Mapping the dynamics of research networks in ecology and evolution using co-citation analysis (1975–2015)

Denis Réale[a], Mahdi Khelfaoui[b], Pierre-Olivier Montiglio[a] & Yves Gingras[1b]

[a] Département des Sciences Biologiques, Université du Québec A Montréal, CP8888, Succursale centre-ville, Montréal, Québec, Canada, H3C3P8;

[b] Centre Interuniversitaire de Recherche sur la Science et la Technologie, Université du Québec A Montréal, CP8888, Succursale centre-ville, Montréal, Québec, Canada, H3C3P8.

[1] To whom correspondence may be addressed. email: gingras.yves@uqam.ca

phone: (1) 514 987 3000 (7053#)

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 ideas have motivated research activity in subfields, and how long have these ideas attracted the attention of the scientific community? Contrary to what we 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 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; 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 the research subjects within a field can help us to understand the 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 theoretic and conceptual basis [i.e., Dobzhansky's (1973) "nothing in biology makes sense except in the light of evolution"]. However, some authors have noted the lack of interest for evolutionary ideas in ecological research (Bradshaw 1984), and discussions between colleagues quickly show how disparate subfields can be in terms of historical and theoretic backgrounds, fundamental questions, and traditions.

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 a research 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. The 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, Bean and Myers (2016), 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, Nabout and Bini (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, Diniz-Filho and Bini (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 identity 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. We warn readers who may search for their name in the various networks not to feel frustrated if they do not see it or if they feel that their node should be larger, since it does not mean that their work did not have any impact. 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 five 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 (Table 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.

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 1973, 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 Frich 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 1961)]. 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 Slayter 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 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 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 will 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 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 ’80s, 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 (Avise et al. 1987, 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 CONNEL-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 Kodrick-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 keystone 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 (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.

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 et al. 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.

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 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; PARADIS-E; 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 Donogue 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 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 series of 5-year network shows, 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 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 revolution (Fig. 7, Fig. 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 Fig. 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 on 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 then has 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; Fig. 2 and 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 taxaoriented 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 (Fig. 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 (Fig. 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 phenomena 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. Charnov 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 Rolhf 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.

Acknowledgments

We thank Beatrix Beisner and Pedro Peres-Neto for their constructive comments on a previous draft and Yimen Araya-Ajoye, Anne Charmantier, Niels Dingemanse, and Dave Westneat for discussions on the results. We are grateful to Carolyn Hall for editing the English Part of this work, done in part while D Réale was a visiting scholar at the Centre d'Écologie Fonctionnelle et Évolutive CNRS Montpellier, France. D Réale and PO Montglio are members of the Quebec Center for Biodiversity Science an excellence research center funded by the Fonds de Recherche Québec Nature Technologies. M Khelfaoui and Y Gingras are members of the Centre Interuniversitaire de Recherche sur la Science et la Technologie (CIRST).

Competing interests

We declare that no competing interests exist.

References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3-4), 227-266.

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature*, 299(5886), 818-820.

Andersson, M. (1986). Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution*, 40(4), 804-816.

Andersson, M. B. (1994). *Sexual selection.* Princeton: Princeton University Press.

Araujo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33(10), 1677-1688.

Avise, J. C. (1992). Molecular population structure and the biogeographic history of a regional fauna: A case history with lessons for conservation biology. *Oikos*, 63(1), 62-76.

Avise, J. C., Arnold, J., Ball, R. M., Bermingham, E., Lamb, T., Neigel, J. E., Reeb, C.A. & Saunders, N. C. (1987). Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, 18, 489-522.

Birkhead, T. R. & Møller, A. P. (1992). *Sperm Competition in Birds: Evolutionary Causes and Consequences*. Tim Birkhead: Academic Press.

Blondel, V. D., Guillaume, J. L., Lambiotte, R., & Lefebvre, E. (2008). Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and experiments*, 10:P10008.

Bradshaw, A. (1984). The importance of evolutionary ideas in ecology and vice versa. In Shorrocks (Ed.), *Evolutionary Ecology* (pp. 1-25). Oxford, UK: Blackwell.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist*, 124(2), 255-279.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771-1789.

Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58(2), 445-449.

Burley, N., & Willson, M. (1983). *Mate Choice in Plants*. Princeton: Princeton University Press.

Burnham, K. P., & Anderson, D. R. (1998). *Model selection and multimodel inference: a practical information-theoretic approach*. New-York: Springer-Verlag.

Carneiro, M.C., Nabout, J.C. and L.M. Bini. (2008). Trends in the scientific literature on phytoplankton. *Limnology*, 9(2), 153-158.

Carvalho, P., Diniz-Filho, J.A.F. and L.M. Bini (2005). The impact of Felsenstein's “Phylogenies and the comparative method” on evolutionary biology. *Scientometrics*, 62(1), 53-66.

Chapin, III F. S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 11, 233-260.

Charlesworth, B., & Charlesworth, D. (1978). A model for the evolution of dioecy and gynodioecy. *American Naturalist*, 112(988), 975-997.

Charnov, E. L. (1976). Optimal foraging the marginal value theorem. *Theoretical Population Biology* 9(2), 129-136.

Charnov, E. L. (1982). *The Theory of Sex Allocation*. Princeton: Princeton University Press.

Charnov, E. L., & Krebs, J. R. (1974). On clutch size and fitness. *Ibis*, 116(2), 217-219.

Cherven, K. (2013). *Network graph analysis and visualization with Gephi*. Packt Publishing.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton: Princeton University Press.

Clutton-Brock, T. H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296(5565), 69-72.

Clutton-Brock, T. H. (Ed). (1988). *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. Chicago: University of Chicago Press.

Cody, M.L. (1974). *Competition and the structure of bird communities*. Princeton: Princeton University Press.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42(4), 710-723.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), 1302-1310.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 111(982), 1119-1144.

Courchamp, F. and Bradshaw, C. J. (2018). 100 articles every ecologist should read. *Nature Ecology & Evolution* 2(2), 395-401.

Cuddington, K. and Beisner, B. (2005). *Ecological paradigms lost: routes of theory change*. Elsevier Academic Press.

Cummins, K. W. (1974). Structure and function of stream ecosystems. *BioScience*, 24(11), 631-641.

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: Murray London.

Darwin, C. (1871). *Sexual selection and the descent of man*. London: Murray London.

Dingemanse, N. J., Kazem, A. J., Réale,. D. and Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, 25(2), 81-89.

Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *American Biology Teacher*, 35(3), 125-129.

Drummond, A. J. and Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7(1), 214.

Elith, J. and Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*, 40(1), 677-697.

Emlen, S. T. and Oring, L. W. (1977). Ecology sexual selection and the evolution of mating systems. *Science*, 197(4300), 215-223.

Excoffier, L., Laval, G. and Schneider, S. (2005). Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics*, 1(1), 47-50.

Excoffier, L., Smouse, P. E. and Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, 131(2), 479-491.

Felsenstein, J. (1981). Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution*, 17(6), 368-376.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39(4), 783-791.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature* 405(6783), 220-227.

Gingras, Y. (2002). Les formes spécifiques de l'internationalité du champ scientifique. *Actes de la Recherche en Sciences Sociales*, vol. 141-142, 31-45.

Gingras, Y. (2009). Revisiting the "quiet debut" of the double helix: a bibliometric and methodological note on the "impact" of scientific publications. *Journal of the History of Biology*, 43(1), 159-181.

Gingras, Y. (2010). Mapping the structure of the intellectual field using citation and co-citation analysis of correspondences. *History of European Ideas*, 36(3), 330-339.

Gordon, D. M. (2011). The fusion of behavioral ecology and ecology. *Behavioral Ecology*, 22(2), 225-230.

Goudet, J. (1995). FSTAT version 12.: a computer program to calculate F-statistics. *Journal of Heredity*, 86(6), 485-486.

Grime, J. P. (1979). *Plant strategies and vegetation processes*. New York: Wiley Chichester.

Gross, M. R. (1994). The evolution of behavioural ecology. *Trends in Ecology and Evolution*, 9(10), 358-360.

Grossetti, D., M., Eckert, D., Gingras, Y., Jegou, L., Lariviere, V., & Milard, B. (2014). Cities and the geographical deconcentration of scientific activity: a multilevel analysis of publications (1987-2007). *Urban Studies*, 51(10), 2219-2234.

Hamilton, W. D. (1964). The genetical evolution of social behaviour II. *Journal of Theoretical Biology*, 7(1), 17-52.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2), 295-311.

Hanski, I. (1994). A practical model of metapopulation dynamics. *Journal of Animal Ecology*, 63(1), 151-162.

Hanski, I. and Gilpin, M. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42(1-2), 3-16.

Hanski, I., Hansson, L. and Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, 60(1), 353-367.

Harper, J. and White, J. (1974). The demography of plants. *Annual Review of Ecology Evolution and Systematics*, 5(1), 419-463.

Harper, J. L. (1977). *Population biology of plants*. London: Academic press.

Harper, J. L., Lovell, P. H. and Moore, K. G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, 1(1), 327-356.

Harvey, P. H. and Pagel, M. D. (1991). *The Comparative method in evolutionary biology*. Oxford: Oxford University Press.

Heinrich, B. and Raven, P. H. (1972). Energetics and pollination ecology. *Science*, 176(4035), 597-602.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965-1978.

Hinde, R. A. (1976). Interactions relationships and social structure. *Man*, 11(1), 1-17.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12(2), 197-229.

Hubbell, S. P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19(1), 166-172.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, 93(870), 145-159.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104(940), 501-528.

Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology Evolution and Systematics*, 2(1), 465-492.

Katz, J. S. and Hicks D. (1997). How much is a collaboration worth? A calibrated bibliometric model. *Scientometrics*, 40(3), 541-554.

Krebs, C. J. (1972). *Ecology: the experimental analysis of distribution and Abundance*. New York: Harper and Row.

Krebs, J. R. (1978). Optimal foraging: decision rules for predators. *Behavioural ecology: an evolutionary approach*. Krebs, J. R. and Davis, N. B (eds). Sunderland: Sinauer, 23-63.

Krebs, J. R., Erichsen, J. T., Webber, M. I. and Charnov, E. L. (1977). Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour*, 25(1), 30-38.

Lack, D. L. (1954). *The natural regulation of animal numbers*. Oxford: The Clarendon Press.

Lack, D. L. (1968). *Ecological adaptations for breeding in birds*. London: Chapman & Hall.

Lande, R. (1979). Quantitative genetic analysis of multivariate evolution applied to brain:body size allometry. *Evolution*, 33(1), 402-416.

Lande, R. and Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, 37(6), 1210-1226.

Larivière, V., Ni, C., Gingras, Y., Cronin, B. and Sugimoto, C. R. (2013). Bibliometrics: global gender disparities in science. *Nature*, 504(7479), 211-213.

Larivière, V., Vigola-Gagné, E., Villeneuve, C., Gélinas, P. and Gingras, Y. (2011). Sex differences in research funding productivity and impact: an analysis of Québec university professors. *Scientometrics*, 87(3), 483-498.

Legendre, P. and Legendre, L. (1998). *Numerical Ecology*. London: Elsevier.

Leimu, R. and J. Koricheva (2005). Does Scientific Collaboration Increase the Impact of Ecological Articles? *BioScience*, 55(5), 438-443.

Levin, D. A. (1984). Inbreeding depression and proximity-dependent crossing success in Phlox drummondii. *Evolution*, 38(1), 116-127.

Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. Princeton: Princeton University Press.

Lewontin, R. C. (1974). *The genetic basis of evolutionary change*. New York: Columbia University Press.

Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation:a review and prospectus. *Canadian Journal of Zoology*, 68(4), 619-640.

Lloyd, D. G. (1979). Some reproductive factors affecting the selection of self-fertilization in plants. *American Naturalist*, 113(1), 67-79.

Logan, J.M., Bean, S.B. and A.E. Myers. (2017). Author contributions to ecological publications: What does it mean to be an author in modern ecological research? PLoS One, 12(6): e0179956.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Raffaelli, Schmid, D., Tilman, D. and Wardle, D. A. (2001). Biodiversity and ecosystem functioning:current knowledge and future challenges. *Science* 294:804-808.

Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. and Rodríguez-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, 279(5359), 2115-2118.

MacArthur, R. H. (1972). *Geographical ecology: patterns in the distribution of species*. Princeton: Princeton University Press.

MacArthur, R. H. and Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist*, 100(916), 603–609.

MacArthur, R. H. and Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17(4), 373–387.

MacArthur, R. H. and Wilson, E. O. (1967). *The theory of island biogeography*. Princeton: Princeton University Press.

May, R. M. (1974). Biological populations with nonoverlapping generations: stable points stable cycles and chaos. *Science*, 186(4164), 645-647.

May, R. M. (1976). Simple mathematical models with very complicated dynamics. *Nature*, 261(5560), 459-467.

Maynard-Smith, J. (1974). The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, 47(1), 209-221.

Maynard-Smith, J. and Parker, G. A. (1976). The logic of asymmetric contests. *Animal Behaviour*, 24(1), 159-175.

Maynard-Smith, J. and Price, G. R. (1973). The logic of animal conflict. *Nature*, 246(5427), 15-18.

Mayr, E. (1970). *Populations, species, and evolution: an abridgment of animal species and evolution*. Harvard: Harvard University Press.

McCallen, E., Knott, J., Nunez-Mir, G., Taylor, B., Jo., I. and S. Fei. (2019). Trends in ecology: shifts in ecological research themes over the past four decades. *Frontiers in Ecology and Evolution*, 17(2), 109-116.

Medina, A.M. (2018). Why do ecologists search for co-authorships? Patterns of co-authorship networks in ecology (1977–2016). *Scientometrics*, 116(3), 1853-1865.

Merton, R. K. (1988). The Matthew effect in science II. Cumulative advantage and the symbolism of intellectual property. *Isis*, 79(4), 606-623.

Møller, A. P. (1994). Sexual selection and the barn swallow. In Dugatkin L. A. (ed.). *Model systems in behavioral ecology: integrating conceptual theoretical and empirical approaches*. Princeton: Princeton Unversity Press, 359-380.

Møller, A. P. and Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, 32(3), 167-176.

Montgomerie, R. (2010). The end of behavioral ecology. *Evolution*, 65(4), 1212-1214.

Mooney, H. A. (1972). The carbon balance of plants. *Annual Review of Ecology and Systematics*, 3(1), 315-346.

Neff, M.W. and E.A. Corley. (2009). 35 years and 160,000 articles: A bibliometric exploration of the evolution of ecology. *Scientometrics*, 80(3), 657-682.

Nei, M. (1972). Genetic distance between populations. *American Naturalist*, 106(9), 283-292.

Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, 89(3), 583-590.

Odum, E. (1992). Great ideas in ecology for the 1990s. *BioScience*, 42(7), 542-545.

Owens, I. P. F. (2006). Where is behavioural ecology going? *Trends in Ecology and Evolution*, 21(7), 356-361.

Paine, R. T. (1966). Food web complexity and species diversity. *American Naturalist*, 100(910), 65-75.

Paine, R. T. (1980). Food webs: linkage interaction strength and community infrastructure. *Journal of Animal Ecology*, 49(3), 667-685.

Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Review*, 45(4), 525-567.

Parker, G. A. (1979). Sexual selection and sexual conflict. In Blum, M. S. and Blum. S. A (eds.). *Sexual selection and reproductive competition in insects*. Academic Press, 123-166.

Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42.

Pianka, E. R. (1966). Latitudinal gradients in species diversity:a review of concepts. *American Naturalist*, 100(910), 33-46.

Pianka, E. R. (1970). On r-and K-selection. *American Naturalist*, 104(9), 592-597.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4(1), 53-74.

Posada, D. and Crandall, K. A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14(9), 817-818.

Pritchard, J. K., Stephens, M. and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155(2), 945-959.

Pyke, G. H., Pulliam, H. R. and Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 52(2), 137-154.

R Core Team. (2014). *R:A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna: Austria. http://www.R-project.org/.

Raymond, M. and Rousset, F. (1995). An exact test for population differentiation. *Evolution*, 49(6), 1280-1283.

Ricklefs, R. E. (1969). *An analysis of nesting mortality in birds*. Washington: Smithsonian Contribution to Zoology (no. 9).

Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235(4785), 167-171.

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7(1), 1-15.

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge: Cambridge University Press.

Roughgarden, J. (2009). Is there a general theory of community ecology? *Biology and Philosophy*, 24(4), 521-529.

Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Schluter, D. (2001). Ecology and the origin of species. *Trends in Ecology and Evolution*, 16(7), 372-380.

Schoener, T. W. (1969). Models of optimal size for solitary predators. *American Naturalist*, 103(931), 277-313.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2(1), 369-404.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27-39.

Sih, A., Crowley, P., McPeek, M., Petranka, J. and Strohmeier, K. (1985). Predation competition and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16(1), 269-311.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, 236 (4803), 787-792.

Slatkin, M. (1993). Isolation by distance in equilibrium and non-equilibrium populations. *Evolution*, 47(1), 264-279.

Small, H. (1973). Co-citation in the scientific literature: a new measure of the relationship between two documents. *Journal of the American Society for Information Science*, 24(4), 265-269.

Sokal, R. R. and Rolhf, F. J. (1969). *Biometry: the principles and practices in biological research*. New York: W.H. Freeman.

Song, Y. and T. Zhao (2013). A bibliometric analysis of global forest ecology research during 2002–2011. *SpringerPlus*, 2:204. https://doi.org/10.1186/2193-1801-2-204

Stearns, S. C. (1976). Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, 51(1), 3-47.

Stearns, S. C. (1977). The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics*, 8(1), 145-171.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging theory*. Princeton: Princeton University Press.

Sutherland, W. J. et al. (2012). Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101(1), 58-67.

Swofford, D. L., Olsen, G. J., Waddell, P. J. and Hillis, D. M. (1996). Phylogenetic inference. Molecular Systematics. Eds. Hillis, D. M., Moritz, C., B. K. Sunderland: Sinauer Massachusetts, 407-514.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., et al. (2004). Extinction risk from climate change. *Nature* 427(6970), 145-148.

Thornhill, R. (1983). Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *American Naturalist*, 122(6), 765-788.

Thornhill, R. and Alcock, J. (1983). *The evolution of insect mating systems*. Harvard: Harvard University Press.

Tilman, D. (1982). Resource competition and community structure. Princeton: Princeton University Press.

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities*. Princeton: Princeton University Press.

Tilman, D. (1994). Competition and biodiversity is spatially structured habitats. *Ecology*, 75(1), 2-16.

Tinbergen, N. (1963). On aims and methods of ethology. *Ethology*, 20(4), 410-433.

Traag, V., Waltmann, L. and Van Eck, N. J. (2018). From Louvain to Leiden: guaranteeing well-connected communities. https://arxiv.org/abs/1810.08473.

Trivers, R. L. (1972). Parental investment and sexual selection. *Sexual selection and the descent of Man*. Trivers, R. L (ed.). Blackwell Science, 135-179.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14(1), 249-264.

Trivers, R. L. and Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068), 90-92.

Weir, B. S. and Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, 38(6), 1358-1370.

Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64(6), 1540-1548.

Westneat, D. F., Sherman, P. W. and Morton, M. L. (1990). The ecology and evolution of extra-pair copulations in birds. *Current Ornithology*, 7, 331-369.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21(2-3), 213-251.

Wiens, J. J. and Donogue, M. J. (2004). Historical biogeography ecology and species richness. *Trends in Ecology and Evolution*, 19(12), 639-644.

Wiens, J. J. and Graham, C. H. (2005). Niche conservatism:integrating evolution ecology and conservation biology. *Annual Review of Ecology Evolution and Systematics*, 36(1), 519-539.

Williams, G. C. (1966). Natural selection the costs of reproduction and a refinement of Lack's principle. *American Naturalist*, 100(916), 687-690.

Williams, G. C. (1975). *Sex and evolution*. Princeton: Princeton University Press.

Williams, G. C. (1979). The question of adaptive sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society of London, Series B*, 205(1161), 567-580.

Wilson, E. O. (1975). *Sociobiology: The modern synthesis*. Cambridge: Belknap.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16(2), 97-159.

Wright, S. (1949). The genetical structure of populations. *Annales of Human Genetics*, 15(1), 323-354.

Table 1. Evolution of world share (%) of publications in Ecology and Evolution

Country	1975-79	1980-84	1985-89	1990-94	1995-99	2000-04	2005-09	2010-14
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

Figure Legends

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.

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.

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.

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.

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.

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.

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.

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.

Fig. 1. Réale et al.:period 1975-79.

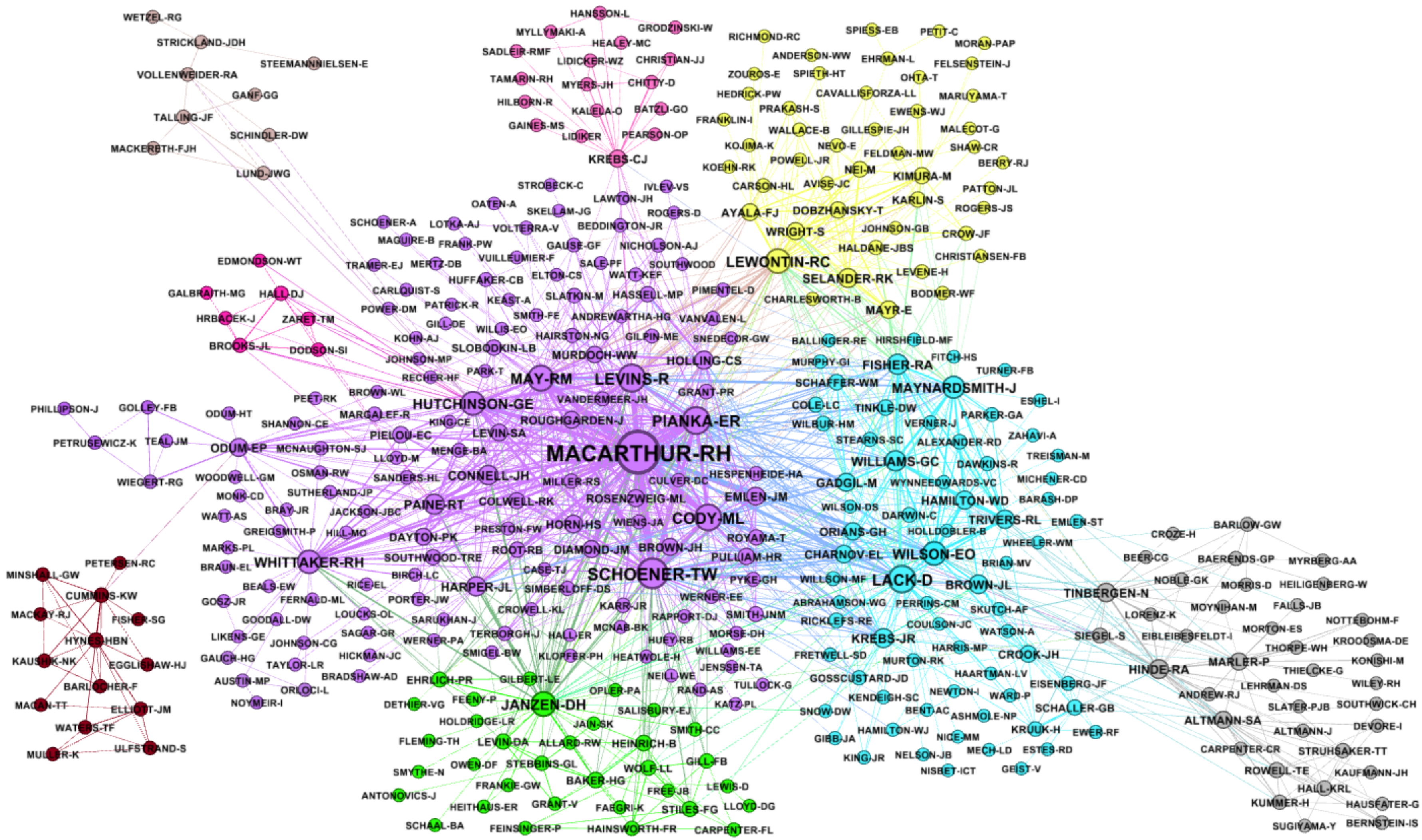


Fig. 2. Réale et al.: period 1980-84

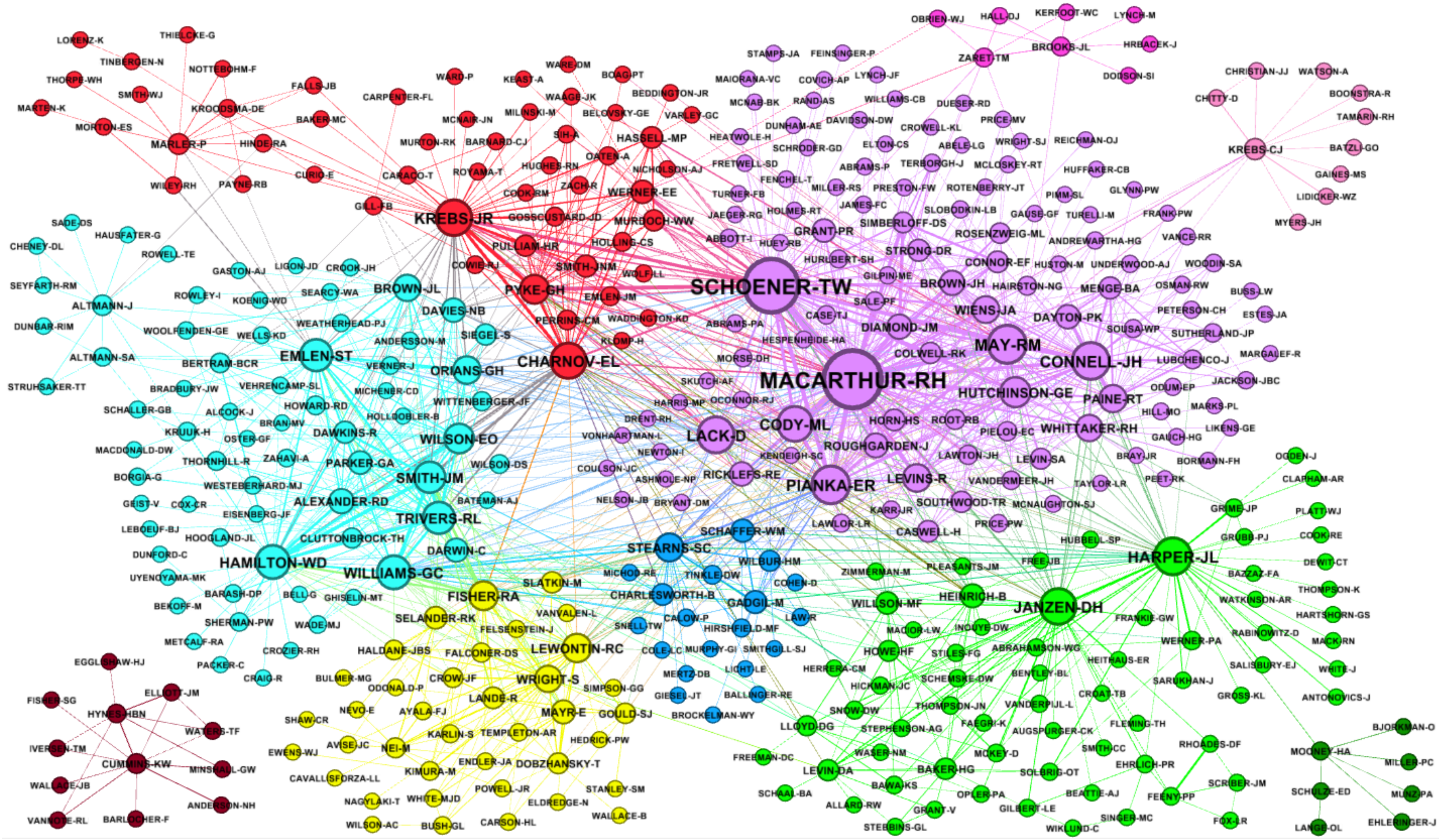


Fig. 3. Réale et al.: period 1985-89

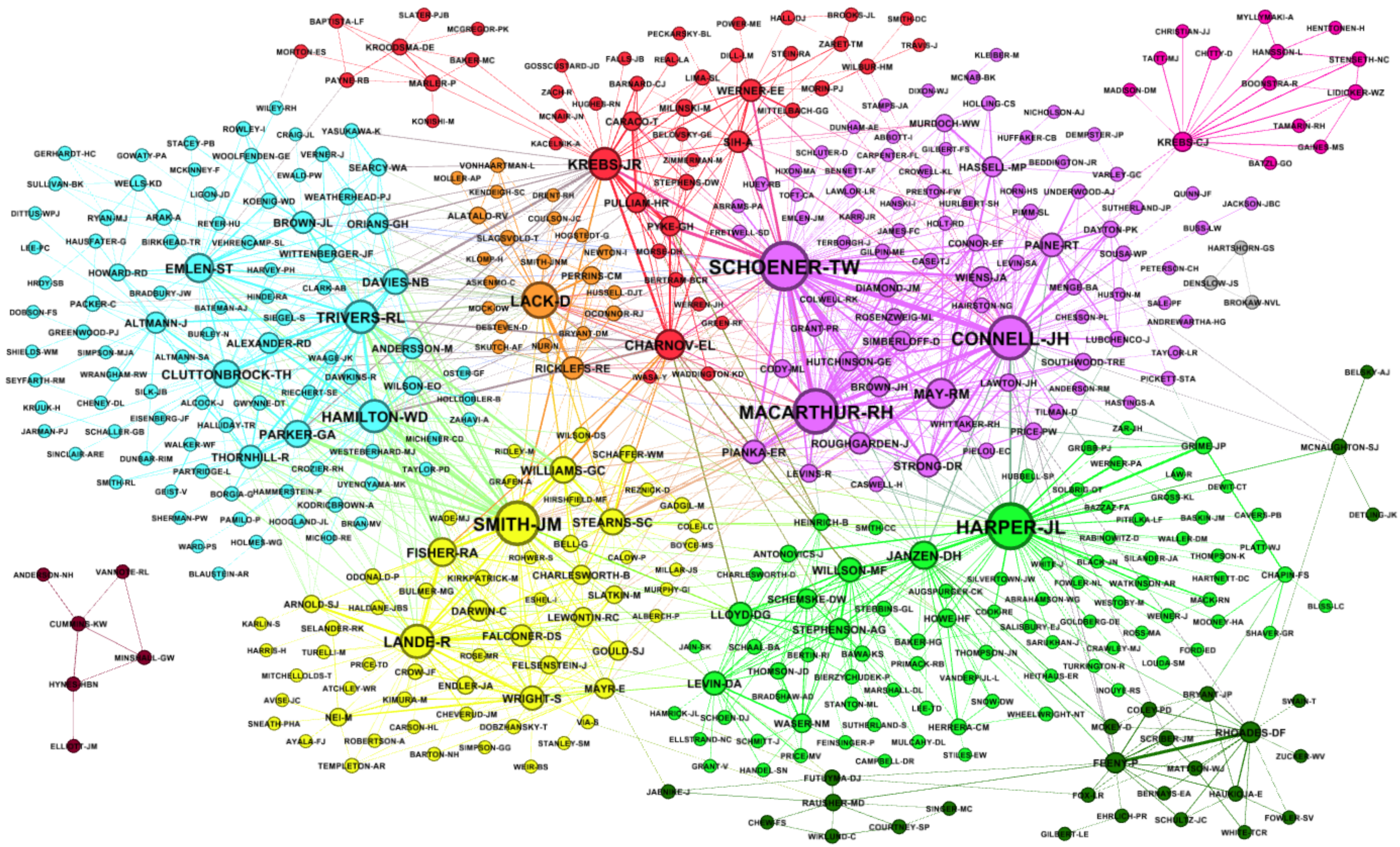


Fig. 4. Réale et al.: period 1990-94

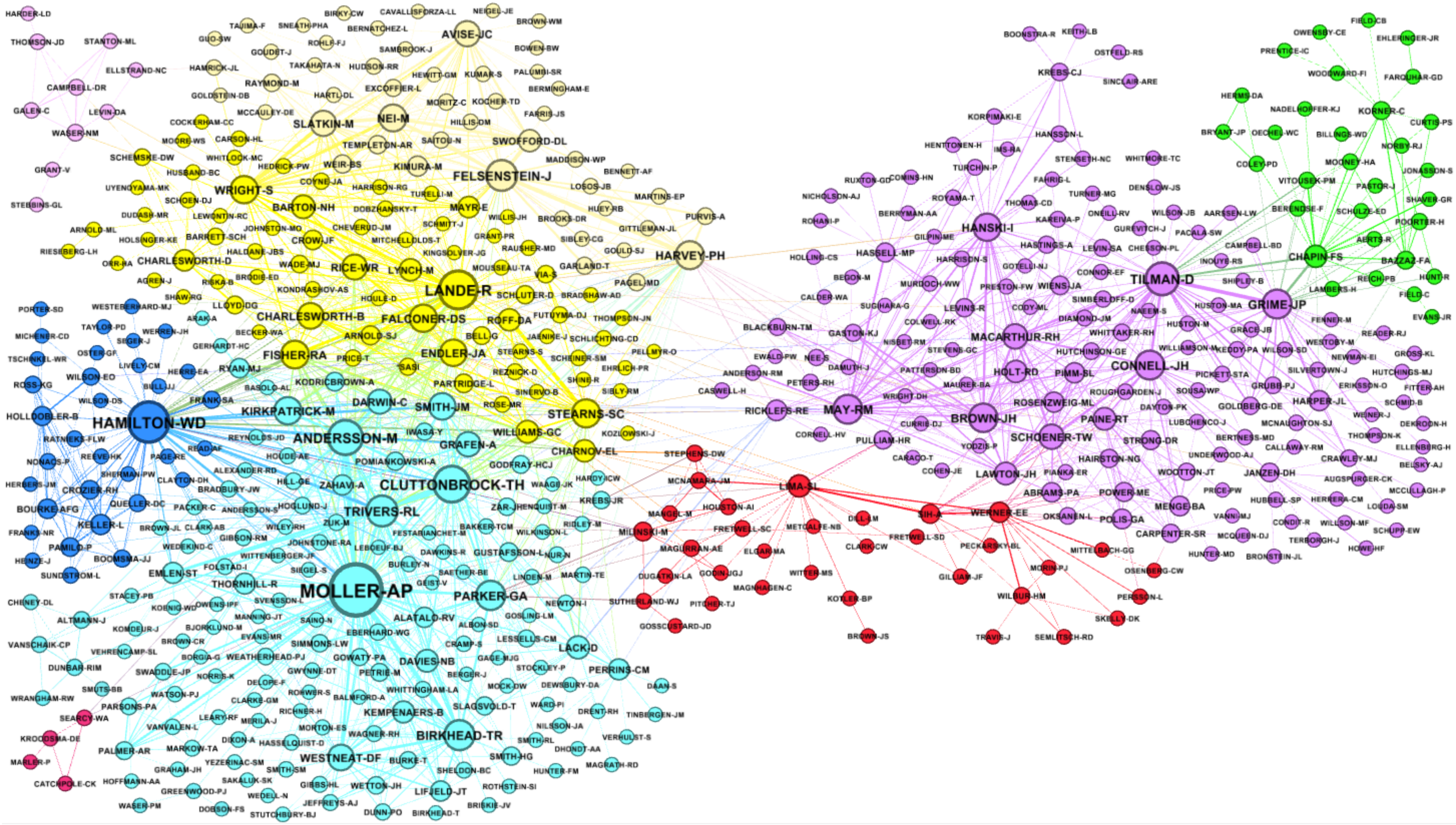


Fig. 5. Réale et al.: period 1995-99

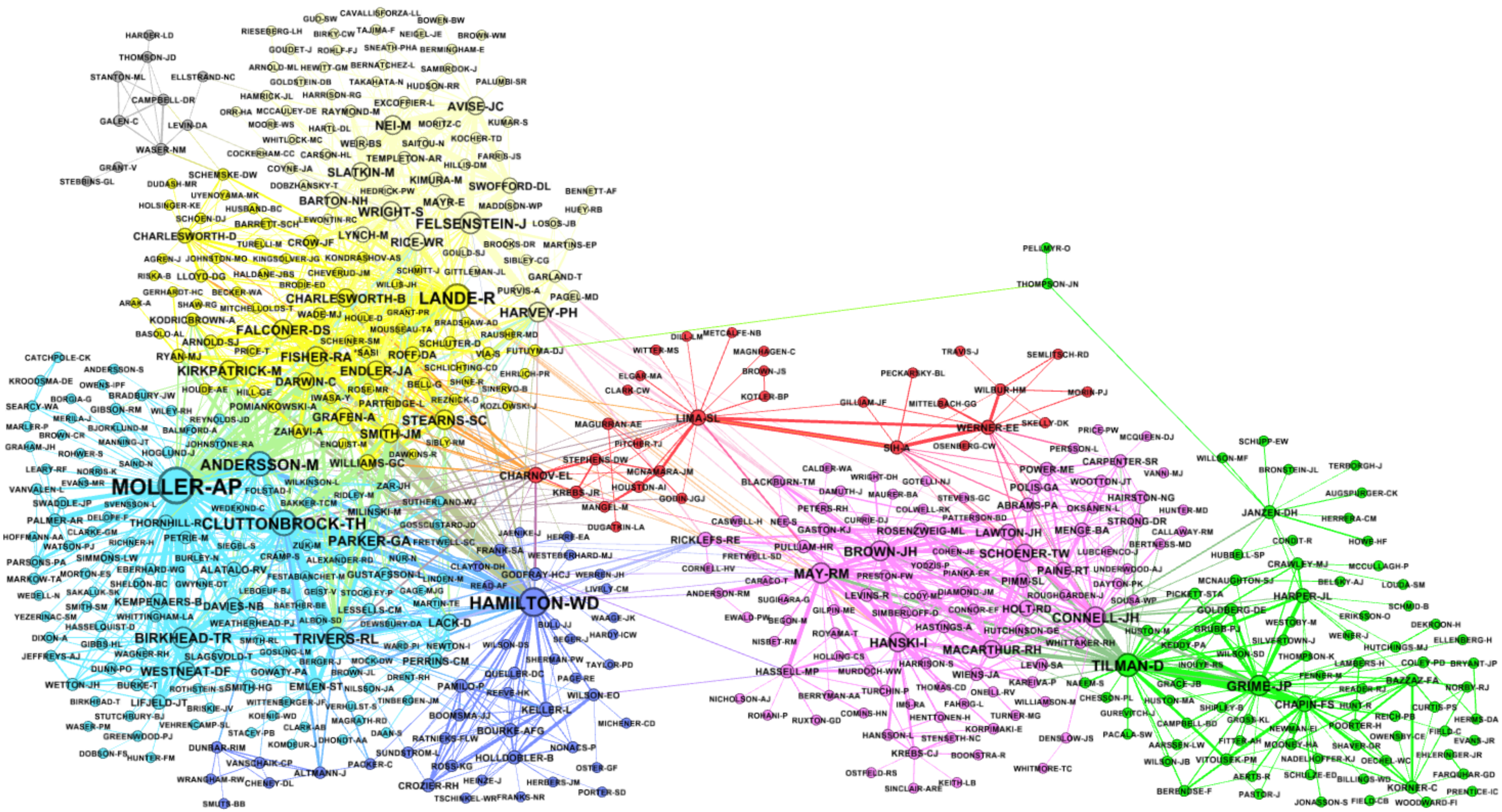


Fig. 6. Réale et al.: period 2000-04

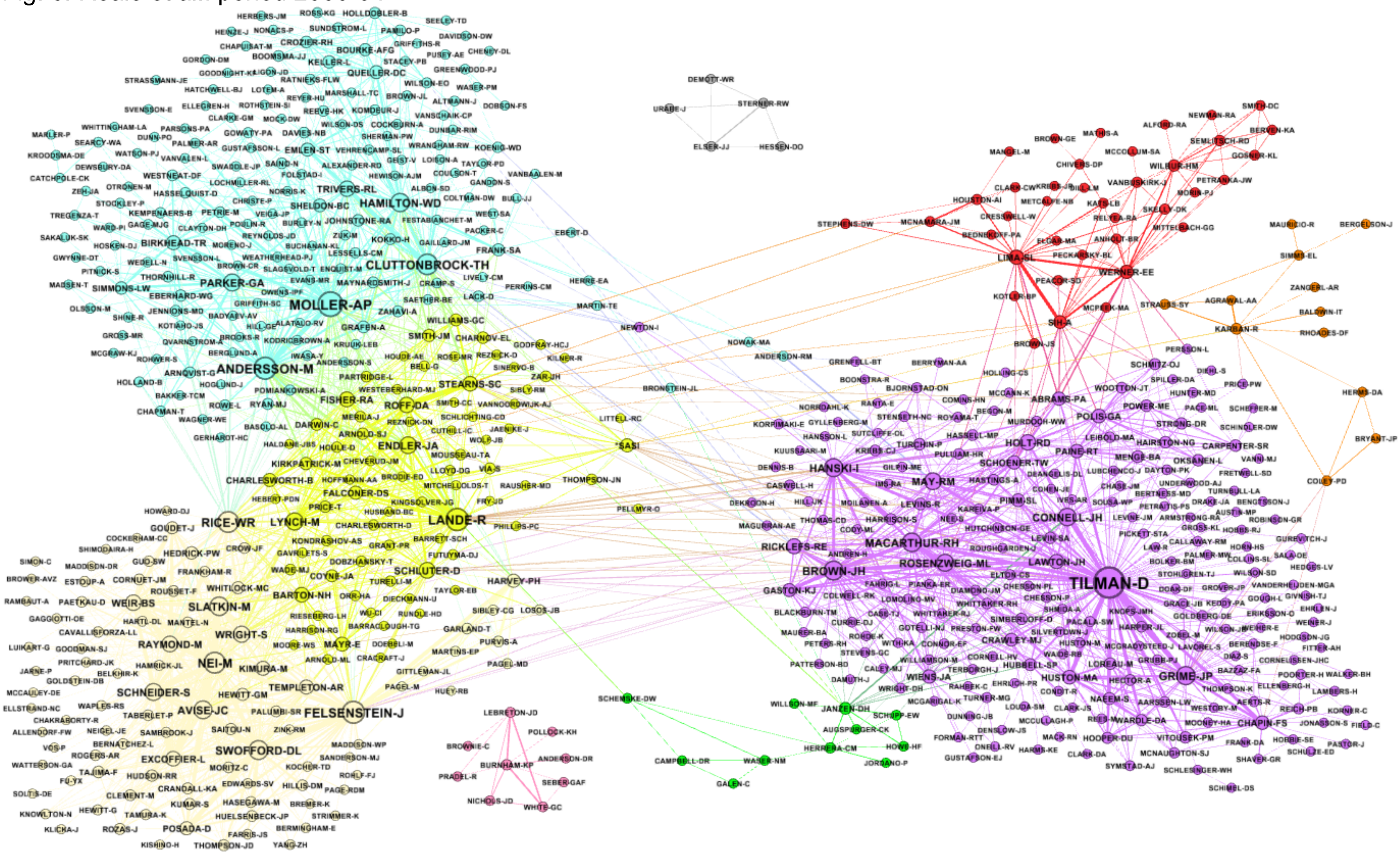


Fig. 7. Réale et al.: period 2005-09

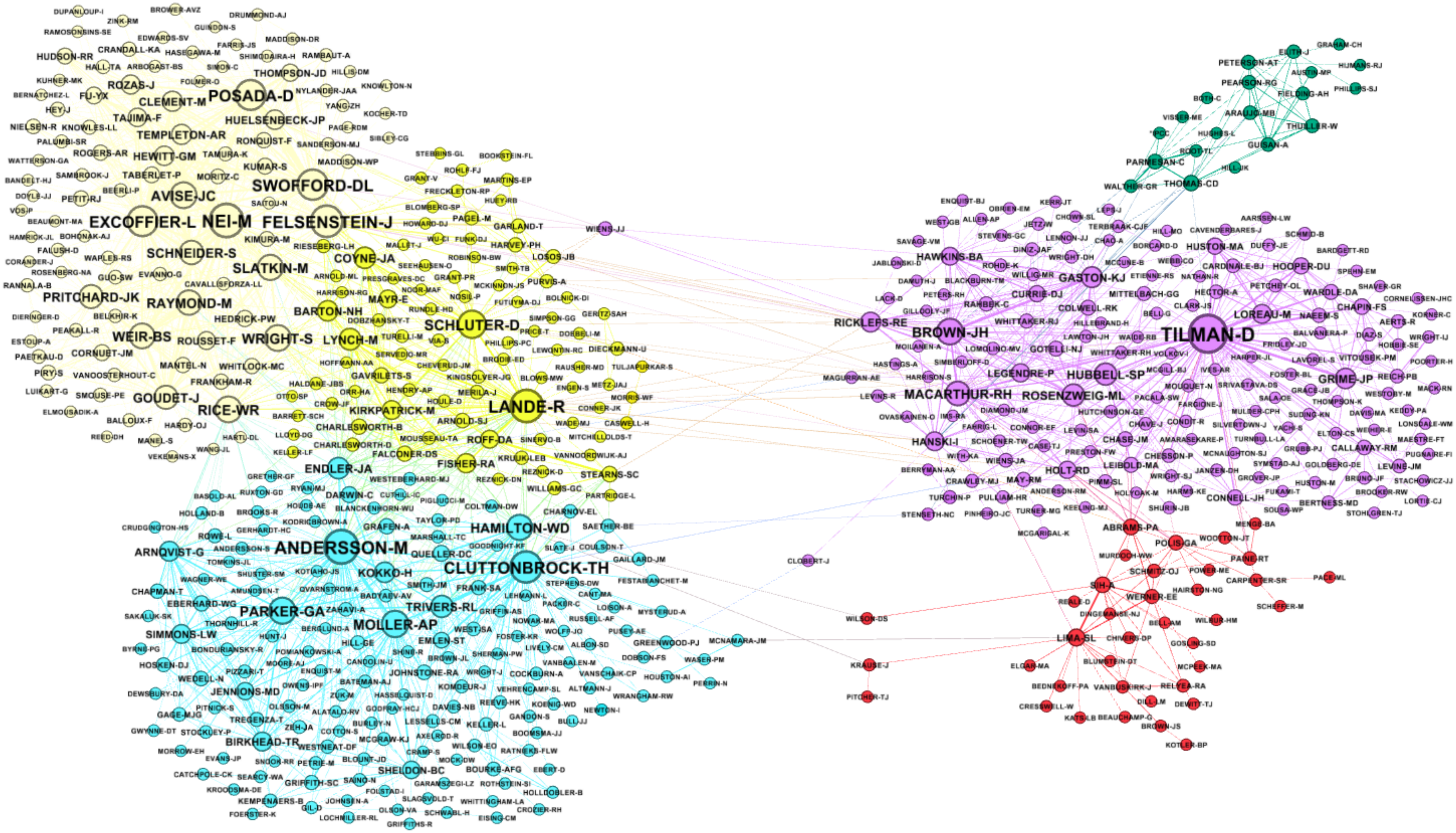
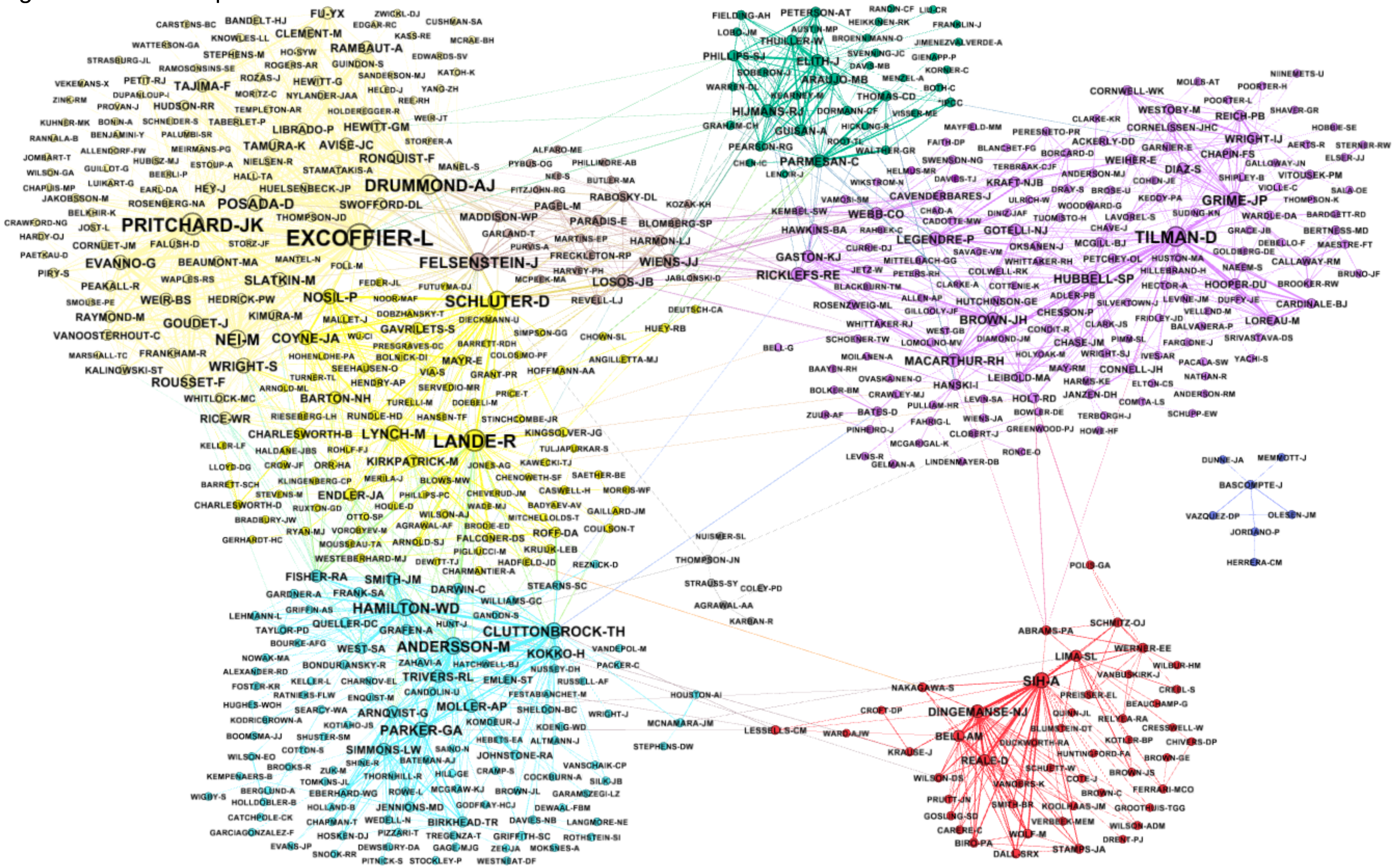


Fig. 8. Réale et al.: period 2010-14



Supplementary information

Table S1. List of the journals used to generate the co-citation networks, and the period of coverage for each journal.

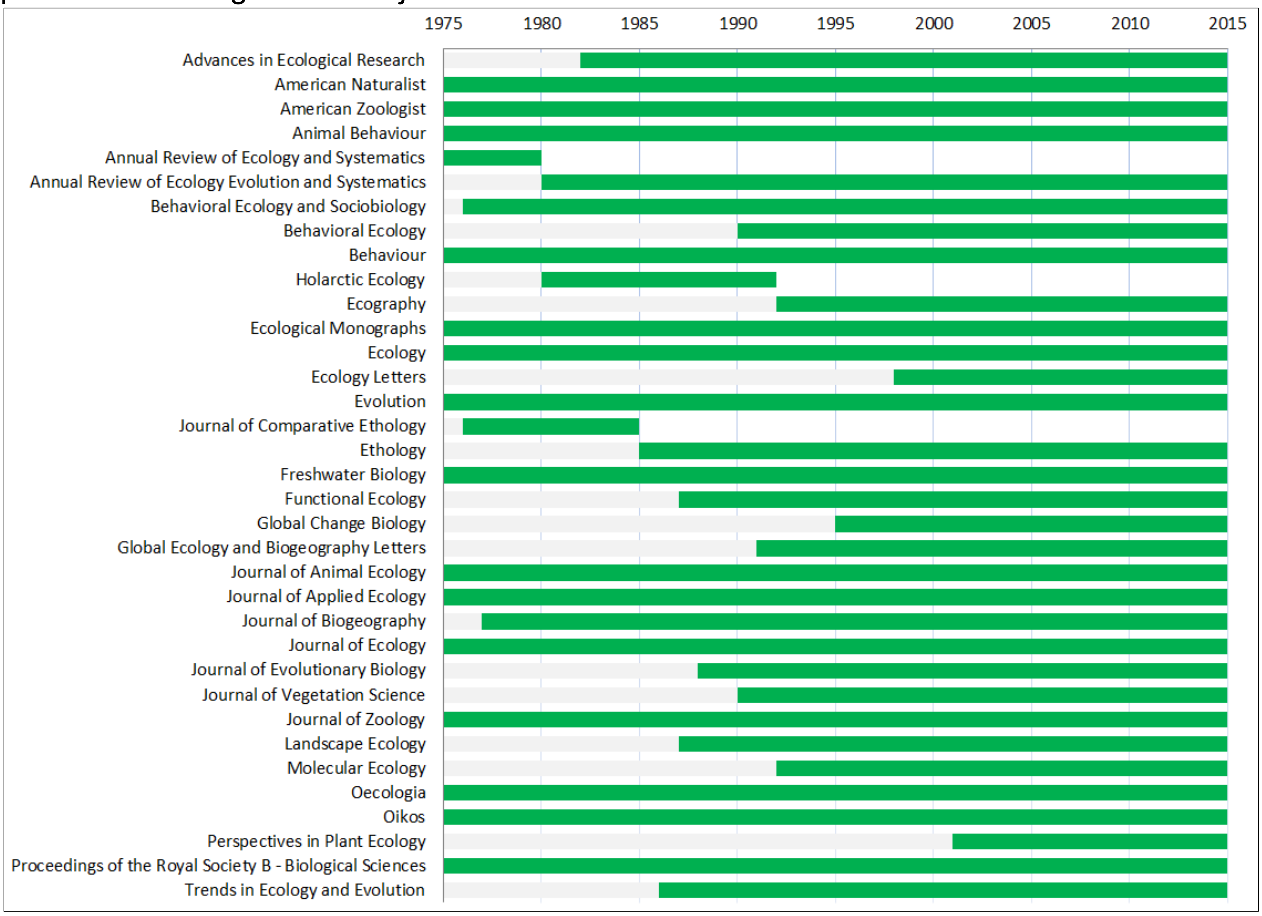


Table S2. Number of articles and references per 5-year period

Period	Number of articles	Number of references
1975-1979	7448	217,621
1980-1984	9999	311,253
1985-1989	11,399	400,199
1990-1994	13,135	498,834
1995-1999	18,415	764,399
2000-2004	22,008	1,046,803
2005-2009	26,439	1,386,571
2010-2014	29,131	1,679,795

Table S3. Proportion of nodes in each cluster (% of the total network).

Cluster	1975-79	1980-84	1985-89	1990-94	1995-99	2000-04	2005-09	2010-14
Purple	35.8	31.4	18.7	27.5	18.7	33.8	28.3	21.7
Turquoise	18.4	17.4	21.0	26	24.2	27.0	27.9	19.5
B. Yellow	12.1	9.3	13.8	14.4	13.3	12.1	15.3	13.2
L. Yellow	-	-	-	9.4	12.6	13.5	17.9	18.3
Red	-	13.3	10.6	6.8	5.6	5.9	6.4	8.2
Green	8.7	16.9	6.1	5.8	15.3	1.7	-	-
Pink	4.5	2.4	3.2	0.9	-	-	-	-
D. Blue	-	4.9	-	6.8	8.4	-	-	-
D. Green	-	-	-	-	-	-	3.5	6.3
L. Brown	-	-	-	-	-	-	-	4.6
Gray	10.3	-	-	-	-	-	-	-
Brown	2.9	2.9	1.5	-	-	-	-	-

Table S3. Proportion of internal links in each Cluster (% of the total network).

Cluster	1975-79	1980-84	1985-89	1990-94	1995-99	2000-04	2005-09	2010-14
Purple	35.9	32.0	20.3	23.2	16.9	30.5	22.0	18.2
Turquoise	14.4	15.0	16.1	25.3	20.5	19.3	21.7	14.7
B. Yellow	7.4	7.0	13.1	13.2	13.1	10.6	9.9	10.1
L. Yellow	-	-	-	7.3	11.3	18.8	30.2	25.7
Red	-	7.9	7.0	3.0	2.6	3.3	2.6	5.9
Green	4.3	8.5	3.6	2.5	8.1	0.5	-	-
Pink	1.5	0.6	1.5	0.3	-	-	-	-
D. Blue	-	2.2	-	4.8	5.4	-	-	-
D. Green	-	-	-	-	-	-	2.1	5.2
L. Brown	-	-	-	-	-	-	-	3.7
Gray	6.1	-	-	-	-	-	-	-
Brown	1.9	1.1	0.5	-	-	-	-	-

Table S5. Clusters with the most links in common (% of the total network)

1975-79		**1980-84**		**1985-89**		**1990-94**	
Cluster Pair	**% links**	**Cluster Pair**	**% links**	**Cluster Pair**	**% links**	**Cluster Pair**	**% links**
Purp – Turq	10.2	Purp – Red	4.3	Turq – B. Yel	5.4	Turq – B. Yel	5.8
Purp – Green	4.3	Purp – Green	3.3	Purp – Red	2.2	B. Yel – L. Yel	4.2
Purp – B. Yel	2.9	Purp – Turq	3.2	Turq – Red	2.1	Turq – D. Blue	1.9
Turq – B. Yel	2.7	Turq – B. Yel	3.1	Purp – Green	2.1	Purp – Green	1.0
Turq – Gray	2.7	Turq – Red	2.9	Purp – B. Yel	1.6	Purp – Red	1.0

1995-99		**2000-04**		**2005-09**		**2010-14**	
Cluster Pair	**% links**	**Cluster Pair**	**% links**	**Cluster Pair**	**% links**	**Cluster Pair**	**% links**
B. Yel – Turq	5.4	B. Yel – Turq	4.5	B. Yel – L. Yel	4.1	B. Yel – L. Yel	2.7
B. Yel – L. Yel	4.8	B. Yel – L. Yel	4.1	B. Yel – Turq	3.3	B. Yel – Turq	2.5
Purp – Green	2.1	B. Yel – Purp	1.2	Turq – L. Yel	1.2	L. Brow – L. Yel	1.6
D. Blue – Turq	1.9	Turq – L. Yel	0.9	Purp – B. Yel	1.0	L. Brow – Purp	1.5
Purp – Red	0.9	Purp – Red	0.9	Purp – Red	0.7	L. Brow – B. Yel	1.2

Table S6. Top-20 cited publications in each period

N	Publication (1975-1979)	Publication (1980-1984)	Publication (1985-1989)
1	SIEGEL-S NONPARAMETRIC STATIS 1956	SOKAL-RR BIOMETRY 1969	SOKAL-RR BIOMETRY 1981
2	SOKAL-RR BIOMETRY 1969	SIEGEL-S NONPARAMETRIC STATIS 1956	HARPER-JL POPULATION BIOL PLAN 1977
3	MACARTHUR-RH THEORY ISLAND BIOG 1967	HARPER-JL POPULATION BIOL PLAN 1977	SIEGEL-S NONPARAMETRIC STATIS 1956
4	MACARTHUR-RH GEOGRAPHICAL ECOL 1972	PYKE-GH Q REV BIOL 52 1977	TRIVERS-RL SEXUAL SELECTION DES 1972
5	LEVINS-R EVOLUTION CHANGING E 1968	MACARTHUR-RH THEORY ISLAND BIOG 1967	FALCONER-DS INTRO QUANTITATIVE G 1981
6	SCHOENER-TW ANN REV ECOL SYST 2 1971	MACARTHUR-RH GEOGRAPHICAL ECOL 1972	MACARTHUR-RH THEORY ISLAND BIOG 1967
7	TRIVERS-RL SEXUAL SELECTION DES 1972	TRIVERS-RL SEXUAL SELECTION DES 1972	ALTMANN-J BEHAVIOUR 49 1974
8	WILLIAMS-GC ADAPTATION NATURAL S 1966	STEARNS-SC QUART REV BIOL 51 1976	FISHER-RA GENETICAL THEORY NAT 1930
9	MAY-RM STABILITY COMPLEXITY 1973	SCHOENER-TW ANN REV ECOL SYST 2 1971	ZAR-JH BIOSTATISTICAL ANAL 1974
10	SNEDECOR-GW STATISTICAL METHODS 1967	SCHOENER-TW SCIENCE 185 1974	SCHOENER-TW AM NAT 122 1983
11	MAYR-E ANIMAL SPECIES EVOLU 1963	WILSON-EO SOCIOBIOLOGY NEW SYN 1975	SMITH-JM EVOLUTION THEORY GAM 1982
12	WILSON-EO SOCIOBIOLOGY NEW SYN 1975	LEVINS-R EVOLUTION CHANGING E 1968	THORNHILL-R EVOLUTION INSECT MAT 1983
13	LACK-D ECOLOGICAL ADAPTATIO 1968	FISHER-RA GENETICAL THEORY NAT 1930	EMLEN-ST SCIENCE 197 1977
14	FISHER-RA GENETICAL THEORY NAT 1930	SNEDECOR-GW STATISTICAL METHODS 1967	STEARNS-SC QUART REV BIOL 51 1976
15	PIANKA-ER AM NATURAL 104 1970	EMLEN-ST SCIENCE 197 1977	GRIME-JP PLANT STRATEGIES VEG 1979
16	WILSON-EO INSECT SOC 1971	WILLIAMS-GC ADAPTATION NATURAL S 1966	PYKE-GH Q REV BIOL 52 1977
17	CLAPHAM-AR FLORA BRIT ISLES 1962	WILLIAMS-GC SEX EVOLUTION 1975	CONNELL-JH AM NAT 122 1983
18	SCHOENER-TW SCIENCE 185 1974	HAMILTON-WD J THEORET BIOL 7 1964	LACK-D ECOLOGICAL ADAPTATIO 1968
19	HAMILTON-WD J THEORET BIOL 7 1964	ALTMANN-J BEHAVIOUR 49 1974	SOKAL-RR BIOMETRY 1981
20	SCHOENER-TW ECOLOGY 49 1968	CONNELL-JH SCIENCE 199 1978	HARPER-JL POPUL BIOL PLAN 1977

N	Publication (1990-1994)	Publication (1995-1999)	Publication (2000-2004)
1	SOKAL-RR BIOMETRY 1981	SOKAL-RR BIOMETRY 1981	SOKAL-RR BIOMETRY 1995
2	ZAR-JH BIOSTATISTICAL ANAL 1984	ZAR-JH BIOSTATISTICAL ANAL 1984	ZAR-JH BIOSTATISTICAL ANAL 1999/1996/1984
3	HARPER-JL POPULATION BIOL PLAN 1977	RICE-WR EVOLUTION 43 1989	RICE-WR EVOLUTION 43 1989
4	TRIVERS-RL SEXUAL SELECTION DES 1972	ANDERSSON-M SEXUAL SELECTION 1994	ANDERSSON-M SEXUAL SELECTION 1994
5	SAS USERS GUIDE STAT 1985	STEARNS-SC EVOLUTION LIFE HIST 1992	STEARNS-SC EVOLUTION LIFE HIST 1992
6	FISHER-RA GENETICAL THEORY NAT 1930	HARVEY-PH COMP METHOD EVOLUTIO 1991	RAYMOND-M J HERED 86 1995
7	STEPHENS-DW FORAGING THEORY 1986	TRIVERS-RL SEXUAL SELECTION DES 1972	WEIR-BS EVOLUTION 38 1984
8	SIEGEL-S NONPARAMETRIC STATIS 1956	FISHER-RA GENETICAL THEORY NAT 1930	ROFF-DA EVOLUTION LIFE HIST 1992
9	FALCONER-DS INTRO QUANTITATIVE G 1981	HARPER-JL POPULATION BIOL PLAN 1977	LIMA-SL CAN J ZOOL 68 1990
10	ALTMANN-J BEHAVIOUR 49 1974	GRIME-JP PLANT STRATEGIES VEG 1979	NEI-M MOL EVOLUTIONARY GEN 1987
11	EMLEN-ST SCIENCE 197 1977	LIMA-SL CAN J ZOOL 68 1990	HARVEY-PH COMP METHOD EVOLUTIO 1991
12	HAMILTON-WD J THEOR BIOL 7 1964	BIRKHEAD-TR SPERM COMPETITION BI 1992	EXCOFFIER-L GENETICS 131 1992
13	MACARTHUR-RH THEORY ISLAND BIOG 1967	ROFF-DA EVOLUTION LIFE HIST 1992	TRIVERS-RL SEXUAL SELECTION DES 1972
14	GRIME-JP PLANT STRATEGIES VEG 1979	HAMILTON-WD J THEOR BIOL 7 1964	FELSENSTEIN-J AM NAT 125 1985
15	DARWIN-C DESCENT MAN SELECTIO 1871	FELSENSTEIN-J AM NAT 125 1985	ROSENZWEIG-ML SPECIES DIVERSITY SP 1995
16	ENDLER-JA NATURAL SELECTION WI 1986	DARWIN-C DESCENT MAN SELECTIO 1871	FISHER-RA GENETICAL THEORY NAT 1930
17	THORNHILL-R EVOLUTION INSECT MAT 1983	EMLEN-ST SCIENCE 197 1977	MACARTHUR-RH THEORY ISLAND BIOG 1967
18	SMITH-JM EVOLUTION THEORY GAM 1982	FALCONER-DS INTRO QUANTITATIVE G 1989	HOLLDOBLER-B ANTS 1990
19	HURLBERT-SH ECOL MONOGR 54 1984	MACARTHUR-RH THEORY ISLAND BIOG 1967	HAMILTON-WD J THEOR BIOL 7 1964
20	RICE-WR EVOLUTION 43 1989	SOKAL-RR BIOMETRY 1981	HARPER-JL POPULATION BIOL PLAN 1977

N	Publication (2005-2009)	Publication (2010-2014)
1	SOKAL-RR BIOMETRY 1995	*RDEVCORTEAM R LANG ENV STAT COMP
2	ANDERSSON-M SEXUAL SELECTION 1994	BURNHAM-KP MODEL SELECTION MULT 2002
3	BURNHAM-KP MODEL SELECTION MULT 2002	PRITCHARD-JK GENETICS 155 2000
4	POSADA-D BIOINFORMATICS 14 1998	ANDERSSON-M SEXUAL SELECTION 1994
5	RAYMOND-M J HERED 86 1995	DRUMMOND-AJ BMC EVOL BIOL 7 2007
6	WEIR-BS EVOLUTION 38 1984	HIJMANS-RJ INT J CLIMATOL 25 2005
7	RICE-WR EVOLUTION 43 1989	EXCOFFIER-L EVOL BIOINFORM 1 2005
8	PRITCHARD-JK GENETICS 155 2000	EVANNO-G MOL ECOL 14 2005
9	STEARNS-SC EVOLUTION LIFE HIST 1992	COYNE-JA SPECIATION 2004
10	EXCOFFIER-L GENETICS 131 1992	RONQUIST-F BIOINFORMATICS 19 2003
11	ZAR-JH BIOSTATISTICAL ANAL 1999	STEARNS-SC EVOLUTION LIFE HIST 1992
12	FELSENSTEIN-J AM NAT 125 1985	HUBBELL-SP UNIFIED NEUTRAL THEO 2001
13	LEGENDRE-P NUMERICAL ECOLOGY 1998	HAMILTON-WD J THEOR BIOL 7 1964
14	TRIVERS-RL SEXUAL SELECTION DES 1972	LEGENDRE-P NUMERICAL ECOLOGY 1998
15	NEI-M MOL EVOLUTIONARY GEN 1987	WEIR-BS EVOLUTION 38 1984
16	CLEMENT-M MOL ECOL 9 2000	PARMESAN-C ANNU REV ECOL EVOL S 37 2006
17	COYNE-JA SPECIATION 2004	CRAWLEY-MJ R BOOK 2007
18	HUBBELL-SP UNIFIED NEUTRAL THEO 2001	FISHER-RA GENETICAL THEORY NAT 1930
19	FISHER-RA GENETICAL THEORY NAT 1930	RAYMOND-M J HERED 86 1995
20	HAMILTON-WD J THEOR BIOL 7 1964	PARMESAN-C NATURE 421 2003

Fig. S1. Period 1995-1999, including SOKAL-RR

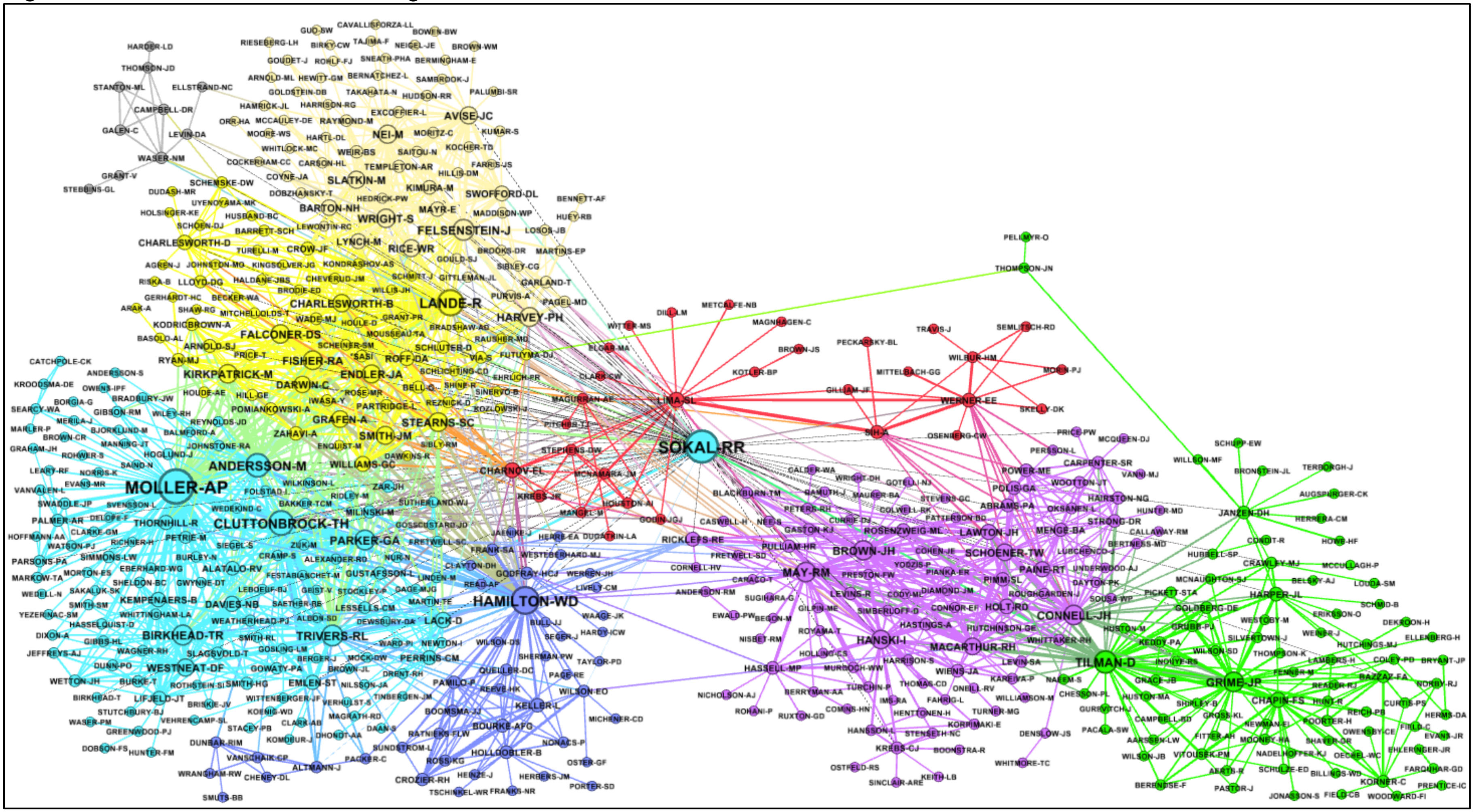


Fig. S2. Réale et al.: period 2010-14 including *RDEVCORTEAM

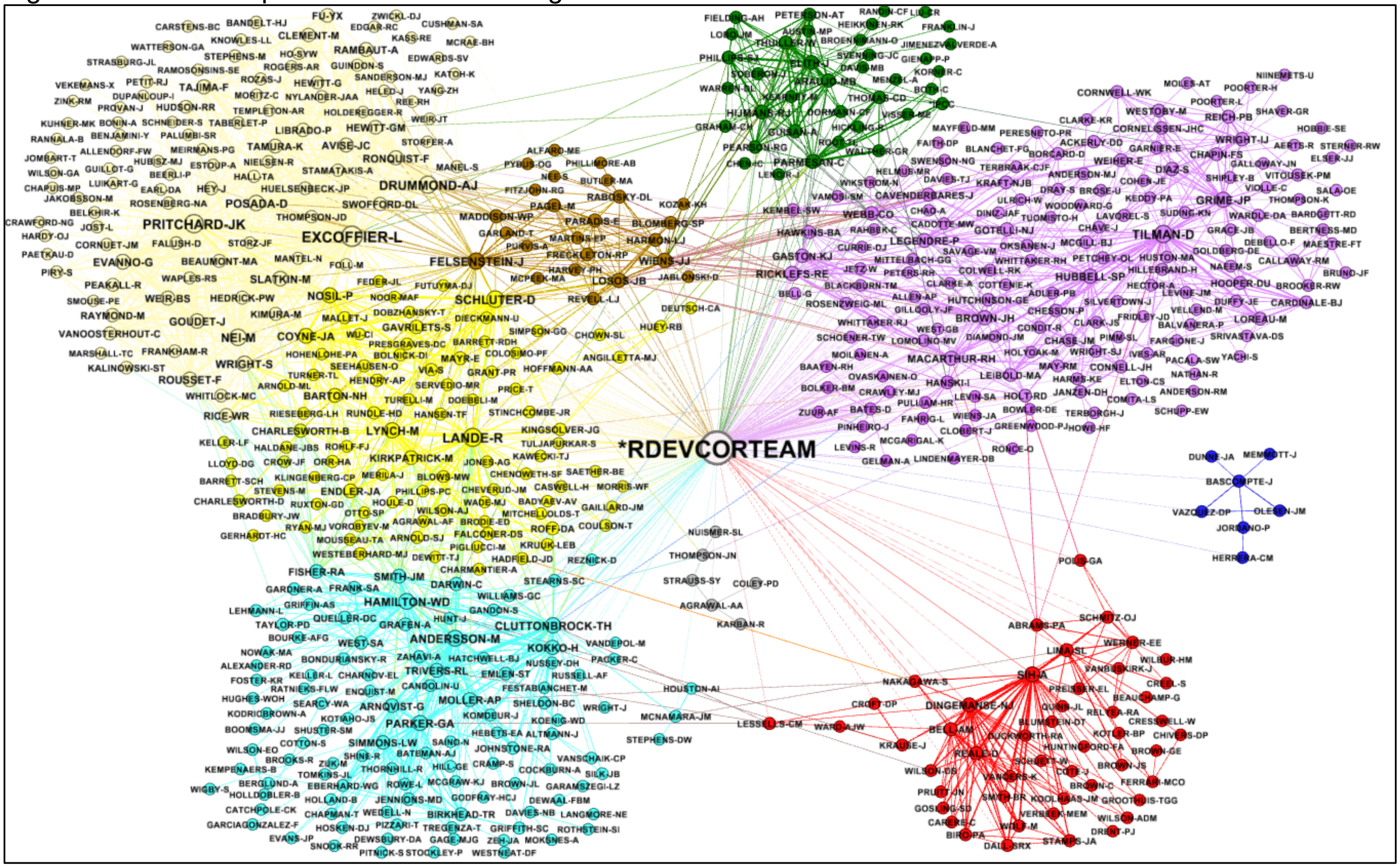


Fig. S3. Réale et al.: period 2010-14 including BURNHAM-KP