small bee	*Ardisia pusilla*	Myrsinaceae	VI	s	n	h	w	a	o	1	
3	small bee	*Bredia hirsuta*	Melastomataceae	X	s	n	h	pk	a	r	7	C9
3	small bee	*Pollia japonica var. minor*	Commelinaceae	VI	p	n	h	w	a	o	3	
3	small bee	*Psychotria sepens*	Rubiaceae	V-VII	l	n	d	w	a	c	10	C12
3	small bee	*Ranunculus sieboldii*	Ranunculaceae	V-X	p	n	h	y	a	o	3	
3	small bee	*Reynoutria japonica*	Polygonaceae	XII	p	n	h	w	a	o	11	C12
3	small fly	*Alocasia odora*	Araceae	VI	p	n	m	w	a	a	25	C12
3	small fly	*Croomia japonica*	Stemonaceae	V-VII	p	n	h	c	a	o	5	
3	small fly	*Litsea japonica*	Lauraceae	X	t	n	d	c	a	o	14	C9
3	small fly	*Piper kadzura*	Piperaceae	V	l	n	h	w	a	a	3	C9
3	syrphid fly	*Blastus cochinchinensis*	Melastomataceae	VIII	s	n	h	w	z	r	1	
3	syrphid fly	*Rhynchotechum discolor*	Gesneriaceae	VIII	p	n	h	w	z	c	2	C7
3	*Tetralonia*	*Rubus grayanus*	Rosaceae	III	s	n	h	w	a	r	1	
3	various insects	*Mosla dianthera*	Lamiaceae	X	p	n	h	w	z	c	12	C9
4	beetle	*Pandanus odoratissimus*	Pandanaceae	VIII	s	n	m	c	a	a	11	C12
4	beetle?	*Melothria liukiuensis*	Cucurbitaceae	XII	l	n	h	g	a	o	1	
single	?	*Lasianthus japonicus*	Rubiaceae	XII	s	n	h	w	a	t	2	
single	beetle	*Eurya japonica*	Theaceae	XII-II	t		d	c	a	o	1	
single	wind	*Pinus luchuensis*	Pinaceae	II	t	n	m	c	a	a	2	

We also note that plants that are not part of a community based on plant-similarity are plants with low degree (i.e. specialists), although they seem to share many of the observable traits with other plants that are in a community. From explorations with a test network of lower species richness[18], we observed that this effect is exacerbated in pollination networks of a smaller than the one we used here. Most pollination networks are not as ambitious in scope as Kato 2000, so our methods may not be as effective for networks with less resolution or smaller spatial sampling.

Our results indicate that cross-discipline methodology in ecology and economics is a productive research direction. Ideas for future work include:

- An interesting difference between for instance country-product and plant-pollinator networks is that in the plant-pollinator networks both node types are species and can be introduced and removed from the system. In the case of countries this is not the case. Hence in an ecological system we can for example try and predict which species can or should be introduced or removed together.
- We can apply economic methods to infer how species richness and composition in plant-pollinator networks change over time. We would expect species with more features to have entered the system later. In the case of the product space, there is a clear direction of countries moving from simple products to complex products hence showing path-dependency.
- Both plants and pollinators can be considered as agents with capabilities and their partners as products with requirements. We can make a comparison between a plant-pollinator network and an economic network that also consists of two types of agents (i.e. that can be removed or introduced), for example the occupation-industry network for a particular city. Industries (plants) require occupations (pollinators) and occupations (pollinators) provide service to industries (plants). Hence these interactions can be interpreted as mutualistic, and some policy implications for economic diversification may follow based on insights from ecology.

8 Conclusion

Here, we provide evidence that similarity analyses on ecological networks may successfully recover the requirements and capabilities of species interactions. In concert with field observations, this may be a productive means of uncovering ecological dependencies than simple ecological trait measurements, because of lack of data and human sensory biases in the process of choosing and categorizing traits relevant to other species.

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Author contributions statement

A.v.D. and K.R.S.H. conceived of this study. A.v.D. and S.H. performed the network projections and visualizations. K.R.S.H. performed the ecological analysis. All authors reviewed the manuscript.

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