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The rise of Network Ecology: Maps of the topic diversity and scientific collaboration

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ABSTRACT

Network ecologists investigate the structure, function, and evolution of ecological systems using network models and analyses. For example, network techniques have been used to study community interactions (i.e., food-webs, mutualisms), gene flow across landscapes, and the sociality of individuals in populations. The work presented here uses a bibliographic and network approach to (1) document the rise of Network Ecology, (2) identify the diversity of topics addressed in the field, and (3) map the structure of scientific collaboration among contributing scientists. Our aim is to provide a broad overview of this emergent field that highlights its diversity and to provide a foundation for future advances. To do this, we searched the ISI Web of Science database for ecology publications between 1900 and 2012 using the search terms for research areas of *Environmental Sciences & Ecology* and *Evolutionary Biology* and the topic *ecology*. From these records we identified the Network Ecology publications using the topic terms *network*, *graph theory*, and *web*, while controlling for the usage of misleading phrases. The resulting corpus entailed 29,513 publications between 1936 and 2012. We found that Network Ecology spans across more than 1500 sources with core ecological journals being among the top 20 most frequent outlets. We document the rapid rise in Network Ecology publications per year reaching a magnitude of over 5% of the ecological publications in 2012. Drawing topical information from the publication record content (titles, abstracts, keywords) and collaboration information from author listing, our analysis highlights the diversity and clustering of topics addressed within Network Ecology. The largest connected component of the topic network contained 73% of the corpus, and exhibited strong clustering (clustering coefficient 0.93). The co-authorship network revealed that while network ecologists are generally collaborative, the field is deeply fragmented into topic and co-author cliques. The largest component of the co-author network comprised 46% of the authors and contained 149 distinct clusters. We suggest ways to build on the collaborative spirit and reduce the field fragmentation so as to improve the development and spread of ideas. We conclude that Network Ecology will likely continue to grow because the forces driving its increase are likely to persist.

"I map, therefore I am" Katharine Harmon (2004)

"Networks are everywhere" Manuel Lima (2011)

"Ecology is networks... to understand ecosystems will be to understand networks" Bernard Patten, quoted by Fritjof Capra (1996)

1. Introduction

Network concepts, tools, and techniques have a long history of use in ecology, but in recent years their use appears to have grown rapidly (Ings et al., 2009; Proulx et al., 2005). For example, Summerhayes and Elton, 1923 mapped the food-chains and food-cycles for biotic communities on Bear Island, creating prototype food webs (Elton, 1927). Bernard C. Patten formally recognized the importance of network models in ecology in his 1968 recruitment lecture at the University of Georgia titled "The network variable in ecology" (Patten and Fath, 2000: p. 178). More recently, scientists have used network models to investigate communities of mutualistic species (Bascompte et al., 2003; Bascompte and Jordano, 2007;

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Guimarães et al., 2011), general properties of ecosystems (Higashi and Burns, 1991; Jørgensen et al., 2007; Ulanowicz, 1986), and the movement of genes and organisms across landscapes (Holland and Hastings, 2008; Jacoby et al., 2012; Urban and Keitt, 2001). In this paper, we investigate the broad use of network concepts, tools, and techniques to investigate ecological and evolutionary questions. Following Borrett et al., 2012, we call this science *Network Ecology*.

Fundamentally, network models map one or more relationships among a set of objects or actors (Brandes and Erlebach, 2005; Higashi and Burns, 1991; Newman, 2003; Wasserman and Faust, 1994). As such, they are a way of describing how objects are arranged with respect to each other that accounts for mutual dependencies and higher order characteristics in the resulting pattern. Analytically, networks can be represented as mathematical graphs (G) composed of a set of nodes or vertices (V) and edges (E) such that $G=(V, E)$. Both vertices and edges can have multiple characteristics such as different types or weights. Further, edges can be undirected (symmetric relations) or directed (asymmetric relations), which is visually indicated by arrows. For example, in a food web the vertices represent different species, functional groups of species, or abiotic resource pools like detritus, and the directed edges map the relationship "is eaten by" as represented by arrows (directed edge) pointing from prey to predator. Vertices in a food web might be weighted by biomass or organism body size and edges can be weighted by the amount of energy or biomass transferred.

Ecologists have used multiple types of network models. For example, ecologists interested in animal behavior and social structure have mapped the interactions among individuals of a population (Croft et al., 2004; Finn et al., 2014; Foster et al., 2012; Wey et al., 2008). At the community level, Ings et al., 2009 identify three broad types of ecological networks: food webs, mutualistic networks, and host-parasitoid networks. This classification scheme builds upon the nine possible qualitative interaction types between two species identified by Burkholder, 1952 using a pairwise cross of positive (+), neutral (0), and negative (−) effects of one species on another. In this scheme, mutualism is indicated as (+,+). Ecosystem ecologists are interested in the same relationships, but infer those relationships from transactive network models that trace the flow of a thermodynamically conserved tracer like energy or nutrients (nitrogen, phosphorus, etc.) through a given system (Fath et al., 2007; Fath and Borrett, 2006). Such networks may represent food webs like in the community ecology networks (Cross et al., 2011; Martinez, 1991), but they may also map non-trophic processes such as death and excretion (Baird and Ulanowicz, 1989; Olff et al., 2009; van Oevelen et al., 2011) or biogeochemical processes (Christian et al., 1996; Reiners, 1986; Small et al., 2014; Whipple et al., 2014). More recently, ecologists have considered how to combine the variety of different ecological network perspectives to develop a broader understanding (Belgrano et al., 2005; Fontaine et al., 2011; Knight et al., 2005). From these examples, we might infer that network models and analytical tools have been used broadly in ecology. The question is how broadly?

Our objective in this study was to identify and characterize the domain of Network Ecology. We addressed three primary questions. First, has the size of the domain changed over time? Second, what topics are ecologists addressing using the network approach, and third what is the nature of the scientific collaboration among these ecologists? The examples previously presented suggest that there are a large number of topics being studied by a community of scholars that is divided into distinct clusters. As publications are a key product of the scientific process, we used a computational approach to infer from the publication record both the primary topics in the field and the structure of scientific collaboration. This bibliographic approach draws topical information from the content of publication records (titles, abstracts, keywords), collaboration information from author listing, and prominence and subfield information from citations. While our approach is different from a traditional in-depth review of the literature, it serves as a broad and high-level review of the field that provides a foundation for future work.

2. Materials and methods

To address our research questions, we used a combination of bibliographic techniques and network modeling. Similar network approaches to bibliometric studies have been used successfully to characterize the social structure of collaboration in many fields, including sociology (Moody, 2004), physics, biomedical research, and computer science (Newman, 2001a, 2001b), the study of ecosystem services (Costanza and Kubiszewski, 2012), and the evolution of collaboration in the US Long Term Ecological Research network (Johnson et al., 2010). Topical modeling for science-studies is similarly widespread, mapping detailed portraits of particular fields (Börner, 2010; Evans and Foster, 2011; Moody and Light, 2006).

2.1. Bibliographic data: search and selection criteria

To identify the Network Ecology publications, we searched the ISI Web of Science (WoS). We chose this bibliographic database because it is a large general index for science that includes extensive indexing of ecological science. Within the WoS, we limited our search to the Science Citation Index Expanded and Social Science Index Expanded citation databases between 1900 and 2012. We excluded two conference proceedings databases because they cover a smaller period of time (1990–present) and because the discipline of ecology values journal article publications more highly than conference proceedings.

Network ecology lies at the intersection of (A) ecological science and (B) network concepts, tools, and techniques. To identify the broad domain of ecological science in the WoS, we searched the union of two WoS research areas, *Environmental Science & Ecology* and *Evolutionary Biology*, and the topic tag of *ecology*. This is broadly inclusive of ecological science, but it is dependent on the WoS research area classifications that are applied to whole journals. To find the network science within this ecological science, we further searched the results for the union of three topic terms: *network*, *graph theory*, and *web*. These terms are frequently used within network science and can be regarded as signals for research using network concepts or models. The use of *web* captured science from spider webs to food webs, but it also included some spurious references to topics like the World Wide Web.

Ecologists use the term *network* in a variety of ways. The introductory examples illustrated the construction and analysis of network models to characterize communities and ecosystems. However, there are common uses of the term network that are less related to the type of network science we sought. To address this challenge, we excluded those records that our initial search identified only due to their use of a few selected phrases. Specifically, we excluded records that were initially included only because they entailed the phrases *neural network* or *Bayesian belief network*. These phrases are common statistical techniques unrelated to the broader network science that was our target. We also excluded records identified solely on the terms *monitoring network*, *transportation network*, and *railway network* because these phrases did not typically recover research where network science was applied to ecological problems.

We downloaded the final selection of records from WoS on May 13, 2013. We analyzed the resulting corpus with network analysis tools in SAS, Pajek, and R.

Table 1
Percent of ecology publications that include selected concepts and methods in ecology, including the 50 most important concepts in ecology as ranked by British ecologists in 1986 (Cherrett, 1989).

2012 Rank	Concept	*N*	% of 64,115	1986 Rank	2012 Rank	Concept	*N*	% of 64,115	1986 Rank
1	Species	17,126	26.7%		32	Succession	595	0.9%	2
2	Model	16,853	26.3%		33	Plant herbivore	555	0.9%	21
3	System	12,707	19.8%		34	*3/2* thinning *law*	551	0.9%	49
4	Population *cycles*	11,225	17.5%	19	35	Managed reserve	466	0.7%	28
5	Pattern	9158	14.3%	32	36	Density-dependent *regulation*	424	0.7%	15
6	Community	8456	13.2%	8	37	Environmental heterogeneity	394	0.6%	13
7	Ecosystem	6853	10.7%	1	38	Life history strategies	370	0.6%	9
8	*Species* diversity	6448	10.1%	14	39	Carrying capacity	363	0.6%	17
9	Evolution	5384	8.4%		40	coevolution	263	0.4%	24
10	Conservation *of resources*	4926	7.7%	4	41	Biome	252	0.4%	47
11	Energy *flow*	4897	7.6%	3	42	(Diversity or biodiversity) and stability	248	0.4%	
12	*Materials* cycling	3808	5.9%	7	43	Guild	240	0.4%	50
13	Landscape	3387	5.3%		44	Stochastic processes	208	0.3%	25
14	Indicator *organisms*	2698	4.2%	29	45	Island biogeography *or biogeographic theory*	178	0.3%	22
15	Organism	2680	4.2%		46	Allometry	174	0.3%	
16	Regression	2337	3.6%		47	Parasite-host interactions	170	0.3%	38
17	*Ecological* adaptation	2200	3.4%	12	48	Structural equation modeling	131	0.2%	
18	Disease	2136	3.3%		49	Ecotype	105	0.2%	40
19	Competition	1939	3.0%	5	50	Species packing	87	0.1%	48
20	*Natural* disturbance	1661	2.6%	26	51	Keystone species	85	0.1%	46
21	Systems ecology	1634	2.5%		52	Allocation theory	78	0.1%	43
22	Trophic *level*	1415	2.2%	31	53	Optimal foraging	72	0.1%	37
23	*Habitat* restoration	1344	2.1%	27	54	Competition and species exclusion	63	0.1%	30
24	Limiting factors	1220	1.9%	16	55	Territoriality	58	0.1%	42
25	Niche	1108	1.7%	6	56	Maximum sustainable yield	32	0.0%	18
26	Food webs	1017	1.6%	11	57	Climax	25	0.0%	41
27	Stable isotope	882	1.4%		58	Pyramid *of numbers*	14	0.0%	45
28	Predator-prey *interactions*	790	1.2%		59	R and K selection	11	0.0%	33
29	ANOVA or analysis of variance	758	1.2%		60	Intrinsic regulation	9	0.0%	44
30	Species-area relationships	751	1.2%	39	61	Socioecology	8	0.0%	36
31	Bioaccumulation *in food chains*	704	1.1%	23	62	Plant-animal coevolution	7	0.0%	34
					63	Ecosystem fragility	5	0.0%	10

Note: Plural forms of concepts listed were also searched and are included in the counts. For concepts and methods that seemed overly specific, we selected to search a more general form (excluding italicised words). For example, the phrase *energy flow* is very specific, so we also searched the term *energy* by itself. We added the 13 concepts that are not ranked in the BES 1986 survey.

2.2. Analysis

2.2.1. Publication volume

Given the Network Ecology corpus, we characterized the volume of the publications using several metrics. First, we examined how the number of publications changed through time. Given that any observed change in publication numbers could be influenced by the general publication inflation in ecology, we report the raw number of network articles and show this as a percent of the annual number of publications in ecology (WoS search for ecology as described previously without applying the search for network concepts). This normalization should remove the expected inflationary trend in ecology publication volume. Our second approach for characterizing the publication volume was to quantify three aspects of the publications in the corpus. We described the distribution of (1) the WoS research area categories, (2) the journals in which the papers are published, and (3) the article citation frequency within the corpus.

To evaluate the relative importance of the Network Ecology publication volume in the most recent year analyzed (2012), we compared it to the relative frequency of selected concepts and tools in the broader ecology corpus in WoS. We started with the 50 concepts that were identified by members of the British Ecological Society (BES) as important ecological concepts in 1986 (Cherrett, 1989), generalizing when appropriate. We then added 13 additional terms to capture newer topics of apparent importance (e.g. *disease*) and common analytical techniques (e.g. *regression*) (Table 1).

2.2.2. Corpus validation

To evaluate the quality of the Network Ecology corpus discovered, we determined if the corpus included recent publications considered important by a community of experts. Participants were surveyed online and asked to identify up to 5 Network Ecology publications between 2007 and 2012 that they considered most important (Supplementary Table A1). The survey was created using Qualtrics software and distributed to the Ecological Society of America's Ecolog-L electronic mailing list, which currently boasts more than 17,000 subscribers. We also sent the survey directly to a targeted group of 56 known Network Ecology experts. A reminder was sent after about a week and participants were encouraged to further distribute the survey link. 59 respondents completed the survey. The resulting convenience sample was intended to be a positive control on our discovery of key Network Ecology publications. Accordingly, we classified the references identified by the expert community into three categories: (1) not included in WoS, (2) included in WoS but missing from the corpus, and finally (3) included in the corpus.

2.2.3. Topics in Network Ecology

To identify the predominant topics in Network Ecology, we built a network of papers linked by similar terms used in the title, abstract, and keyword records. Edges are weighted by the similarity of their term use, using the standard tf-idf formulation (Börner et al., 2003), which discounts the similarity of common terms and favors more rare terms. Edges were included in the topic network when they indicated a minimum percentage of co-term similarity. We constructed two versions of this co-term network; one composed of all papers in the corpus (35% minimum similarity) and a second with 5-year moving windows (25% minimum similarity). By this construction, papers on similar topics can be identified using cluster detection techniques (Moody and Light, 2006). We applied the Louvain community detection algorithm (Blondel et al., 2008) on a weighted graph as implemented in PAJEK. To visualize the results, we constructed two-dimensional maps of the topic space by applying space-based layout routines to the similarity network. These routines place papers that have much in common near each other. Since the resultant networks are too dense to be visually informative, we overlaid contour maps that reflect the paper density in the topic space and labeled these maps with the most frequent terms used in each cluster (Moody and Light, 2006 for this particular technique; Börner, 2010, for the general approach). Labels are generated automatically using the most commonly used terms within each cluster.

In addition to identifying the clusters within these temporal waves, we characterized the topic distribution using network community detection metrics. The first is the *modularity score* (Newman and Girvan, 2004), which captures the extent of clustering beyond random chance. A value of 1.0 indicates completely disconnected clusters, while a value of 0 indicates no difference from random assignment. The second is the *heterogeneity index*, which captures the distribution of topics across clusters. The heterogeneity index is the probability that two papers chosen at random would fall within the same cluster.

2.2.4. Structure of scientific collaboration

To characterize the structure of scientific collaboration in Network Ecology, we constructed a co-authorship network in which nodes represent individual authors, and weighted edges connect two authors by the number of papers they have co-authored. Since publication records are often inconsistent in name use, we applied a light name-cleaning routine to combine names that are obviously similar ("Stuart J. Whipple" & "S.J. Whipple") by matching on uncommon last names and combinations of first and middle initials (see Moody, 2004). This is a deliberately conservative name correction routine, as the network costs of conflating common names (potentially creating a bridge between groups that are unconnected) are typically worse than leaving them separate (which, while potentially increasing isolates, tends to preserve collaboration groups). Once constructed, we identified the connectivity structure and examine diversity in collaboration groups. We again applied the Louvain community detection algorithm to identify collaboration clusters (default unit-weighted resolution parameter).

3. Results

3.1. Publication volume

The total number of Network Ecology articles discovered prior to any exclusions based on selected phrases was 33,900 (Table 2).

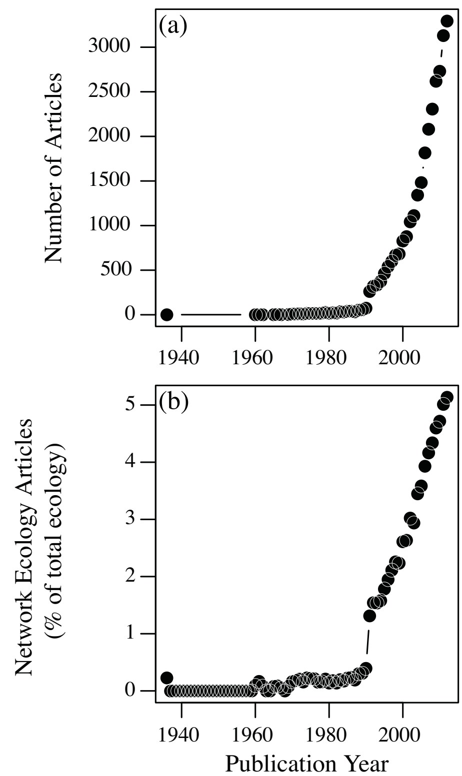

Fig. 1. (a) Number of Network Ecology publications per year, and (b) as percent of total ecology publications discovered in our bibliographic search.

The majority (59%) of these records was discovered by the intersection of the WoS research area *Environmental Science & Ecology* and topic term *network*, and 88% of the articles were discovered by the intersection of the same WoS research area and the topic terms *network*, *graph theory*, and *web*. In contrast, the intersection of these three network topic terms with the WoS research area *Evolutionary Biology* only found 8% of the records and only 4% of these were unique. From this initial corpus, we excluded records based on their use of phrases that entail the term *network* but do not necessarily refer to research that applies network science to ecological problems (# affected): *neural* (2444), *Bayesian belief* (259), *monitor* (1263), *railway* (232), and *transport network* (244). Combined, these exclusion phrases removed 3962 records or 12% of our initial sample. The remaining 29,513 records are the Network Ecology corpus that we further analyzed.

The number of Network Ecology articles published each year has grown rapidly (Fig. 1). The first ecology article discovered by our methods appeared in 1936, by Griswold and Crowell on "The Effects of Humidity on the Development of the Webbing Clothes Moth"; however, this article seems to have been identified due to the common name of the organism rather than its use of a formal

Table 2
Number of records returned using search terms for two dimensions of Network Ecology: Ecological science (WoS research areas *Environmental Science & Ecology* and *Evolutionary Biology* and topic *ecology*) and network science (topics *network*, *graph theory* and *web*).

			Ecological Science					
			Null	Environmental Science & Ecology	Evolutionary Biology	Ecology		
			0	A	B	C	A or B	A or B or C
Network Science	Null	0		1,002,490	139,706	106,825	1,075,483	1,144,552
	Network	X	666, 367	19,987	1900	2751	21,005	22,534
	Web	Y	110, 868	10,567	846	2978	10,749	12,196
	Graph theory	Z	6198	183	22	76	189	207
		X or Y or Z	769, 435	29,877	2688	5450	31,068	33,900

Note: Number at the intersection of the search terms are the set intersection (∩) of the row and column terms; "or" in the table represents the set union (∪) of search terms.

network approach. Instead, Gimingham's (1961) investigation of the network of variation in heath communities appears to be the first ecological publication identified by our search that explicitly uses a network model. From these early publications, the number of Network Ecology publications increased quickly to 3063 articles in 2012.

The growth in Network Ecology research cannot be explained by the general inflation in ecology publications. Relative to the total number of ecology publications, Network Ecology publications noticeably increased in the early 1960s (Fig. 1b). Between 1990 and 1991 the percent of Network Ecology articles jumped by almost 1%. Following this jump, Network Ecology publications have steadily increased from less than 1.5% in 1991 to over 5% in 2012. This suggests that Network Ecology is a large and rapidly growing area of research.

The Network Ecology corpus includes work from a wide range of WoS research areas and publication sources, which indicates the diversity of research in this field (Fig. 2). Our corpus entailed publications pertaining to 122 unique, though non-exclusive WoS research areas. The most common area was *Environmental Science & Ecology*, which is not surprising as this was one of our search criteria. The next three most frequent research areas were *Marine & Freshwater Biology*, *Engineering*, and *Water Resources*. Other WoS research areas represented in our corpus included disparate disciplines such as *Geography*, *Urban Studies*, and *Public Administration*.

Network Ecology publications in our corpus were distributed across nearly 1500 different publication outlets. These are primarily journals, though sometimes proceedings from conferences. Note that we did not correct for merging or changes in journal names over time. The journals Marine Ecology Progress Series and Water Resources Research contained the most Network Ecology papers, but each only contained 3–4% of the articles (Fig. 2b). Core ecology journals such as Ecology, Oikos, Oecologia, and Ecology Letters were among the top 20 most frequent sources. More general journals such as Science of the Total Environment and Proceedings of the Royal Society B: Biological Sciences also made the top 20.

The frequency of citations to articles in the corpus (Fig. 3) roughly follows the expected long-tail distribution of a Zipfs or power-law form; however, there were fewer citations at the low-end than is typical for such distributions (Zipf, 1949). The modal value is 0 (13.8%) while 51% of papers are cited 8 or more times, 25% more than 23 times, 10% more than 50 times, and the top 5% received more than 78 citations. Only 3.3% of papers are cited 100 times or more.

In 2012, the Network Ecology publications listed in WoS were 5.1% of the total publications in ecological science as defined above (Fig. 1b). To put this proportion into perspective, we found the percentage of ecological publications in 2012 that contained other key ecological concepts including the 50 identified in the 1986 BES survey (Cherrett, 1989). The respective proportions range from 26.7% for *species* and 26.3% for *model* to approximately 0% for terms like *island biogeographic theory*, *pyramid of numbers*, and *3/2 thinning law* (Table 1). Some of the 1986 BES concepts continue to show relevance in 2012. For example, 17.5% of the ecology publications in 2012 included the term *population*, which represents a generalized form of the concept *population cycle*, which ranked fourth in the BES survey. *Ecosystem* was the highest ranked concept on the BES survey and it appeared in 10.7% of the ecology articles published in 2012. When compared to the relative frequency of these 63 terms, our definition of *Network Ecology* (which includes food webs) would have a rank of 15.

3.2. Corpus validation

The online survey was completed by 59 people who identified 118 unique publications. Of these, 22 fell outside our target time frame (2007–2012). Of the remaining 96, respondents showed agreement on some of the most important papers as multiple people identified the same papers. Out of the 96 publications identified, 13 (14%) were mentioned twice and 2 (2%) references were mentioned three times (Table 3). Five of the references were not included in the WoS database. Three of these missing references were books or book chapters (Olesen et al., 2012; Whitehead, 2008; Ulanowicz, 2009), which are not indexed by WoS, and the other 2 were published in journals not indexed by WoS (Rudnick et al., 2012; Ulanowicz, 2011). The remaining 91 publications were found in the WoS database, and thus were discoverable by our search. However, only 55 of the 91 discoverable references (60%) identified by the experts were represented within our Network Ecology corpus. This indicates the challenge of discovering relevant Network Ecology articles even when using a broad bibliographic search like ours.

3.3. Topics in Network Ecology

3.3.1. Corpus topic network

To identify the topic structure of the Network Ecology corpus, we constructed a similarity network based on co-word frequency. Fig. 4 illustrates this process by walking out from a single paper to its local neighborhood and the clusters they link to. Panel (a) plots just the focal paper and its nearest neighbors. At an edge-threshold of at least 35% co-term similarity, this paper is directly adjacent to 15 other papers, all generally on aspects of food webs and grazers. Stepping out two more links as shown in panel (b), we reach nearly 300 papers and find this small cluster embedded within a wider field of 7 or 8 clusters, ranging in topics from algae in alpine environments to the invasive consequences of crayfish. Since the layout algorithm pulls similar papers near each other, these clusters emerge as tight groups in the network diagram. Many papers here are related in one way or another to water-based ecosystem studies, and were we to step out even further we would likely find those nested within a broader set of papers related to aquatic environments. To ease recognition, we visualized clusters by fitting a 2-d kernel density surface and overlaying the resultant contours shown in the example.

The complete topic network is comprised of 29,513 vertices representing the papers in the corpus connected by 106,795 edges indicating topic co-word similarity with a minimum of 35% similarity. This topic network is comprised of several separate components (disconnected subnetworks) of varying sizes. The largest component contains 21,636 vertices (73% of total). The remaining 27% of the papers appear in smaller components. The second largest component contains 15 papers (0.05%). The majority of papers not in the largest component (5908 or 20% of total) are isolated nodes (components of size 1) with no edges connecting them to other papers. This isolation indicates that either their topics do not appear related to other papers in the corpus or that their WoS records did not contain enough information to identify the similarity. We focused our subsequent analysis on the giant component of this topic network, which should reduce the potential bias of less relevant references initially captured in our search.

Fig. 5 provides a contour diagram of the topic structure revealed in the giant component of the topic network. The overall topology of this topic network resembles a ring structure with multiple topic-centered peaks joined at their peripheries to a neighboring subfield. Starting at the north central region of the contour diagram, we find a large number of clusters generally related to aquatic ecosystems, rivers, and lakes. Moving in a clockwise direction, we then encounter a small ridge of work related to soil, nematodes, food web and communities that then links to work on predator–prey food webs and communities. The southeast of this map is composed of work on landscapes, habitats and conservation with a

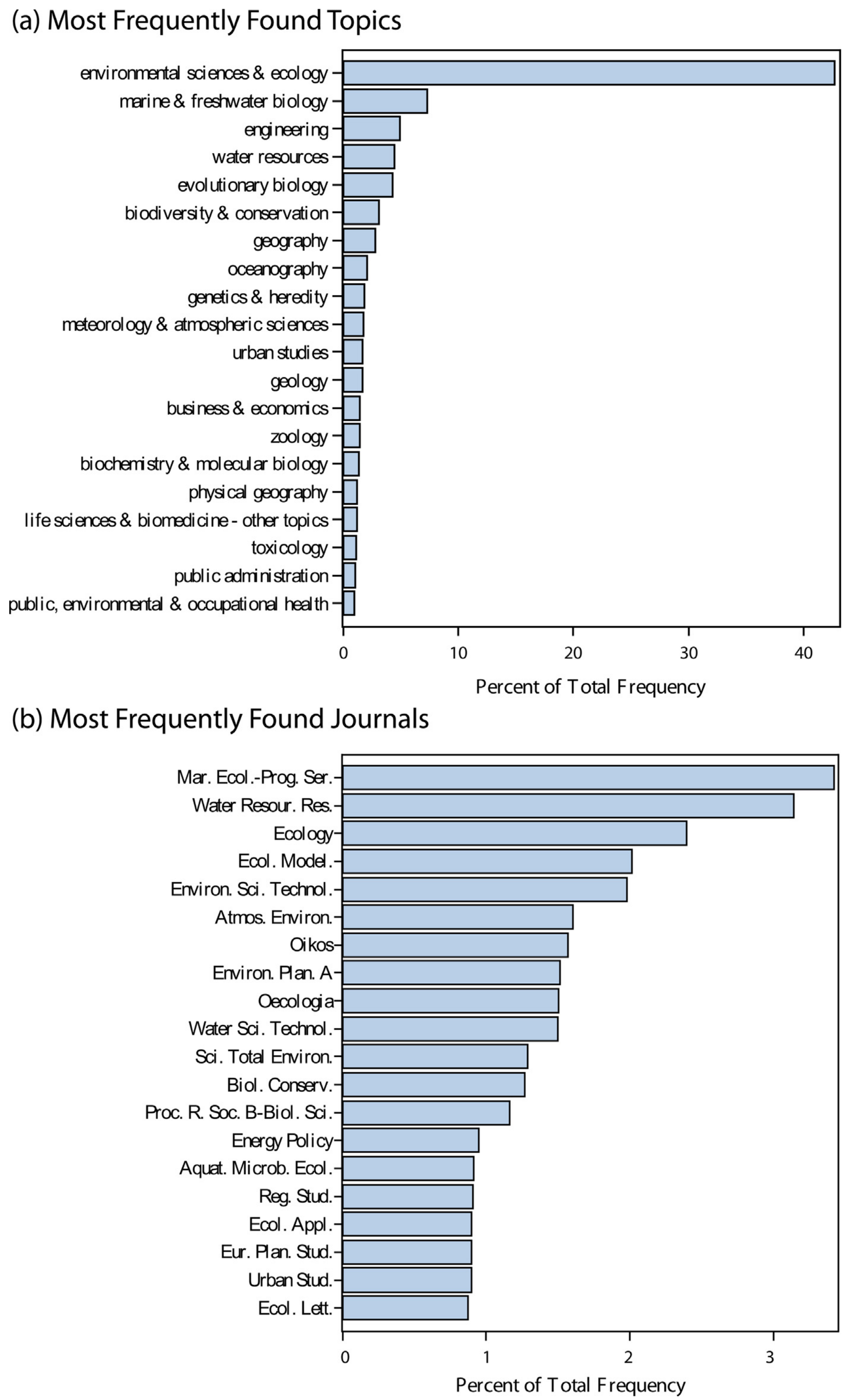

Fig. 2. Top 20 WoS research areas (a) and journal titles (b) for Network Ecology research.

large genetic cluster. The common theme of land-use bridges from the southeast corner to the southwest which shows work on the intersection of human activity and ecosystems, particularly urban planning, policy & energy use. The far west of the diagram relinks with water system models through groundwater and distribution topics. Descriptive network statistics of the five largest clusters are indicated in Table 4.

3.3.2. Temporal waves

To identify possible temporal variation of topics and topic structure in Network Ecology, we constructed and analyzed topic networks in temporal waves. We combined the years 1980 to 1989 due to the small number of papers. From thereon we constructed waves in 5 year moving windows. Table 4 shows the 5 largest topic clusters in each of the waves. Except in the years 1980 to 1989,

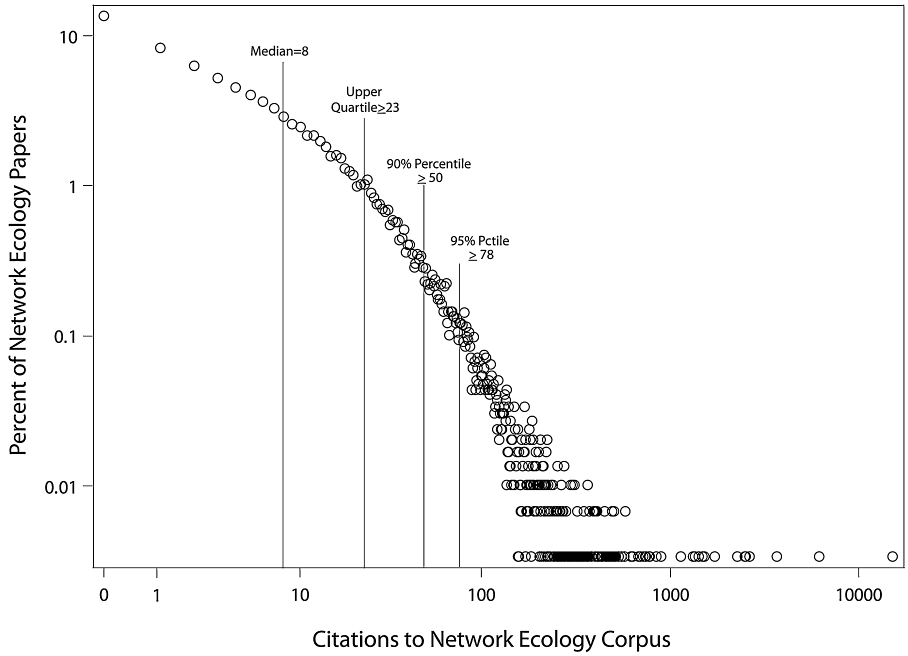

Fig. 3. Citation distribution for articles in the Network Ecology corpus.

the modularity score as well as the heterogeneity index shows remarkable stability across the waves. The modularity score as well as the heterogeneity index for the full corpus is substantially larger than that for each individual wave, which signals that the topics addressed did change across the waves as either new topics emerged, old topics disappeared, or the terminology used to address the same topic changed (our analysis cannot differentiate between these possibilities). Not only the size of the largest component, but also the average cluster size steadily increased from 38 for the years 1980 to 1989, to an average of 238 between 2005 and 2009—a level that was subsequently almost reached within only 3 years (2010–2012).

Our analysis reveals a strongly clustered pattern of the topic networks. The modularity score is over 0.82 in all waves since 1990, and 0.93 for the full corpus. This strong clustering is expected in a topical network for science studies, since most publications are designed to speak carefully to a particular research problem. The distribution of cluster sizes suggests that no single topic dominates the field of Network Ecology; the largest clusters typically account for between 5% and 7% of the topics in a wave. The topic network for the full corpus is even more dispersed with the largest clusters entailing only about 4% of the papers. The network for the full corpus allows us to identify more specialized topics that might not appear in any of the smaller waves as there would be too few papers. The more dispersed nature of the full corpus is reflected in the high heterogeneity scores, typically topping out over 0.95 in later years. Since all of these papers have a foundational commonality in Network Ecology, this suggests an extremely topically

Table 3
Most frequently cited papers by experts asked to identify important Network Ecology papers published between 2007 and 2012.

Authors	Year	Title	Journal
Mentioned Three Times			
Dale and Fortin	2010	From graphs to spatial graphs	Ann. Rev. Ecol. Evol. Syst.
Fontaine et al.	2011	The ecological and evolutionary implications of merging different types of networks	Ecol. Lett.
Mentioned Two Times			
Aizen et al.	2012	Specialization and rarity predict nonrandom loss of interactions from mutualist networks	Science
Allesina and Pascual	2009	Googling food webs: can an eigenvector measure species' importance for coextinctions?	PLoS Comp. Biol.
Baird et al.	2008	Nutrient dynamics in the Sylt-Romo Bight ecosystem, German Wadden Sea: An ecological network analysis approach	Estuar. Coast. Shelf Sci.
Bascompte and Jordano	2007	Plant-animal mutualistic networks: The architecture of biodiversity	Ann. Rev. Ecol. Evol. Syst.
Berlow et al.	2009	Simple prediction of interaction strengths in complex food webs	Proc. Nat. Acad. Sci. USA
Chen et al.	2008	Network position of hosts in food webs and their parasite diversity	Oikos
Dunne and Williams	2009	Cascading extinctions and community collapse in model food webs	Philos. Trans. R. Soc., Lond. B
Nuismer et al.	2013	Coevolution and the architecture of mutualistic networks	Evolution
Otto et al.	2007	Allometric degree distributions facilitate food-web stability	Nature
Ramirez	2012	Population persistence under advection-diffusion in river networks	J. Math. Biol.
Thébault and Fontaine	2010	Stability of ecological communities and the architecture of mutualistic and trophic networks	Science
Urban et al.	2009	Graph models of habitat mosaics	Ecol. Lett.
Wey et al.	2008	Social network analysis of animal behavior: a promising tool for the study of sociality	Anim. Behav.

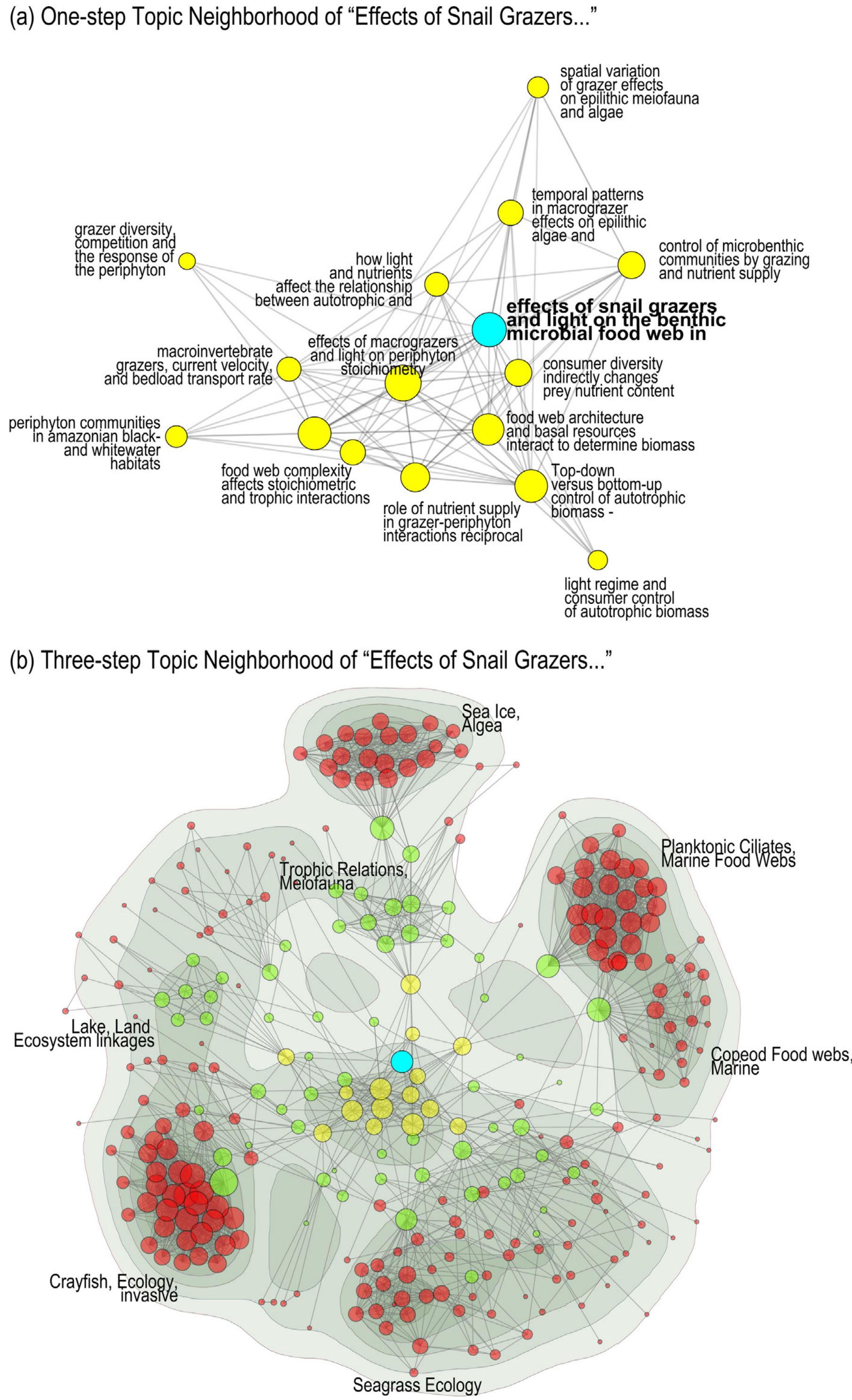

Fig. 4. Topic network construction example: (a) the one-step local neighborhood around the exemplar paper Burgmer et al., 2010 which is colored blue, and (b) the topic clusters that appear 3 steps from the focal paper. A contour map overlay created with a 2-d kernel density surface algorithm also shows the paper clusters in (b). Clusters are labeled with the most common terms. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

diverse body of work employing network concepts, tools, and techniques.

While the sheer diversity of the topical networks makes identifying temporal trends difficult, we did find some patterns of interest. We see similarities across the largest topics in each year as themes related to water and aquatic systems, predator-prey models, conservation, and network methodology reoccurs. In particular, topics related to predator-prey models reappear throughout most waves. Furthermore, topics related to water and aquatic systems (*lake*, *fish*, *phytoplankton*) seem to have become more central between 1995 and 1999 and gained further relevance thereafter (*stream*, *river*, *water*, *rain*). Between 2000 and 2004 conservation and the influence of human living and production on the environment become apparent (*reserve*, *pollution*, *air*, *concentration*, *road*, *emission*, and eventually also *firm*, *innovation*) which might be due to a more general interest in sustainable living and environmental

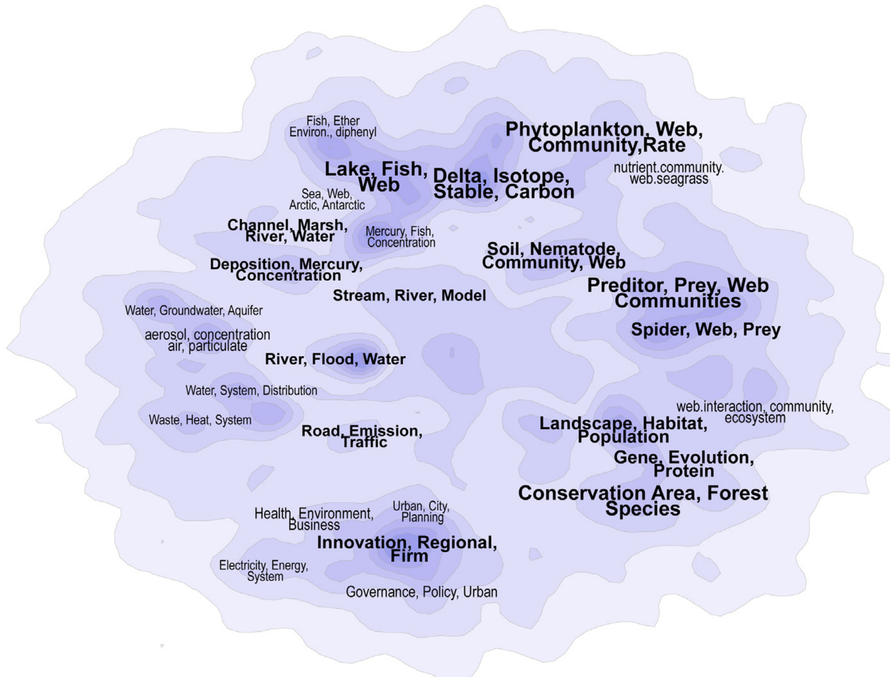

Fig. 5. Contour plot of the topic network giant component. Regions are labeled with the most common terms found in the clusters and font size corresponds to term frequency.

protection. Between 2010 and 2012, themes related to urban living (*urban*, *city*) and the topic *temperature* appears, which could be due to an increased interest in climate change and the application of ecological network analysis to built environments.

3.4. Scientific collaboration

3.4.1. Overview

To map the structure of scientific collaboration in Network Ecology, we constructed a co-authorship network from the publications in our corpus. Whenever two scientists collaborate on a paper, it creates a connection that extends through all co-authors and thus collaboration networks provide a useful model for communities of science. In Network Ecology collaboration is common (Fig. 6). Most of our papers contain multiple authors and the median paper has 3 authors (inter-quartile range (IQR) 2–4), though there is a fairly large tail (with the largest paper having 82 authors). The incidence of collaboration has been growing over time, from an average of 2 co-authors per paper in the 1980s to over 4 currently.

Concatenating across all publications we built the full collaboration network. In this network, the vertices represent authors that are connected by an edge if they have co-authored a paper in the corpus (co-authorships among these authors on papers other than those in our corpus are not considered). Edges are weighted to indicate the number of papers co-authored. The corpus contains 69,564 uniquely named authors.

Fig. 7 provides an image of the full collaboration network using the same contour overlay strategy as previously described. The largest connected component contains 46% of these authors. Only 2695 (3.9%) of the authors appear as isolated nodes having not co-authored a publication. The component size distribution is skewed, such that the next largest component has 75 people. The diameter of the large component is 27 steps, while the average path length is 7.7. Within the largest component, the largest bi-connected component contains 58% of authors (19,015), and 85% of this set are members of at least a 3-core—sharing at least three neighbors in common with every other member of the set. It is possible for most of the members of the largest connected component to reach each other via multiple collaboration paths. Thus, at a high-level of analysis, these results show a well-connected research community

3.4.2. Clustering

Despite the broad connectivity within the community, there are a large number of distinct clusters in the largest co-authorship component (Fig. 8). The Louvain community detection algorithm (Blondel et al., 2008) identified 149 clusters ranging in size from 6 to 1618. The small clusters (<25 or so) are generally fringe cases that are only weakly connected to the rest; looking at only those with larger sized communities the median is 190 people (IQR: 87–354). The clusters congregate around three distinct larger communities, evident as peaks in the overall sociogram (Fig. 7).

To better characterize the largest co-authorship clusters, we identified the three authors with the highest betweenness centrality within the cluster (Supplementary Table A2). At this scale of analysis, these clusters represent groups of authors who generally work together on similar scientific problems or topics. Embedded within the clusters are also traces of collaborative working groups that may be based on a single primary investigator or a small group of collaborative principles. For example, G. Woodward, J. Memmott and N. Martinez have the highest betweenness centrality in cluster 13, which contains 1618 authors (about 2.5% of all authors, 5% of the largest component). These authors work on a variety of topics, but they appear to also have a common focus on community networks like food webs and pollination networks (Woodward et al., 2005, 2008; Martinez, 1991; Williams and Martinez, 2000; Memmott, 2009). Furthermore, several authors within this cluster have collaborated on recent synthetic publications (Brose, 2006; Ings et al., 2009).

The modularity score for the overall clustering of the co-authorship network is 0.92, suggesting relatively distinct clusters. Just over 94% of co-authorship occurs within clusters, and 80% of authors have only within-cluster ties. The remaining 20% of authors create the links that pull together the entire network. Within cluster density averages 0.09 (IQR: 0.02–0.12), but since density is strongly affected by cluster size average degree is perhaps more telling. On average, authors collaborate with 9.2 other authors in their

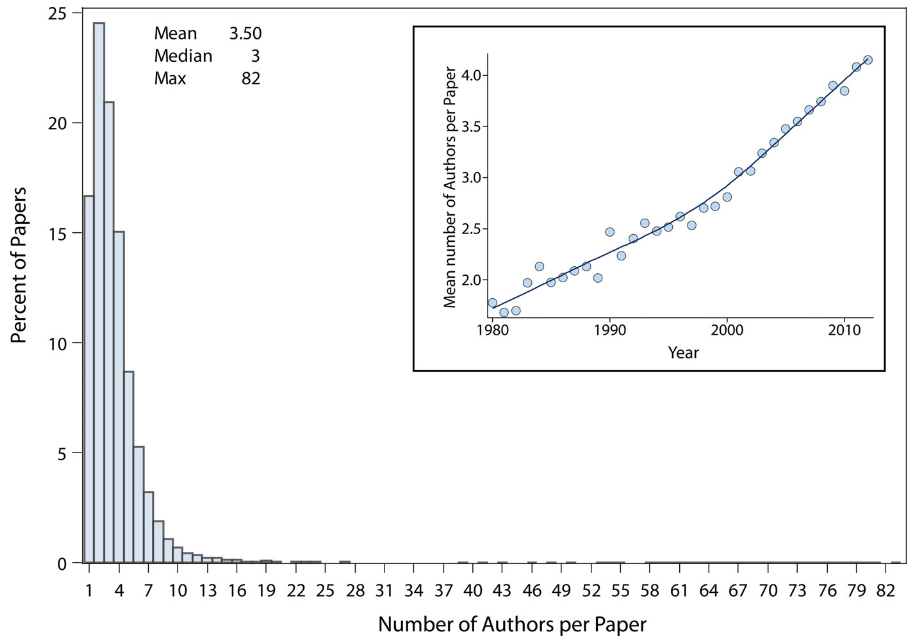

Fig. 6. Frequency distribution of the number of co-authors of Network Ecology articles and the temporal trend in collaboration (inset).

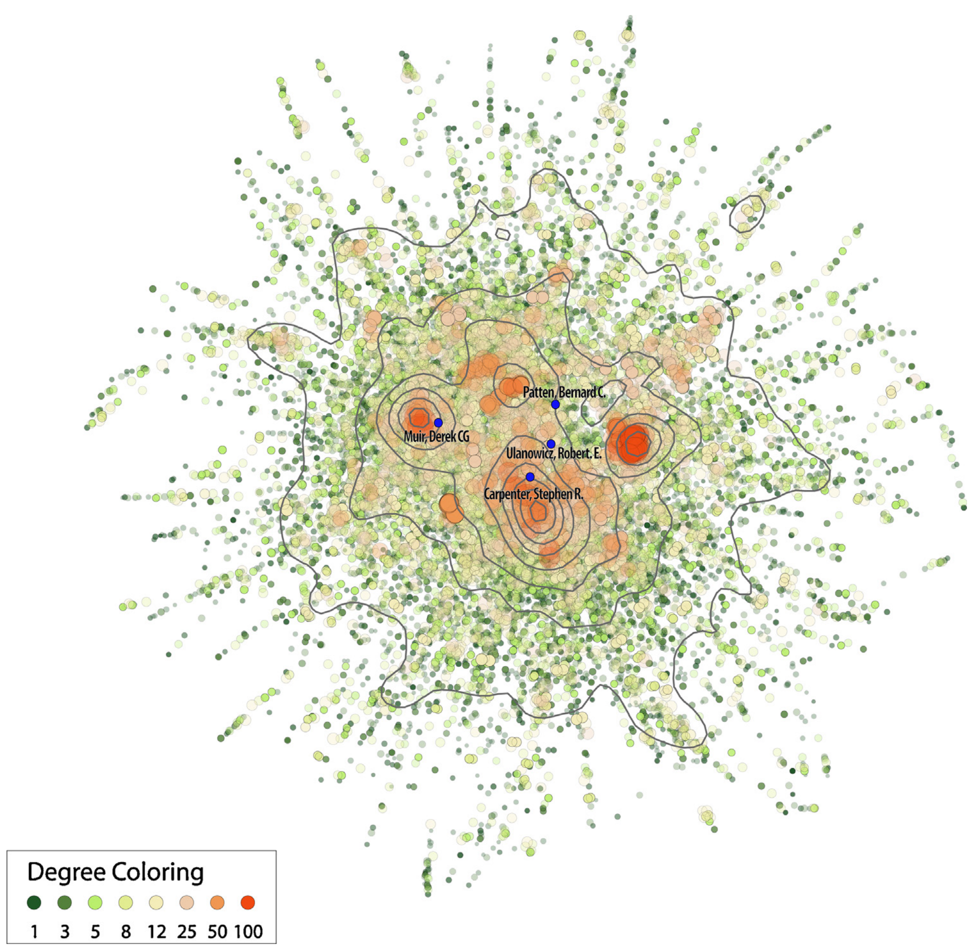

Fig. 7. Collaboration by scientists publishing in Network Ecology as indicted by co-authorship (network node size and color proportional to degree, contour lines capture overall density of the academic field).

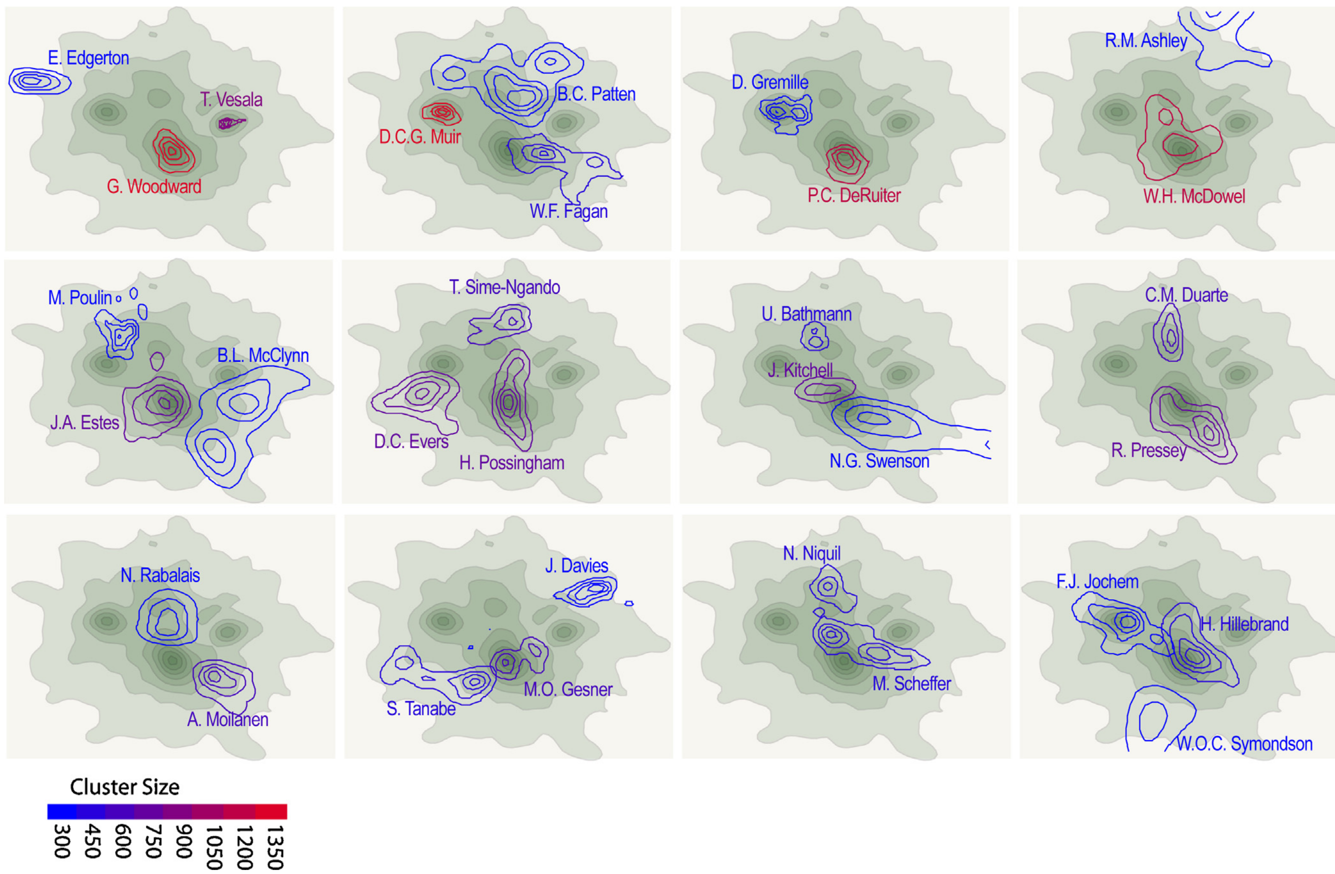

Fig. 8. Clustering in co-authorship network for Network Ecology publications. Each panel highlights distinct clusters in the co-authorship network and indicates the cluster size, dispersion, and the most central author (betweenness).

clusters (Median: 7.8l; IQR: 6.3–9.6). The structure within clusters is composed of overlapping cliques formed by sharing authorship on papers. This ranges from very fragile structures where a few key nodes chain across multiple large papers to very robust groups that collaborate across many papers.

3.4.3. Ego networks

We can further highlight features of the Network Ecology collaborative structure by focusing on selected individual authors. Fig. 9 shows the ego co-authorship networks for Bernard C. Patten, Robert E. Ulanowicz, Stephen R. Carpenter, and Derek C. G. Muir. These ego networks show the co-author structure from the perspective of a specific individual. Here, we have also included the co-authorships that most directly link Patten and Ulanowicz to visualize the hypothesized historical separation between their research programs (see Scharler and Fath, 2009). Within the Network Ecology corpus, Patten has 62 direct co-authors, Ulanowicz has 67, and Carpenter and Muir have 128 and 226, respectively.

Each author's ego network tells different stories. Unpacking those highlights the variety of factors that can influence the structure of scientific collaborations. For example, Patten's ego net displays a couple of different working groups. The first is comprised of his former Ph.D. students (e.g., S. J. Whipple, S. R. Borrett, S. R. Schramski) and the Systems Ecology and Engineering colleagues at the University of Georgia (e.g., D. K. Gattie and C. Kazanci). Another work group is comprised of S. E. Jørgensen, and M. Straskraba. Brian D. Fath appears to be loosely part of both of these groups; he was also a Ph.D. student with Patten. Another cluster of co-authorships appears in the lower region of the plot and includes P. G. Verity, M. E. Frisher, and J. C. Nejstgaard. The publications that link these co-authors were a result of an NSF Biocomplexity award (Nejstgaard et al., 2006; Whipple et al., 2007). There is another cloud of co-authors plotted between Patten and Ulanowicz that is a result of a synthetic publication calling for improvement in food web construction co-authored by multiple investigators working on food webs at that time (Cohen et al., 1993).

4. Discussion

Considered together our results highlight three key features of Network Ecology. First, Network Ecology is a large and rapidly growing area of ecology. Related papers are published in a wide variety of journals, touch on a breadth of topics, and co-occur in a broad set of research areas defined in WoS. Second, despite visible temporal continuity, the substantial research topics addressed within Network Ecology are manifold and have varied over time as shown by prominent co-occurrences of words across papers. Third, collaboration as reflected in co-authorship among researchers suggests a highly collaborative science, but one that appears deeply fragmented into distinct clusters of collaborators. We next consider the forces that may have driven the increase in Network Ecology, suggest possible ways to overcome the domain fragmentation, identify the limitations of this study with possible next research steps, and highlight emerging frontiers of Network Ecology.

4.1. Forces shaping Network Ecology

4.1.1. Growth

Our results show Network Ecology to be a broad and rapidly growing area of research. While this change was not evident in a recent survey of trends in ecological research (Carmel et al., 2013), our finding is consistent with previous research both in ecology

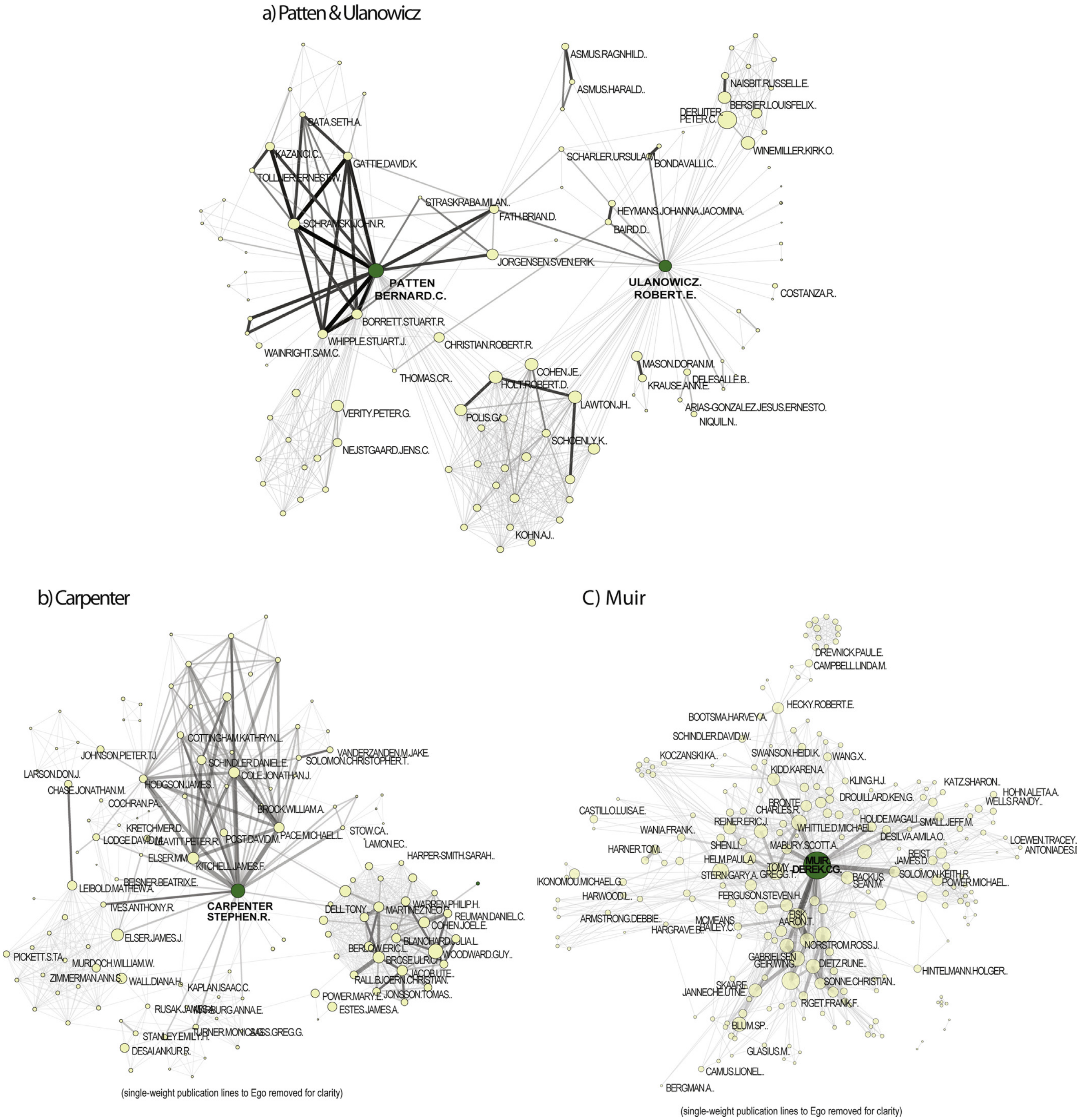

Fig. 9. One-step ego networks of (a) Bernard C. Patten and R.E. Ulanowicz, (b) S.R. Carpenter and (c) D.C.G. Muir.

and in other areas of network science. Ings et al., 2009 used a more constrained survey of papers published in 12 selected journals to show the rapid increase of networks in ecology between 1970 and 2007. For 2007, they found that approximately 12% of the papers published in these journals were related to food webs, host-parasitod, or mutualist networks. This rapid expansion in ecology mirrors developments in other fields. For example while network modeling and analysis has a long history in the social sciences (Wasserman and Faust, 1994; Freeman, 2004), Borgatti and Foster, 2003 document a similar growth pattern in social network publications between 1970 and 2000. We speculate that at least three factors may have contributed to the observed growth in Network Ecology.

The first factor is the positive feedback from a critical mass of theoretical developments, applications, and tools by network pioneers across many fields (e.g., Wasserman and Faust, 1994; Fath and Patten, 1999; Newman et al., 2006). These investigators solved essential methodological problems and successfully demonstrated their substantial utility. In ecology, examples of this are the early theoretical analysis of binary food webs (Pimm, 1982), analysis of flows and cycling in ecosystems (Finn, 1976; Baird and Ulanowicz, 1989), and the development of the Ecopath software for model construction and its inclusion of network analysis tools (Christensen and Pauly, 1992). Beyond ecology, Watts and Strogatz's (1998) paper on the small-world phenomenon is often cited as a tipping point in the development of network science. This publication was

Table 4
Topic cluster distributions and descriptions of the largest 5 topic clusters in the whole network and in the six temporal waves.

Rank	Proportion	Most common terms
Total: P = 21,636, C = 86, M = 0.927, TH = 0.98, Mean cluster size (S.D.): 251 (185)		
1	0.038	Conservation, area, forest, species
2	0.034	Lake, fish, web, concentration
3	0.033	Phytoplankton, web, community, rate
4	0.029	Delta, isotope, stable, carbon
5	0.029	Predator, prey, web, community
2010–2012: P = 8606, C = 37, M = 0.828, TH = 0.96, Mean cluster size (S.D.): 232 (142)		
1	0.061	Conservation, habitat, landscape, area
2	0.054	Urban, city, network, system
3	0.054	Lake, community, temperature, web
4	0.049	Stream, river, water, flow
5	0.047	Species, interaction, plant, specie
2005–2009: P = 9764,C = 41, M = 0.824, TH = 0.96, Mean cluster size (S.D.): 238 (165)		
1	0.066	Network, development, innovation, paper
2	0.059	Conservation, area, forest, species
3	0.056	Stream, river, water, model
4	0.051	Water, system, model, result
5	0.050	Predator, prey, interaction, plant
2000–2004: P = 4828, C = 31, M = 0.831, TH = 0.96, Mean cluster size (S.D.): 156 (98)		
1	0.078	Reserve, conservation, specie, area
2	0.078	Predator, prey, community, specie
3	0.060	Innovation, regional, network, firm
4	0.056	Air, concentration, road, emission
5	0.053	Water, river, model, rainfall
1995–1999: P = 2665, C = 31, M = 0.838, TH = 0.95, Mean cluster size (S.D.): 86 (68))		
1	0.093	Network, development, firm, paper
2	0.092	Production, phytoplankton, bacterial, rate
3	0.069	Lake, fish, web, concentration
4	0.065	Conservation, area, forest, landscape
5	0.061	Species, predator, interaction, prey
1990–1994: P = 1124,C = 29, M = 0.851, TH = 0.95, Mean cluster size (S.D.): 39 (25)		
1	0.075	Deposition, concentration, precipitation, urban
2	0.070	Web, specie, species, ecosystem
3	0.070	Region, development, information, network
4	0.061	Level, biomass, increase, production
5	0.061	Fish, isotope, specie, winter
1980–1989: P = 418, C = 11, M = 0.642, TH = 0.90, Mean cluster size (S.D.): 38 (15)		
1	0.153	Spider, web, prey, araneae
2	0.141	Distribution, model, national, water
3	0.108	Network, fracture, measure, simulation
4	0.108	Analysis, plan, relationship, network
5	0.100	Web, dynamic, pattern, landscape

P = papers in largest component, C = number of topic clusters, M = modularity score, TH = Topic Heterogeneity $\{= 1 - \text{sum}(p_k{}^2)\}$.
Note: A lower edge threshold is used for the individual waves (0.25) than for the total corpus (0.35) to counterbalance the lower power in judging paper similarity based on co-word frequency.

followed closely by Barabási and Albert's (1999) work examining the distribution of degree centralities in network models of several types of complex systems, and the calculation of the diameter of the World Wide Web (Albert et al., 1999). Papers like these generated widespread interest that led to both new mathematics and science. This has surely contributed to the rise of network science in general.

A second critical factor is technological development. Since network models are data intensive, the rise of Network Ecology is partly due to our increasing ability to collect, store, and access data of all types (Proulx et al., 2005; Michener and Jones, 2012; Stafford, 1993). For example, the methodological innovation of using stable isotopes to estimate diet and trophic position in the food web (Peterson et al., 1985; Peterson and Fry, 1987) has enabled an increase in the development and quantification of food web data. More recent efforts for open access ecological data repositories (Reichman et al., 2011) and emphases on synthesis (Carpenter et al., 2009) further drive this work. Barabási, 2012 argued that network thinking is growing in part because of its ability to synthesize high volume data in ways that aid studying complex systems.

Third, ecology is fundamentally a relational science. Its central questions are about the relationships among species and their physical, chemical, and social environments, and how these ultimately create and constrain the empirically observed patterns of species distribution, abundance, and evolution. Because network concepts and analytical tools are broadly useful to address these relational questions, they have also become important within ecology.

The observed ~1% jump in Network Ecology publications between 1990 and 1991 is an interesting feature of our results that we do not want to overlook; however, we do not have a satisfactory explanation for it. To our knowledge, this time frame does not align with any obviously influential events in ecological science, nor with a jump in social network publications (Borgatti and Foster, 2003). A search of the publication records in the immediately proceeding years failed to identify uniquely influential papers. The cause of this jump remains a mystery.

4.1.2. Fragmentation

Despite the generally well-connected cores of both the topic and co-authorship networks, both networks exhibited a high degree of clustering. This suggests that the Network Ecology domain is deeply fragmented. The clustering in both networks is probably due in part to scientists with common topic interests naturally collaborating, but it is also likely reinforced by proximity, training programs, and funding. Hints of these drivers are in the previously discussed ego network of Bernard Patten. We also wonder if a second factor leading to the current clustering structure is the existence of multiple, mostly independent events in which network ideas and tools were imported into ecology; however, this requires further investigation.

While this fragmentation may have some positive consequences such as allowing the incubation of local ideas or the focus on particular problems, it has the potential to inhibit the spread of generally useful concepts and methodological innovations across the clusters. It can also lead to the development of competing jargon that inhibits communication. For example, Jacoby et al., 2012 used the term edge density for the network statistic that food web ecologists have routinely called connectance (Martinez, 1991; Dunne et al., 2002).

To reduce this fragmentation, several actions are possible. First, one challenge revealed by our work is that of identifying relevant science and scientists because related works in different Network Ecology topic areas or collaboration clusters may not be obvious. Adoption of a common keyword like Network Ecology might increase the discoverability of related work. Second, workshop and symposium organizers might consciously include investigators from different clusters. We expect that organizations like the National Center for Ecological Analysis and Synthesis, the National Institute for Mathematical and Biological Synthesis, the National Socio-Environmental Synthesis Center, and the National Evolutionary Synthesis actively reduce this type of fragmentation in ecology; however, this effort could be enhanced with additional knowledge of the existing cliques. Third, given that the interest in Network Ecology and its utility continues to grow, new training opportunities that explicitly bridge across topic and current co-authorship clusters might be useful. This could include training workshops at conferences.

4.2. Limitations and next steps

There are several limitations of our study that may adversely influence our findings. We next discuss the four primary limitations and conclude with possible next steps in this research.

First, the bibliographic corpus has some limitations due to restricting our search to a subset of the ISI WoS. Our search missed publications, topics, and scientific collaborations that might have emerged if we had expanded our search to conference proceedings or an additional database such as BIOSIS, MEDLINE, Scopus, or Google Scholar. We selected WoS because of its strong and long-term coverage of ecological journals, where ecologists tend to publish their high quality work. That said, our survey of experts suggested that several recent books and book chapters not included in WoS were highly influential in Network Ecology. While the specific results would certainly be different, we do not expect that the broad trends identified would be substantively different if we used a different or combined set of databases.

A second limitation of the WoS database is that not all records in the database are complete. We can illustrate this issue with an example of a paper we would have expected to be in our corpus but that was not. Baird and Ulanowicz, 1989 studied the seasonal dynamics of carbon flux in the Chesapeake Bay by building and analyzing network models to understand the ecosystem, and the article has been an influential Network Ecology paper as evidenced by its 409 cites as of this writing. It was published in Ecological Monographs, a journal that was included within our subject area classifications. However, our Network Ecology search missed this paper because the information provided by the WoS record is missing the author keywords and abstract. This renders the WoS record invisible to our topic term search. Inspection of the paper shows that both our search terms *network* and *web* appear in the abstract and keywords of the paper, so if this information had been included in the WoS database our search would have discovered this paper. As older WoS records tend to be less complete (personal observation), this issue likely introduced a systematic bias to our sampling that suggests that our corpus underrepresents the earlier Network Ecology research.

A third limitation of our bibliographic corpus relates directly to our use of the WoS subject classifications as a means of identifying ecology publications. These research area classifications are applied to the whole journal, rather than being specific to an article. This helps explain why our corpus missed 36 (40%) of the Network Ecology articles between 2007 and 2012 identified by our experts. 21 (58%) of the articles missed were published in journals with a more general scope as indicted by their WoS research area classification of *Science & Technology—Other Topics*. For example, the articles by Allesina and Levine, 2011 and Allesina and Tang, 2012 are both clearly about Network Ecology. However, the first was published in the Proceedings of the National Academy of Sciences and the second was published in the journal Nature, both of which WoS labeled with a research area of *Science & Technology—Other Topics*. Thus, since the term *ecology* was not found in the title, abstract, or keywords, these papers were not identified as ecological articles in our search. This issue might also bias against selected Network Ecology authors who tend to publish their work in journals with different research area classifications. For example, of the 40 articles published by R.E. Ulanowicz through 2012 indexed by WoS with our *network* keywords, only 22 (55%) of these articles were published in a journal labeled as *Environmental Science & Ecology*. 9 or 23% of these publications were published in journals labeled by WoS as *Life Sciences Biomedical Other Topics*. This might also help explain why there were only 87 papers in our corpus that mentioned the Ecopath software despite its expected importance; Ecopath papers are often published in fisheries, marine science, and oceanography journals. This limitation is inherent in any restricted set of journal used for reviews like this (see Carmel et al., 2013 and Ings et al., 2009). More importantly, it suggests that our corpus provides a conservative estimate of the magnitude of Network Ecology.

A fourth challenge to our corpus works in an opposing direction—possibly inflating the volume of our results. In contrast to the Ings et al., 2009 study, we deliberately used a set of broad search terms to identify ecological science and the use of network concepts, techniques and tools within it. Despite the exclusion criteria we subsequently applied, our final corpus still included papers that did not strictly pertain to the area of Network Ecology we sought. For example, as described in section 3.1 the earliest record in our corpus is Griswold and Crowell, 1936, which unfortunately does not report the kind of network science we tried to capture. Further, despite our term exclusions it is clear that some papers were included in our corpus due to their use of *network* as referring to sensor and research networks in particular (e.g., Long Term Ecological Research Network, National Ecological Observatory Network). Although this will have inflated our corpus to an unknown degree, this problem is difficult to avoid and we decided to err on the side of being more inclusive. Further, we focused our topic and co-authorship analysis on the largest network components to reduce the effect of this bias on our results.

We see two specific next steps to extend this research. First, while we have conducted a first analysis of the temporal dynamics of the topics in Network Ecology, we have not considered the temporal dynamics of the co-authorship structure. The current co-authorship network is cumulative, which may obfuscate the changing impact of generations of scientist and/or particular individuals. Further, more established scientists will tend to be more central because they have had more time to publish and develop collaborations. Second, we could extend this analysis by developing a bibliographic coupling graph for the corpus. This network would provide a way to identify the commonality among papers suggested by their joint citations as well as identify influential publications along the lines of a traditional citation analysis.

4.3. Frontiers of Network Ecology

The future of Network Ecology appears bright. This is suggested by the rapid and sustained increase in Network Ecology publications (Fig. 1). While this pace of increase cannot be sustainable, we do not expect the forces driving the rise of network ecology to dissipate soon. In fact, we see at least four frontiers at which Network Ecology might further develop.

One frontier is the application of network concepts, techniques and tools to new areas within the broad field of ecology. For example, Cohen et al., 2012 proposed the development of physiological regulatory networks to investigate organismal ecology and evolution. Similarly, several scientists have begun to use ecosystem network analysis to investigate the sustainability of urban metabolisms (Chen and Chen, 2012; Li et al., 2012; Zhang et al., 2010), industrial networks (Layton et al., 2012), and trade networks (Kharrazi et al., 2013).

A second frontier is the application of existing Network Ecology to address applied questions. Memmott, 2009 illustrates many possible directions in this regard. For example, Network Ecology can be used to assess the effectiveness of management and restoration or the potential impact of climate change. Accordingly, Hines et al., 2013 and Hines and Borrett, 2014 used a comparative network approach to predict the potential impact of sea level rise on the sedimentary nitrogen cycle of the Cape Fear River estuary. Likewise, Small et al., 2014 applied ecological network analysis to investigate the linked N cycling among the Laurentian Great Lakes.

A third frontier emerges from attempts to apply Network Ecology more broadly. To do this effectively, Network Ecology will need to continue to develop methods for model construction (Fath et al.,

2007) and overcome sampling and data limitations (Polis, 1991). Linear inverse modeling is one tool to assist with this (van Oevelen et al., 2010; Vézina and Pace, 1994). Network Ecology will also need to improve its ability to quantify statistical uncertainty in network models and related implications for analysis and conclusions (Borrett and Osidele, 2007; Kaufman and Borrett, 2010; Kones et al., 2009).

A fourth frontier is the combination of multiple network perspectives and models. Fontaine et al., 2011 note that each network model provides a particular and necessarily limited perspective on the ecological systems being studied. Combining multiple perspectives has already led to new ecological insights. For example, Knight et al., 2005 combined both a food web network and a pollination network to show how a predatory fish can facilitate the fitness of nearby terrestrial plants. Likewise, Malcom, 2011 applied an individual based genotype model to a network population model to show that the size and connectance pattern of genetic networks can change the trait heritability in the population and the population recovery from disturbance. In doing so, Malcom also illustrates the opportunity for crossing scales of analysis with network approaches.

These frontiers are only illustrative of the many possible directions that Network Ecology can grow into. Its future will be further enabled by developments in network science more generally. For example, statisticians are beginning to tackle the quantitative challenges of making inferences with networks (e.g., Kolaczyk, 2009) and the challenge to visualize the structural complexity that network approaches can capture (e.g., Moody et al., 2005; Lima, 2011).

4.4. Summary

Network Ecology is comprised of scientists using network models to investigate ecological systems at many different hierarchical levels of organization. Network Ecology is defined by the use of a general model type—a network. Our analysis suggests that this is a large and rapidly growing subfield of ecology. This is reflected in the number of publications, the array of topics, and large number of authors identified in our Network Ecology corpus. These scientists broadly use network concepts, techniques, and tools to (1) characterize the system organization (Croft et al., 2004; Borrett et al., 2007; Borrett, 2013; Ulanowicz, 1983), (2) investigate the consequences of the network organization (Allesina and Pascual, 2009; Borrett et al., 2006, 2010; Dunne et al., 2002), and (3) identify the processes or mechanisms that might generate the observed patterns (Allesina et al., 2008; Guimarães et al., 2007; Ulanowicz, 1986; Williams and Martinez, 2000). Both its topic and co-authorship structure indicates that the field of Network Ecology is divided into clusters, which may inhibit the spread of innovative ideas and tools between the groups. We recommend several actions that might reduce this fragmentation and increase the discoverability of related work, including the use network ecology as a keyword. Network Ecology is a research area with a long history and bright future in part because as Lima, 2011 said “networks are everywhere”.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2014.02.019.

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