



Mapping the dynamics of research networks in ecology and evolution using co-citation analysis (1975–2014)

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Abstract

In this paper we used a co-citation network analysis to quantify and illustrate the dynamic patterns of research in ecology and evolution over 40 years (1975–2014). We addressed questions about the historical patterns of development of these two fields. Have ecology and evolution always formed a coherent body of literature? What dominant ideas have motivated research activity in these two fields? How long have these ideas attracted the attention of researchers? Contrary to what was expected, we did not observe any trend towards a stronger integration of ecology and evolution into one big cluster that would suggest the existence of a single community. Three main bodies of literature have stayed relatively stable over time: population/community ecology, evolutionary ecology, and population/quantitative genetics. Other fields have disappeared, emerged or mutated over time. Besides, research organization has shifted from a taxon-oriented structure to a concept-oriented one over the years, with researchers working on the same topics but on different taxa showing more interactions.

Keywords Ecology · Evolution · Behavioral ecology · Community ecology · Evolutionary ecology · Ecosystem ecology · Plant ecology · Population genetics · History of ecology and evolution · Cocitation networks · Community detection

Introduction

Like all scientific fields, evolution and ecology has changed over time. Interest in topics has waxed and waned, and the number of scientists, publications, and the breadth of research topics has grown. Analyzing temporal changes in subjects within a research field can help

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us understand the historical development of that field and its newest directions. It may also help new researchers in the field to situate their topic within this changing landscape. Ecology and evolution are often seen as a coherent framework with one main theoretical and conceptual basis. Despite Dobzhansky's (1973) well known opinion according to which "nothing in biology makes sense except in the light of evolution", some authors have noted a lack of interest for evolutionary ideas in ecological research (Bradshaw 1984).

Attempts to synthesize the literature in ecology and evolution or its subfields have been common. For instance, Courchamp & Bradshaw (2018) have recently proposed a list of the 100 must read in ecology and evolution. Others have proposed personal opinions on the developments of the field (e.g., Gross 1994; Loreau et al. 2001; Cuddington and Beisner 2005; Owens 2006; Montgomerie 2010; Gordon 2011), tried to encourage new directions of research (Odum 1992; Sutherland et al. 2012), or promoted stronger links between isolated subfields (Bradshaw 1984). These publications have been highly valuable in reviewing and maintaining the dynamism and structure of scientific research in ecology and evolution. These attempts, however, represent subjective, researcher-centric perspectives.

Other studies have tried to analyze ecology with bibliometric tools, less often ecology and evolution. For instance, Medina (2018) studied patterns of co-authorship among ecology researchers using a network approach and found that the effect of authors' reputation and geographic distance on these patterns has declined over time. Authorship in ecology was also studied by Logan et al. (2017), who analyzed the varying contribution of researchers to ecology publications according to their ranking as co-authors. Leimu and Koricheva (2005) studied the impact of ecological research published in the journal *Oecologia* and found that papers written in international collaboration did not have higher citation rates, contrary to what is generally the case (Katz and Hicks 1997). Some subfields of ecology have also been studied from a bibliometric perspective. Song and Zhao analyzed the evolution of forest ecology over a 10-year period (2002–2011) and concluded that the field had, during that period, mainly focused on the topics of forest diversity, conservation, dynamics and vegetation. Similarly, Carneiro et al. (2008) analyzed, using keywords, the changing trends in the subfield of limnology from 1991 to 2005. They concluded that research in this field had shifted from descriptive studies to more diversified topics including genetics, evolution, and the use of technologies such as remote sensing or chemtax. Finally, in ecology and evolution, Carvalho et al. (2005) performed a citation analysis to evaluate the impact of Felsenstein's independent phylogenetic contrast method on the field between 1985 and 2002, and classified his paper as a "citation classic".

Most of the above-cited studies focused on the use of evaluation-based metrics, such as co-authorship trends or citation impact, to characterize ecology. In this paper, our aim is different, since we are rather interested in mapping the global structure and dynamics of research in ecology and evolution. We thus construct networks of co-citations (Small 1973; Gingras 2009, 2010) of research for intervals of 5 years and use community-detection algorithms to identify sub-communities in ecology and evolution and analyze their temporal dynamics over a period of 40 years. Co-citation networks presented in this paper have the advantage over other methods, such as article title co-word analysis (Neff and Corley 2009) or automated text analysis (McCallen et al. 2019) used to identify changing trends in ecology over time, of providing a clearer graphical representation of the research dynamics and interactions between ecology and evolution. Our first question is whether research in these two fields forms a single coherent body of literature or is composed of two or more relatively independent subgroups that rarely cite each other. Ecologists and evolutionary biologists often have intuitive opinions about the structure and development of their scientific community. We provide the first quantitative analysis of these trends, and we ask

whether the subgroups identified by the algorithm resemble the subfields known within the field (e.g., population genetics, behavioral ecology), and whether clear boundaries circumscribe these areas. With the recent technological developments (e.g., statistics, molecular tools, endocrinological assays, stable isotope analyses, bio-logging), and the advancement in editing tools allowing a broader access to the literature (internet, online access to both papers and books), boundaries between different fields may have become more porous than they were previously. We would thus expect to observe a trend towards a higher integration into one big network of co-citations. Our analyses allow us to ascertain if this is really the case. Finally, we determine which works/ideas or countries have been the central actors within the subfields and whether their interactions have changed over time. In other words, we look for ecology/evolution “standards”, whose influences have persisted over the last 40 years. Below we describe and interpret the co-citation networks from 1975 to 2014.

Methods

Our analyses rely on the co-citation frequency of authors, or the number of times two authors are cited together in a list of citing documents (Small 1973). We have used the Web of Science (WoS) bibliographic database, which includes information on authors and their affiliations and all cited references contained in each paper. In these citing documents, a co-cited publication could either be a scientific article, a book, a technical report or any other cited document. The interest of co-citation network analysis—as opposed to simple citation analysis—is that it shows how authors or publications, representing the ideas or concepts they contain, are linked to each other. It therefore allows us to create a visual representation of the structure of a scientific field like ecology, and how it is linked (or not) with other fields like evolution. The method of co-citation analysis also provides a valuable tool to visualize the changing focus of research in a field over time (Gingras 2009, 2010).

The scientific community under scrutiny is all the publications cited in journals in Table S1 between 1975 and 2014. This list of selected journals has been established by first analyzing the journal co-citation network, using a first list of the most prominent journals in ecology and evolution. All the journals that were well represented in the network, but that were not in the first list, were then added to the new list for the final analyses. Citations to books or to papers from journals outside the source list were also included in the analysis, so that the list of cited (and co-cited) journals is much larger than in Table S1. This list is not exhaustive, but it includes most of the journals recognized as central to ecology and evolution. The networks thus represent the field as seen by scientists who publish in the most visible journals, and adding some unselected journals to the analysis does not change the structure of the network, but may only add a few peripheral clusters to it.

To generate co-citation networks we used the open-source network graph analysis and visualization software Gephi (Cherven 2013), which represents a network as nodes connected by edges. Each node represents a set of publications with a first author’s name (name in capital followed by initials in the text and the figures). Edges (or links) represent the number of co-citations between all the publications belonging to two nodes, their thickness being proportional to that number. Node size and edge number/size illustrate the intensity of research activity in one field. A bigger node shows that a (set of) publication(s) on a topic, associated with a first author, has had a large structuring role on the activity of the research domain. Authors may be present in several nodes: one for their publications as first author, and others representing papers where they collaborated as co-author.

Importantly, an author who has published publications only as a co-author will be unnoticed in the network. Of course, co-citations and citations are positively correlated, as publication cannot be co-cited without being cited, but it is, for example, possible to be highly cited but that most citations are outside the studied network. The standardized number of citations an author has received is a better index of the impact of an author in his/her field than the size of the node or the number of links with other nodes. However, “evaluating” the impact of each ecologist and evolutionary biologist is out of the scope of this paper, which focuses on the changing relationships between subfields of research.

Gephi uses the Louvain community detection algorithm (Blondel et al. 2008) to identify relatively coherent subgroups (i.e., clusters) within a main network. The resulting partitioned networks are based on the maximization of their modularity function. To determine if a group of nodes should be identified as a distinct cluster or community, the modularity function maximizes the difference between the actual number of edges within this group and its expected number of edges in the whole network (Traag et al. 2018). Cluster with similar color nodes and edges forms a specialty, that is a scientific community centered on a research topic. We make the hypothesis, largely substantiated in other similar analyses of scientific fields (Gingras 2009, 2010), that the clusters represent the conceptual and specialty structure of the field. A high level of co-citation suggests a strong conceptual relation between the co-cited publications.

We separated the study period into eight sub-periods of 5 years each. Over that 40-year period, we observe a fourfold rise in the number of papers published in the field and an eight-fold increase in the number of cited references (Table S2). Since we base our global analysis on thousands of papers, most of which are signed with initials, we could not measure the role of gender within the networks (Larivière et al. 2011, 2013; Bradshaw and Courchamp). To make each network legible, only the edges above a certain co-citation threshold are shown, and the threshold changes with the period. The edges and nodes that are missed when the thresholds are increased have no effect the global structure of the resulting networks, because their degree distribution, i.e. the distribution of the number of edges among nodes, follows a power law. The missing edges and nodes thus belong to the long tail portion of the power-law distribution.

For clarity reasons, we focused on large, connected clusters and ignored small, unconnected groups unless they later became significant. The reader, however, can pay more attention to these small groups, as they provide some information on research topics that are less connected to the ecology and evolution framework. We concentrated on the most illustrative publications of a cluster. We thus restricted the description of a cluster to its most important nodes, from the list of top cited publications for each period (Table S4). To make each network more easily legible, we increased co-citation threshold from 15 in the 1975–1979 network to 70 in the 2010–2014 network. Consequently, we should not interpret the structure of activity of a subfield in absolute terms, but in comparison with other subfields for the same period. Also, some fields may exist but may not be shown in a network as their general activity (nodes and edges) is below the threshold.

To provide a measure of the importance of a research community in a period, we calculated the proportion of nodes and internal links that belong to each cluster within the global network (Tables S3 and S4). To measure the intensity of interactions between the different research communities we calculated the proportion of external links between the main clusters of each network (Table S5). For generality and clarity, we restricted our description to the main nodes of each cluster to illustrate the ideas they represent. By examining the details of each network, the reader will find more precise information on the structure of each cluster and the ideas exchanged within it. This approach also reveals that

some authors' names move from one group to another depending on the changes in their research activity through time or the impact their ideas had on different groups of researchers. Thus, the name of an author influencing one cluster at one moment might become a node with a high centrality in another cluster later in time. Finally, since we want to follow the evolution of research and not focus on textbooks and similar standard references, we have excluded from the networks some central books that are always referred to (see e.g., SOKAL-RR, Fig. S1; RDEVCORTEAM, Fig. S2; BURNHAM-KP, Fig. S3).

Results

1975–1979: the dominance of population and community ecology (Fig. 1)

Five main clusters were visible in the study period. The core cluster, in purple, was dominated by works on species distribution and coexistence, and on the theory of island biogeography [MACARTHUR-RH (MacArthur and Wilson 1963, 1967; MacArthur 1972)]. This cluster also included publications on species competition [SCHOENER-TW (Schoener 1974)], on the diversity and organization of communities [CODY-ML, PIANKA-ER, HUTCHINSON-GE (Hutchinson 1959; Pianka 1973; Cody 1974)], and on population dynamics [MAY-RM (May 1974, 1976)]. One extension (WHITTAKER-RH) was mostly focused on research on plant communities, successions, and gradient analyses (Whittaker 1972). This population/community ecology group was the most important cluster, and represented 36% of the nodes and links of the network.

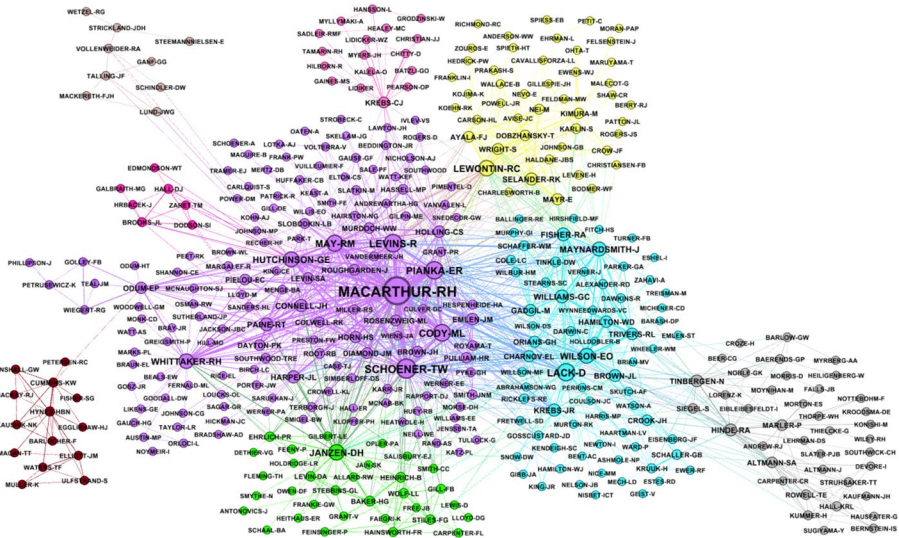


Fig. 1 Network of co-citations in ecology and evolution journals during the 1975–1979 period. The threshold of co-citations used for this figure is 15, which means that a link is shown between two nodes when the two (sets of) papers starting with a senior author were co-cited at least 15 times during that period. The size of a node is proportional to the number of edges with other nodes, and the thickness of a link between two nodes is also proportional to their number of co-citations

The population/community ecology group was centrally connected to three other major groups. It was connected to population genetics, in bright yellow [LEWONTIN-RC (Lewontin 1974)], through the extensions of population ecology models to analyze genetic evolution within populations [LEVINS-R (Levins 1968)]. Population/community ecology was also linked to the turquoise cluster representing evolutionary ecology via shared concepts on life history theories [LACK-D, WILLIAMS-GC, CODY-ML, PIANKA-ER (Lack 1954, 1968; Williams 1966)], and through work on feeding strategies and optimal foraging [SCHOENER-TW (Schoener 1969, 1971)]. The turquoise cluster showed the first signs of a structured research field in sociobiology and behavioral ecology [WILSON-EO, SMITH-JM (Maynard-Smith and Price 1973; Maynard-Smith 1974; Wilson 1975)]. Finally, population/community ecology was connected to a third cluster of work on plant ecology and plant/herbivore interactions [green; JANZEN-DH (Janzen 1970, 1971)] through work on plant population ecology [WHITTAKER-RH, HARPER-JL (Harper et al. 1970; Harper and White 1974; Harper 1977)] and on feeding behavior (SCHOENER-TW).

The gray cluster of work in ethology (bottom right) was peripheral, and structured around TINBERGEN-N and HINDE-RA, who also formed the strongest links with evolutionary ecology (turquoise). Studies by Tinbergen on the causes of behavior (Tinbergen 1963) and by Hinde on learning and on social interactions (Hinde 1976) probably resonated within the evolutionary ecology and behavioral ecology/sociobiology literature. The absence or underrepresentation of work by Konrad Lorenz or Karl von Frisch was surprising, as they received the 1973 Nobel prize in medicine with Tinbergen for their pioneering work in ethology.

Finally, we can also observe a little satellite cluster (top right of the purple cluster) representing research on population dynamics and rodent demographic cycles [KREBS-CJ (Krebs 1972)], and a small cluster slightly linked to population/community ecology (through ODUM-EP) and that represented work on stream ecosystems and trophic relationships in aquatic insects [CUMMINS-KW (Cummins 1974)]. The disconnection between this small cluster and the population/community ecology one, despite similar research topics, illustrates how research communities could be structured around an ecosystem during this period.

1980–1984: the apparent decline of ethology (Fig. 2)

Activity in the main purple cluster still focused on community ecology and diversity, island biogeography (MACARTHUR-RH, SCHOENER-TW), diversity and community organization [CONNELL-JH (Connell 1961, 1978; Connell and Slatyer 1977)], HUTCHINSON-GE, PIANKA-ER, CODY-ML) and population dynamics (MAY-RM). Some work within this cluster concentrated on bird population ecology (i.e., habitat selection, CODY-ML), life history, and population dynamics [LACK-D, RICKLEFS RE (Ricklefs 1969)]. A second cluster, in blue, diverged from the purple one and focused on the evolution of life history in animals [PIANKA-ER, STEARNS-SC (Pianka 1970; Stearns 1976, 1977)] and plants [CHARLESWORTH-B (Charlesworth and Charlesworth 1978)].

Through SCHOENER-TW and MACARTHUR-RH (MacArthur and Pianka 1966), population/community ecology maintained strong links with the red cluster on optimal foraging [KREBS-JR, CHARNOV-EL, PYKE-GH (Krebs et al. 1977; Krebs 1978; Charnov 1976; Pyke et al. 1977)], and with the remnants of ethology (MARLER-P, HINDE-RA, TINBERGEN-N and LORENZ-K). Population/community ecology formed

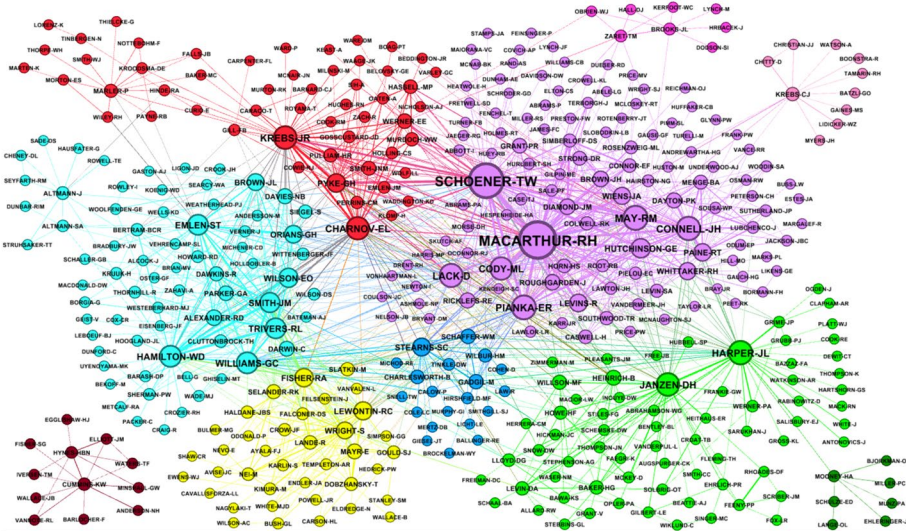


Fig. 2 Network of co-citations in ecology and evolution journals during the 1980–1984 period. The threshold of co-citations used for this figure is 25

a strong group, yet connected with thick edges with several groups doing evolutionary ecology (i.e., red, turquoise and bright yellow).

The turquoise cluster became more dynamic and gathered work on kin selection [HAMILTON-WD, WILSON-EO, TRIVERS-RL (Hamilton 1964, 1971; Trivers 1974; Trivers and Willard 1973)], game theory and the evolution of animal conflict [SMITH-JM (Maynard-Smith and Parker 1976)], and sexual selection and mating systems [TRIVERS-RL, EMLEN-ST (Trivers 1972; Emlen and Oring 1977)]. This field maintained strong edges with life history theories [STEARNS-SC, WILLIAMS-GC (Williams 1975, 1979)] and population genetics (FISHER-RA). Within this cluster, a small group on the left-hand side represented studies in primatology around ALTMAN-J (Altmann 1974).

The theoretical work applying an optimality approach to the evolution of life history, foraging, and sex-ratio allocation [CHARNOV-EL (Charnov and Krebs 1974; Fisher 1930)] played a central role in linking research on population/community ecology (purple cluster), optimal foraging (red cluster), and kin selection, game theory, and mating systems (turquoise). Publications by Darwin were part of this group, but curiously they did not seem to be highly co-cited. Interestingly, we found concepts usually associated to behavioral ecology in the two separated red and turquoise clusters. In contrast ethology was no longer an important and structured field.

Population genetics (in bright yellow) was well connected with the turquoise and purple groups. This group revolved around three sets of publications by FISHER-RA (Fisher 1930), WRIGHT-S (Wright 1931, 1949), and LEWONTIN-RC, and, to a lower extent, publications on evolution and speciation [MAYR-E (Mayr 1970)]. Remarkably both Fisher and Wright have had long-term influence on this field. Publications by Fisher and Lewontin, specifically, connected this field with life history studies (via STEARNS-SC), community ecology (via PIANKA-ER), and kin selection and animal conflicts (via HAMILTON-WD, WILLIAMS-GC, TRIVERS-RL, or SMITH-JM).

Finally, a bicephalous group, in green, regrouped research on plant ecology (HARPER-JL), plant–herbivore interactions (JANZEN-DH), plant–pollinator interactions [HEINRICH-B (Heinrich and Raven 1972)], and plant ecophysiology [MOONEY-HA (Mooney 1972)]. This cluster was mostly linked to the purple cluster through MACARTHUR-RH and CONNELL-JH, but much less to the other clusters. This emphasizes the growing isolation between work on animals and work on plants.

1985–1989: the dawn of evolutionary ecology (Fig. 3)

We can see six main clusters and four satellite sub-clusters: population/community ecology (purple), life history theories and population/quantitative genetics (bright yellow), kin and sexual selection, reproductive effort and mating systems in wild animals (turquoise), optimal foraging and predator–prey relationships (red), bird population and evolutionary ecology (orange), plant ecology and plant/herbivore interactions (light green). The threshold of co-citations used for this figure is 30.

Population/community ecology (purple) was still structured around the trio MACARTHUR-RH, SCHNOENER-TW, and CONNELL-JH. Its relative intensity of activity declined, though, as shown by the decreased density of edges in comparison with the previous period. A group of publications on bird population ecology, reproductive effort, and mating systems (LACK-D) that had started splitting off from population/community ecology (purple) in 1980–1984 formed a new orange cluster and increased its links with the turquoise evolutionary ecology cluster. The red cluster on optimal foraging maintained thick edges with population/community ecology, and to a lower extent with the turquoise and bright yellow clusters.

In parallel, work on life history theories (i.e., STEARN-SC) migrated towards population genetics and evolution (bright yellow), dominated by Maynard-Smith's publications

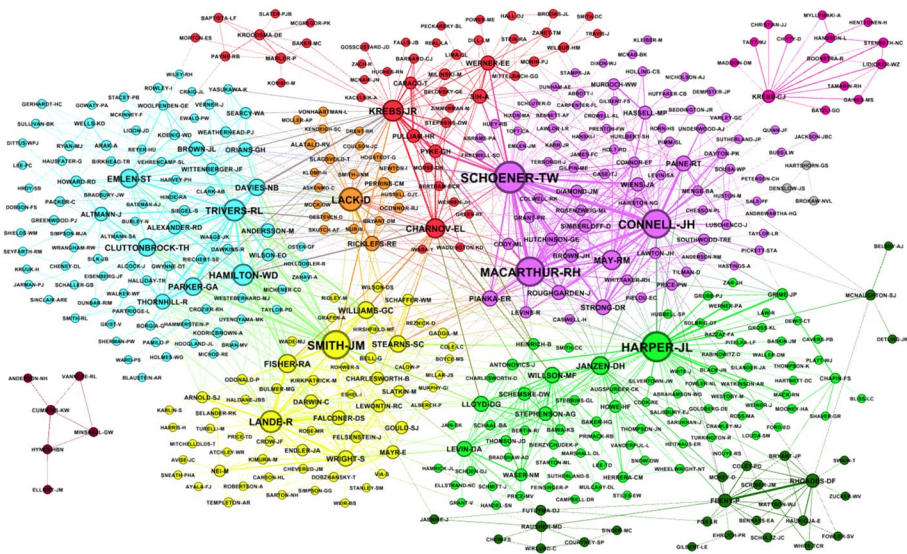


Fig. 3 Network of co-citations in ecology and evolution journals during the 1985–1989 period. The threshold of co-citations used for this figure is 30

on game theory (SMITH-JM). In the bright yellow cluster publications by Maynard-Smith, Williams, and Darwin were highly co-cited with publications from the turquoise cluster (i.e., kin selection, animal conflict and sexual selection). Quantitative genetics and the estimation of natural selection in the wild [LANDE-R (Lande 1979; Lande and Arnold 1983)] emerged as a novel and strong framework in this field. A new cluster appeared [NEI-M (Nei 1972, 1978)], which would become fully formed over the next 5 years.

Things also changed in the turquoise group with studies on reproductive costs, mating systems, and fitness appearing [CLUTTONBROCK-TH (Clutton-Brock et al. 1982; Clutton-Brock 1988)]. We observed the impressive resurgence of Darwin’s ideas (1871) on sexual selection [PARKER-GA, THORNHILL-R (Parker 1970, 1979; Thornhill 1983; Thornhill and Alcock 1983)]. Long-term studies on primates (ALTMANN-J) were part of this group. Although these studies were interested in life history traits, they maintained some independence with life history research (STEARNS-SC, WILLIAMS-GC). Similarly, studies on primates (ALTMANN-J) and ungulates (CLUTTON-BROCK-TH) were using the same general framework as the group working on wild bird populations (LACK-D), but the former two groups were disconnected from the latter.

Harper’s publications, and to a lower extent Janzen’s publication, were still dominating the research activity of plant ecology (light green). Work on evolutionary ecology in plants [LEVIN-DA, LLOYD-DG (Lloyd 1979; Levin 1984)] began connecting the plant ecology group to the population genetic and evolution group (bright yellow). A small satellite group (dark green) working on plant chemical defense emerged from the plant ecology cluster.

1990–1994: The explosion of sex (Fig. 4)

That period shows two weakly connected meta-clusters. On the right-hand side population/community ecology was still linked to plant ecology and plant/herbivore interactions (light green), and had absorbed part of it (e.g., HARPER-JL, JANZEN-DH). On the left-hand

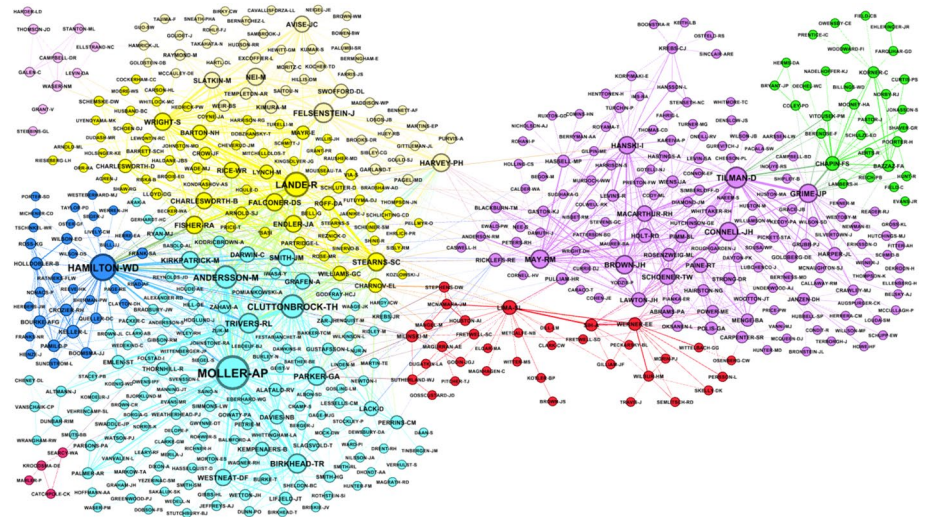


Fig. 4 Network of co-citations in ecology and evolution journals during the 1990–1994 period. Threshold of co-citations used for this figure is 35

side, a broad evolutionary ecology group included four clusters: sexual selection, reproductive effort and mating system (turquoise), life-history theories, population/quantitative genetics (bright yellow), evolution of cooperation and sociality (dark blue), and molecular ecology and phylogeny (light yellow). Work on molecular ecology and phylogeny that had burgeoned during the previous period formed a distinct cluster. The evolutionary ecology meta-cluster showed an activity never seen before: together these four clusters accounted for 50% of the number of nodes in the network and 46% of internal links.

At that period, optimal foraging had almost disappeared as a structured field, and the red group corresponded of publications around predator–prey relationships. KREBS-JR and STEPHENS-DW (Stephens and Krebs 1986) can be seen at the boundary between the turquoise and the red group. In the same way, bird population ecology (LACK-D) became part of the turquoise cluster. Most noticeable is the gigantic development of research on sexual selection. MOLLER-AP (Møller and Pomiankowski 1993; Møller 1994), which had been a minor node in the orange cluster in 1985–1989, was by far the biggest node of the whole 1990–1994 network. This illustrates the craze for sexual selection, sperm competition, and fluctuating asymmetry [BIRKHEAD-TR, ANDERSSON-M, WESTNEAT-DF, PARKER-GA (Andersson 1982, 1986, 1994; Westneat et al. 1990; Birkhead and Møller 1992)] that occurred at the time. Reproductive effort and parental investment were still well-studied topics [TRIVERS-R, CLUTTONBROCK-TH (Clutton-Brock 1991)]. A new cluster (dark blue) on the evolution of cooperation, principally using social insects as models, and centered on the idea of kin selection from HAMILTON-WD, emerged from the evolutionary ecology cluster. Thus, studies on kin selection, a central concept of sociobiology highly criticized outside biology during the '80 s, was forming a very active field of research at this period.

The previous population/quantitative genetics cluster divided into two new clusters. The first one represents quantitative/evolutionary genetics (in bright yellow). It includes quantitative genetics around one main node (LANDE-R), having strong links with life-history specialists (STEARNS-SC) on the right side of the cluster, and plant evolutionary genetics, gravitating around WRIGHT-S and CHARLESWORTH-B on the left. LLOYD-DG and LEVIN-DA left the plant ecology group to join this cluster. Thus, the quantitative/evolutionary genetics cluster (bright yellow) formed a non-taxon centered group. Note that this cluster maintained strong links with the turquoise cluster on sexual selection, reproductive effort and mating systems (FISHER-RA, WILLIAMS-GC, CHARNOV-EL, or SMITH-JM). Indeed, these two clusters shared the highest number of links, as was the case in the previous period (Fig. 6). DARWIN-C (Darwin 1859) represented a small but central node to this large meta-cluster.

The second cluster (in light yellow) originating from the population/quantitative genetics group in 1985–1989 represented the emerging field of molecular ecology [NEI-M, SLATKIN-M, AVISE-JC (Avisé et al. 1987; Avisé 1992; Slatkin 1987, 1993;)], phylogeny [FELSENSTEIN-J (Felsenstein 1981, 1985)], and comparative analyses [HARVEY-PH (Harvey and Pagel 1991)]. Newly developed DNA analyses (e.g., mitochondrial DNA, microsatellites), to study population structure or phylogeny, probably played a role in this new structure.

On the right-hand side, population/community ecology showed a decrease in the influence of the triangle MACARTHUR-RH, SCHOENER-TW and CONNELL-JH. New research topics on competition in plants [TILMAN-D, GRIME-JP (Tilman 1982, 1988; Grime 1979)], species abundance, distribution, and biogeography [BROWN-JH (Brown and Kodric-Brown 1977; Brown 1984)], and metapopulation dynamics [HANSKI-I (Hanski and Gilpin 1991; Hanski 1994)] also appeared. As these topics became more dominant,

Harper’s work on plant ecology (HARPER-JL), and Janzen’s work on plant–herbivore interactions (JANZEN-DH) lost their central role. Studies on plant competition (TILMAN-D, GRIME-JP) were linked to a satellite cluster of work on nutrition in plants [CHAPIN-FS (Chapin 1980)], which included the dark green cluster on plant chemical defense from 1985 to 1989.

Population/community ecology also maintained connections with the small red cluster on predator–prey interactions and predation risk, formed itself by two subgroups, one on guppy antipredator behavior around LIMA-SL (Lima and Dill 1990), and the other on predation risk and its non-consumptive effects on prey, around WERNER-EE (Werner et al. 1983), and linked by SIH-A (Sih et al. 1985). Thus SIH-A may have been acting as a key-stone individual. During this period, the general population/community ecology cluster incorporated the cluster working on rodent cycles through its links with HANSKI-I (Hanski et al. 1991).

1995–1999: stasis in the network (Fig. 5)

Structure during that period was relatively stable. The large evolutionary ecology group was again the most active, with 58% of the nodes and 50% of the internal links. The cluster on sexual selection in turquoise showed a radial shape that illustrates the considerable impact of publications on that subject (MOLLER-AP). A similar phenomenon was visible for studies on the evolution of cooperation (HAMILTON-WD). Molecular ecology and phylogenetics (light yellow), structured around a larger set of co-cited publications, increased in activity. In this evolutionary ecology meta-cluster, sub-clusters displayed intense interactions, mostly through LANDE-RS, ANDERSSON-M, MOLLER-AP, TRIVERS-RL, CLUTTONBROCK-TH, and HAMILTON-WD.

Three clusters formed the population/community ecology meta-cluster. A first cluster (purple) was working on population/metapopulation dynamics and island biogeography

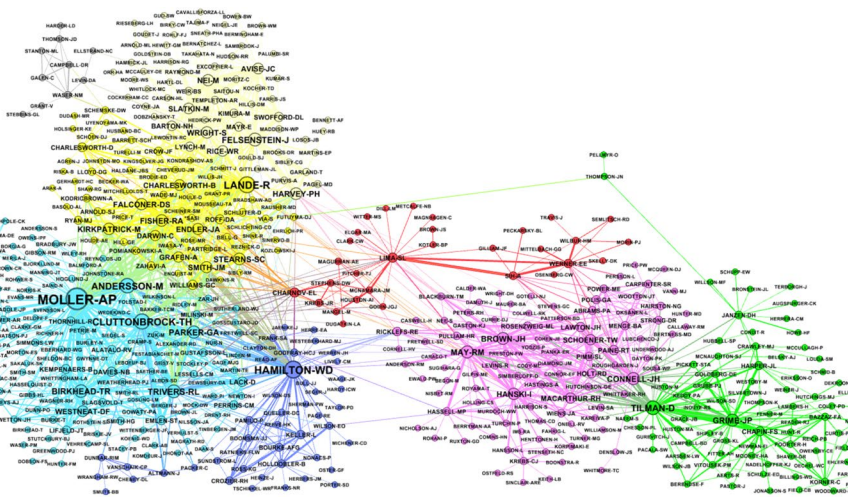


Fig. 5 Network of co-citations in ecology and evolution journals during the 1995–1999 period. Threshold of co-citations used for this figure is 45

(MAY-RM, HANSKI-I, MACARTHUR-RH; BROWN-JH). A second one (green), centered on competition in plants [TILMAN-D (Tilman 1994)], was beginning to have more influence on the structure of the meta-cluster on population/community ecology. A third one (red) developed two subgroups, one on predator–prey interactions (LIMA-SL), and one on predator effects on prey features (WERNER-EE), linked to research on food webs ([PAINE-RT (Paine 1966, 1980)], and which started to drift from population/community ecology.

2000–2004: the rise of molecular ecology (Fig. 6)

Two meta-clusters dominated the period: population/community ecology (purple) and evolutionary ecology (turquoise, bright yellow, light yellow). With 34% of the nodes and 30% of the internal links in the network, the evolutionary ecology meta-cluster continued to increase its activity. This high vigor was particularly obvious for the molecular ecology and phylogeny group (light yellow), with no less than 11 important nodes and some very intense interactions (19% of the internal links). The cluster on the evolution of cooperation was absorbed by the turquoise cluster, which was still dominated by ideas on sexual selection.

Within the community ecology cluster (purple), the centrality of TILMAN-D was still increasing, associated with new ideas on biodiversity and ecosystem function and stability. Research on metapopulation dynamics (HANSKI-I) diverged from that main cluster, but maintained some links with a group working on biogeography & diversity patterns (BROWN-JH, MACARTHUR-RH, RICKLEFS-RE). The cluster on predation risk and non-consumptive effects (in red) increased its activity, and kept being structured around SIH-A, WERNER-EE, and LIMA-SL.

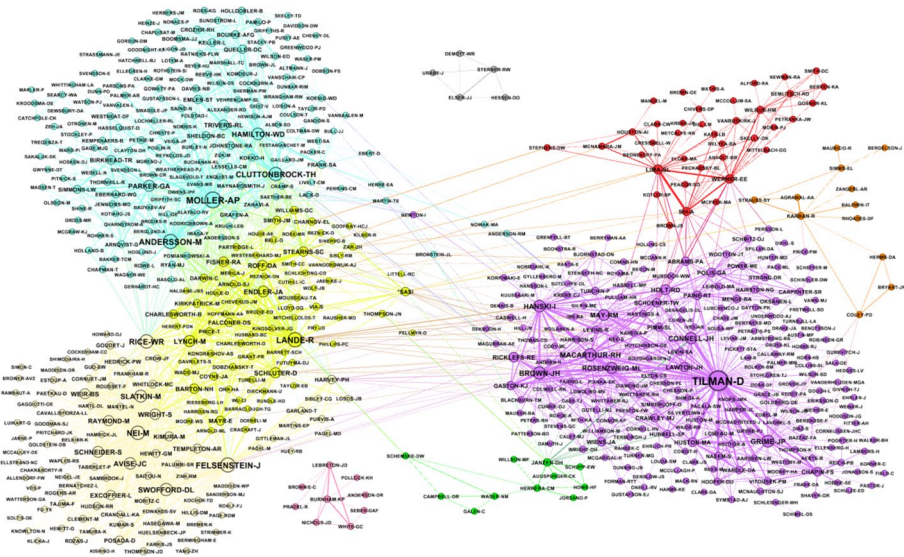


Fig. 6 Network of co-citations in ecology and evolution journals during the 2000–2004 period. Threshold of co-citations used for this figure is 50

2005–2009: molecular ecology: the age of maturity (Fig. 7)

Within the evolutionary ecology meta-cluster, the most striking observation was the growing research activity of molecular ecology and phylogeny, mixed between the light and bright yellow clusters, and probably caused by fast methodological developments [FELSEINSTEIN-J, RAYMOND-M, GOUDET-J, WEIR-BS, PRITCHARD-JK, EXCOFFIER-L, POSADA-D, SWOFFORD-DL (Weir and Cockerham 1984; Excoffier et al. 1992, 2005; Goudet 1995; Raymond and Rousset 1995; Swofford et al. 1996; Posada and Crandall 1998; Pritchard et al. 2000)].

Quantitative genetics, phenotypic selection (LANDE-R), and ecological speciation=[SCHLUTER-D (Schluter 2000, 2001)] dominated the bright yellow cluster. In the turquoise cluster, studies on sexual selection (ANDERSSON-M, PARKER-GA, MOLLER-AP) cohabited with a resurgence of interest for kin selection and the evolution of cooperative breeding [HAMILTON-WD, CLUTTON-BROCK-TH (Clutton-Brock 2002)]. The three groups that constituted the meta-cluster of evolutionary ecology (bright yellow, light yellow and turquoise) accounted for 61% of the nodes and 62% of internal links of the network, an extent never achieved in the previous periods.

Population/community ecology (purple) had both a cloud of intense interactions (28% of nodes and 22% of internal links of the network) related to ideas on island biogeography (MACARTHUR-RH), the metabolic theory of ecology [BROWN-J (Brown et al. 2004)], species diversity [ROSENZWEIG-ML (Rosenzweig 1995)], the neutral theory of species distribution [HUBBELL-SP (Hubbell 2005)], macroecology [GASTON-KJ, RICKLEFS-RE (Ricklefs 1987, 2004; Gaston 2000)], and metapopulations (HANSKI-I). We can see the rise of statistical methods to analyze biogeography/spatial distributions of populations and communities [LEGENDRE-P (Legendre and Legendre 1998)]. Furthermore, TILMAN-D’s ideas were still radiating through the field, reflecting the great interest in biodiversity and ecosystem function.

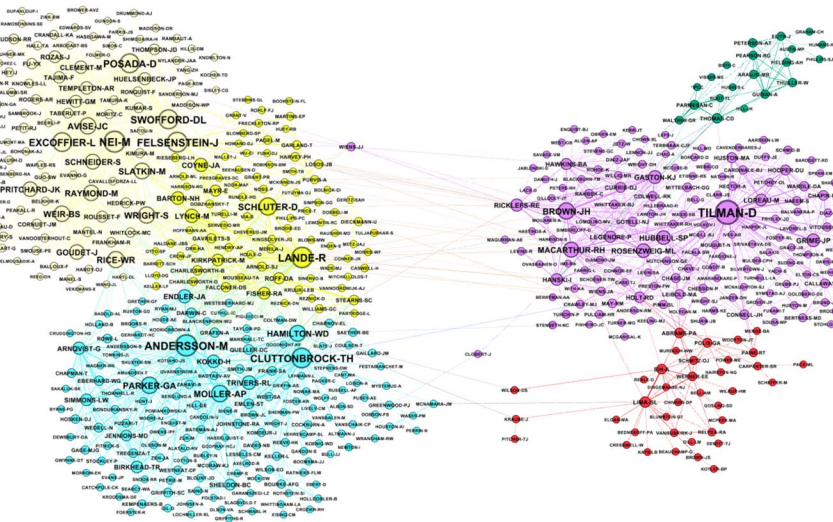


Fig. 7 Network of co-citations in ecology and evolution journals during the 2005–2009 period. Threshold of co-citations used for this figure is 65

The group on predator–prey interactions (in red) remained stable, but it lost links with evolutionary ecology. Instead, it showed stronger relationships with population/community ecology, specifically with food web ecology, competition and predation [CONNELL-JH, HOLT-RD (Holt 1977)]. We also witnessed a new cluster (dark green) emerging on climate change and macroecology studies [IPCC, THOMAS-CD, PARMESAN-C, ARAUJO-MB (Parmesan and Yohe 2003; Thomas et al. 2004; Araujo and Guisan 2006)].

2010–2014: towards a new fusion between evolutionary and community ecology (Fig. 8)?

Work on molecular ecology and phylogeny split into two distinct clusters (light yellow and light brown/pink, respectively). Molecular ecology (light yellow) grew and reached an unequalled density (18.3% of nodes and 18% of internal links of the network). Publications by EXCOFFIER-L played a central role in the field, along with DRUMMOND-AJ (Drummond and Rambaut 2007) and PRITCHARD-JK. Phylogeny (FELSENTEIN-J; PARADISE; FRECKLETON-RP, light brown/pink) developed links with work on speciation and adaptive radiation [LOSOS-JB (Losos et al. 1998)], biogeography [WIENS-JJ (Wiens and Donogh 2004; Wiens and Graham 2005)] and trait-based approaches in community ecology (GASTON-KJ). Interestingly, phylogeny emerged as a hub between evolutionary ecology, population/community ecology, and macro-ecology. The recently developed cluster on climate change and macroecology (in dark green) gained in importance and structure [PARMESAN-C, ARAUJO-MB, HIJMANS-RJ, ELITH-J (Hijmans et al. 2005; Elith and Leathwick 2009)].

Some mutations have occurred in the cluster on predator–prey interaction (in red), which separated from population/community ecology. This may have been caused by the

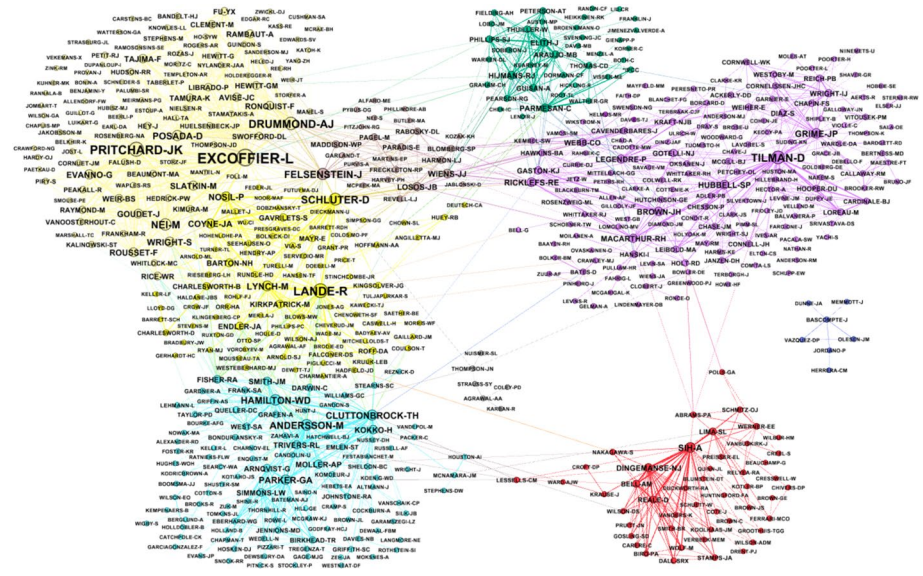


Fig. 8 Network of co-citations in ecology and evolution journals during the 2010–2014 period. Threshold of co-citations used for this figure is 70

emergence of a new research topic on animal personality and individual behavioral variation around SIH-A and DINGEMANSE-NJ (Dingemanse et al. 2010) on the left-hand side of the cluster, and by the old connections between SIH-A and work on predation risk (LIMA-SL) and its consequences for prey dynamics (WERNER-EE), and its cascading effects (SCHMITZ-OJ), including ecosystem fluxes (POLIS-GA).

The internationalization of ecology and evolution

In the 1970s and 1980s, the USA and UK largely dominated the networks in terms of influential publications. The combined world share of publications of these two countries, however, has significantly decreased from 73% in the 1975–1979 period to 41.5% in the 2010–2014 period (Table 1). This decline was accompanied with the rise of countries from continental Europe, such as France, Spain, or Switzerland, whose share of publications have increased from 1.2 to 4.9%, 0.2 to 3.2%, and 0.5 to 3.1%, respectively. Australia has also almost doubled its world share of publications in 30 years, rising from 3.7 to 7.0%. Finally, China, which was not present in the main journals of the field before 1985, represented 1.8% of the world's publications during the 2010–2014 period. These changes illustrate the increasing internationalization of scientific publications, which has been witnessed in all fields of science for the last three decades (Gingras 2002; Grossetti et al. 2014). Indeed, the 12 countries that represented almost 90% of world publications in ecology and evolution in the 1975–1979 period, only accounted for 80.5% in 2010–2014.

Discussion

Our first objective was to analyze the temporal dynamics of research in ecology and evolution and to identify the major themes of research that have structured the whole field. As the 5-year networks show, we can recognize relatively well-defined sub-communities associated with research subjects. Three general bodies of literature have stayed stable over the 40-year period: population/community ecology, evolutionary ecology, and population/quantitative genetics. Our analysis reveals a structure of research that differs from what research communication channels (i.e., scientific societies and journals) would provide. For example, behavioral ecology has commonly been considered as a coherent research field with its international society and journals, under the umbrella theme of the functional approach (Tinbergen 1963). But our analysis shows that it is composed of two or three relatively independent clusters. Our analysis suggests that the most important separation occurred between optimal foraging and predation risk, on the one hand, and sexual selection, mating system evolution, kin selection, and life history theory, on the other hand. In other words, behavioral ecology is not a unified discipline, but forms different communities.

Our analysis also highlights that the structure of research in ecology and evolution is highly dynamic. Over the years, we can observe a very fluid regime of fissions and fusions among studies on life history theory, sociobiology, and sexual selection. Such dynamics appear to be arising from shifts in concepts and research questions. For example, in the '80s publications on life history theory have drifted from population/community ecology to finish absorbed in the population/quantitative genetics and sexual/kin selection/cooperation clusters. Population/quantitative genetics were united conceptually until the late '80s, but beginning in the early '90s population genetics and

Table 1 Evolution of world share (%) of publications in ecology and evolution

Country	1975–1979	1980–1984	1985–1989	1990–1994	1995–1999	2000–2004	2005–2009	2010–2014
USA	44.2	49.9	46.3	40.7	35.6	34.7	33.0	30.9
UK	27.8	21.3	17.5	17.5	17.2	14.1	12.2	10.6
Australia	3.7	3.7	4.2	4.3	4.6	5.2	5.7	7.0
Canada	4.5	5.3	7.3	7.8	6.8	6.2	7.3	6.9
Germany	4.0	3.3	3.7	3.1	3.5	4.3	4.9	5.4
France	1.2	1.0	1.2	2.2	3.7	4.5	4.5	4.9
Spain	0.2	0.4	0.6	1.5	2.4	2.7	3.2	3.2
Switzerland	0.5	0.5	0.5	1.3	2.1	2.5	2.7	3.1
Sweden	2.4	3.0	4.2	4.8	4.2	3.9	3.0	2.6
Netherlands	1.2	1.7	2.1	2.4	2.6	2.5	2.5	2.2
China	0.0	0.0	0.1	0.1	0.1	0.4	0.9	1.8
Japan	0.4	0.8	1.2	1.3	1.5	1.8	1.7	1.7
Other countries	10.1	9.7	11.2	12.9	15.7	17.3	18.5	19.5
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

phylogeny (light yellow) form first one then two groups separated from quantitative and evolutionary genetics or evolutionary biology (in bright yellow). The two groups, however, maintain many connections. Molecular tools represent important techniques in other clusters, which show no links with evolutionary genetics. Thus, the organization of research seems to depend more on concepts than on techniques. Other areas of research have shown a fission–fusion dynamic influenced by taxonomic considerations. For example, throughout the study period, a large diversity of research topics seems to be stably regrouped under the (meta) population/community ecology banner. The fissions and fusions in that group seem mostly related to taxonomic properties (i.e., plants vs. animals).

Several fields have emerged over the years. Sometimes, this emergence seems to follow technological developments. For example, the advent and the explosion of the population genetics/phylogeny cluster coincided with the molecular and the genomic revolutions (Figs. 7, 8). Others have emerged following societal events external to the scientific community. For example, in 2005–2009 we saw the rise of the cluster on climate change and macroecology (dark green in Figs. 7, 8). These findings are consistent with those of Neff and Corley who found, using title co-word analysis in ecology research articles, that «the maturation of ecology has included an increasing focus on subjects such as climate change and genetics subjects». They are also consistent with their findings that some emerging topics in the discipline were enabled by new technological developments such as microsatellite characterization and mitochondrial DNA analysis (Neff and Corley 2009, 679). The shift toward technology-based research areas, or those that require large and complex databases, has also been identified by McCallen et al. (2019). Conversely, some other groups have disappeared as highly structured entities. For example, the ethology group almost vanished from the field at a time coinciding with the emergence of studies using an adaptive approach. Intriguingly, this shift in the approach may mirror Tinbergen's (1963) call for a more integrative approach to the study of behavior.

Other clusters have mutated over the years. The predator–prey relationships group first linked to the optimal foraging group in the '70s, has maintained strong links with population/community ecology over the '80s. It has then changed over time to end up forming a cluster with research on animal personality in the last period, under the shared influence of SIH-A on these two research topics. Finally, we can see the fission of small clusters from the larger ones followed by their fusion. The probabilistic nature of the algorithm in how it assigns a node or a few nodes to a cluster can explain this fission/fusion phenomenon. This artifact could lead to the switch in position of a (group of) node(s) from one cluster to another on different runs of the algorithm. Thus, clusters that stay similar over many periods suggest more robust communities than short-term changes in the clusters.

Although readers may find many more, we identified two absent or underrepresented fields of research in this analysis: conservation biology, and plant/animal ecophysiology, respectively. Conservation biology does not appear as a field, but throughout the different clusters we can detect many scientists who have been active in conservation biology (e.g.: purple: PIMM-S, SIMBERLOFF-D; bright yellow: LANDE-R; light yellow: FRANKHAM-R, HEDRICK-PW; TEMPLETON-AR; turquoise: SUTHERLAND-WJ). Theoretical developments happening within each field, thus, feed the development of conservation biology, but their links may not be strong enough compared to the links developed within each field to generate an independent conservation biology cluster. More importantly, since our list of journals is focused on core ecology and evolution, it excludes the core journals of conservation biology, and hence their main ideas have been undetected in the co-citation indices. One could construct a more general list of journals including all

biological research then see many other fields loosely interacting with the subfield of evolution and ecology that we have prioritized here.

During some periods, scientific activity was structured on a taxon-centric or ecosystem-centric vision: people working on a taxon (e.g., insects, birds, primates, or plants) or on an ecosystem (e.g., aquatic or forest) tended to bias their citations towards that taxon or ecosystem. Sometimes, scientists working on similar concepts but on different taxa were disconnected. For example, Nancy Burley and Mary Willson published a book on mate choice in plants in 1983 (Burley and Willson 1983). In the late '80s Willson had a strong impact in her field (plant ecology; Figs. 2, 3), whereas Burley actively belonged to a group working on sexual selection in animals (Fig. 4). For community ecology, Roughgarden (2009) has argued such a structure would result from the lack of a general theory in the field. However, we can still see some taxa-oriented structure in evolutionary ecology or population genetics, two disciplines characterized by a strong general theoretical background. Sometimes, taxon-oriented clusters may result from the fact that some taxa are highly appropriate to disentangle specific theoretical or conceptual questions. For example, cooperation studies naturally focused on social insects (although not exclusively). In other situations, important network shifts are related to conceptual switches. Plant ecology is a good illustration of it. From this important field in the '80s (Figs. 2, 3) two groups emerged during the late '90s: a first one that merged with community ecologists and a second one that joined evolutionary ecologists (Figs. 6, 7). Interestingly, this shift in the structure of research from a taxon-oriented structure to a more concept-oriented structure seems to happen in the '90s, and coincides with the transformation of many North American zoology and botany departments into either ecology and evolution departments or cell and molecular biology departments.

Some scientists can have tremendous and permanent effects on the structure of a field, although the goal of our analyses is not to evaluate the career of scientists. Ideas from pioneers have strongly influenced most networks. Some actors of the new Darwinian synthesis such as Fisher, Wright, and Mayr show permanent impact in their respective clusters over the 40 years. Others such as Haldane, or Simpson do not seem to have such lasting effects. Darwin himself never has a central position in the networks, although natural selection is at the core of evolutionary ecology. This corresponds to the phenomenon of “obliteration by incorporation” according to which classic sources stop being cited (e.g., Darwin) when they become accepted and taken for granted (Merton 1988). Hence, authors cite contemporary authors, although they have based their ideas on Darwin's work (e.g., sexual selection, natural selection, cooperation). Among the pioneers in ecology, MacArthur has probably had the strongest and longest-lasting influence. In contrast Hutchinson's influence at the level of the global network has declined rapidly. Lack and Schoener maintain very strong impact over the years, but seem to vanish in the 2000s. Others, such as Lotka, Elton, Gleason, or Odum, disappeared very early.

Some authors occupy a remarkably central position in their field (e.g., Lande, Tilman, Excoffier or Hamilton). For these authors, a radiating structure reveals that their publications are co-cited with many other sets of publications: the whole field focuses on the ideas these authors propose. A more reticulated section of the network is the sign of a more diverse circulation of ideas. If we use this index to evaluate the intellectual dynamism of the latest network (Fig. 8) we could say that although some current players can be highly influential (e.g. Tilman, Lande, Clutton-Brock, Excoffier), all the clusters are reticulated and thus show signs of a highly dynamic and diverse exchange of ideas. Other authors shape the whole network by linking two or more fields. One brilliant example of this is Charnov, who worked on such a diversity of topics that he linked all the major clusters in the 1985–1989 period.

What factors could explain the relative importance of sets of publications in a network? We might expect more general publications, like books, to be central: some, like Fisher, Maynard-Smith, or MacArthur have probably influenced the structure of their field with their books. But this is not always the case: others occupy a central position without having published any book (Hamilton; Excoffier; Pritchard). Alternatively, methodological publications can provide a crucial status within a field. For example, Sokal and Rohlf's book on biostatistics (Sokal and Rohlf 1969), the R software (R Core Team 2014), or several authors of computer programs in population genetics and phylogeny have played a dominant role in ecology and evolution.

Over the last 40 years, British and American scientists have dominated ecology and evolution. The main nodes in the early networks were British or American, and these two countries had a high share of the world publications. Most of the early pioneers were also from the UK or USA, and in 1975–1979 these two countries produced more than 70% of the publications in the field. However, the prominence of these two nations declined over time: the world share of publications went down to about 40% in the latest period, and a growing number of scientists from other countries start structuring all the clusters. Nevertheless, the increasing proportion of publications released by new players in the field does not yet translate into their presence in the network of co-citations. It is hard to predict how long it could take for authors of these countries to reach a position of leadership in the subfields.

Conclusion

Our goal in this paper was to answer the question: have ecology and evolution formed a coherent network of ideas over the last 40 years. Our analyses, using co-citation networks and community detection algorithms, identified two main subgroups that we can describe as ecology (purple, green, red clusters), and evolutionary fields (yellow, turquoise, bright yellow and dark yellow). Although these two communities show connections with each other, most of the scientific activity is happening within, rather than between, them. However, we should not take this separation for granted. We can see periods of intense exchange between these different subfields, particularly in the '70s and early '80s. The impression of isolation between these two groups may also come from the increasing activity within the networks that forced us to raise the co-citation threshold used to show an edge. Links between the two large networks may increase considerably over the years but not as much as links within them. We expected that the development of online publication access could reduce the boundaries between the fields, but the increase in the number of publications probably constrains researchers to restrict their investigation to their subfield. Given the growing trend towards specialization in research, one should not anticipate that ecology and evolution will form a unique community of closely connected researchers in the future.

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Compliance with ethical standards

Conflict of interest We declare that no competing interests exist.

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