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A network approach reveals surprises about the history of the niche

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Abstract. The ecological niche is a prominent theoretical concept in many ecological fields, central to ecological understanding of species interactions and community structure. To better understand this important concept, and the impact it has had on ecology, we used a citation analysis to examine the history of the niche through citation patterns during the 20th century. In particular, we sought to document the spread of the niche across ecological subdisciplines, to evaluate whether the existence of different niche definitions facilitated the spread of the niche, and to see whether the conceptual integration stemming from adoption of the niche has also yielded an integration of the niche literature across subdisciplinary boundaries. We show that the ecological niche has been adopted by a number of subdisciplines, but that this success does not appear to have relied strongly on the different niche definitions, nor has it led to general integration of the niche literature across subdisciplinary boundaries. Our analysis thus not only examines the history of one of ecology's central concepts but also suggests that despite the conceptual unification that resulted from the broad adoption of the niche, a unified niche literature had not emerged by the close of the 20th century.

Key words: citation network; disciplinary integration; ecological niche; history of ecology.

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Introduction

The ecological niche is one of the key concepts in community ecology, central to our understanding of competitive exclusion (Grinnell and Storer 1924, Gause 1934, Hardin 1960), the trophic structure of communities (Elton 1927, Thompson et al. 2012), the relationship between organismal fitness and environmental conditions (Hutchinson 1957), and trait evolution (MacArthur and Levins 1967). Despite its fundamental status in ecology today, the niche did not appear in ecological literature until well after the development of ecology as a discipline. The term is widely reported to have first appeared in the ecological literature with Johnson (1910), who uses the term just once without an explicit definition to refer to environmental spaces, each of which is expected to be occupied by a different species. The first major development of a niche definition quickly followed in 1913 by Joseph Grinnell and colleagues (e.g., Grinnell and Swarth 1913, Chandler 1914, Grinnell 1914, 1917, Taylor 1916), who effectively defined the niche as an ecological opportunity in the community that was sufficient for just one species.

As ecology matured over the course of the 20th century, a number of niche definitions joined that of Grinnell et al., notably those of Elton (1927) and Hutchinson (1957) (Box 1). Elton proposed a niche concept that was focused on demonstrating similarities in the structures of different

Box 1. The niche definitions of Grinnell, Elton, and Hutchinson

Over the course of its history, a number of different definitions of the niche have been proposed. Here, we summarize the definitions of Joseph Grinnell, Charles Elton, and G.E. Hutchinson.

Grinnell's niche: At its core, the Grinnellian niche describes an ecological opportunity of sufficient breadth to support one, and only one, species (Grinnell and Swarth 1913, Grinnell 1914). Grinnell spent much of his professional life attached to the museum of Vertebrate Zoology at Berkeley (Hutchinson 1978), and his publications were often focused on species distributions and community composition. Grinnell's niche was embedded in a complex system for classifying species distributions (Grinnell and Swarth 1913), and importantly, much of the influence of environmental conditions was dealt with in other levels of this framework (e.g., the life zone and fauna), leaving the niche free for the consideration of interactions between species. Consequently, many of Grinnell's observations about niches dealt with ecologically similar species that were not found in sympatry, or noted that no two-species with identical niches could be established together (e.g., Grinnell 1914, 1917), which Grinnell occasionally explicitly attributed to competitive exclusion (e.g., Grinnell and Storer 1924). While Grinnell invoked the niche to explain differences in community biodiversity and population abundance (Grinnell 1922), the Grinnellian niche primarily served to mark the taxonomic differences in ecologically similar associations by tracking the different species that occupied each opportunity-space in each community.

Elton's niche: If Grinnell's niche was defined by the opportunities available in a community, Elton's niche was more focused on the role of a species in its community. Indeed, Elton (1927) went so far as to explicitly invoke socioeconomic parallels to the niche, famously suggesting that one should think of a badger as having a role in its community just as vicars have a role in human communities. In particular, Elton's original uses of the niche were strongly focused on the trophic roles of species and were coupled with a bioenergetics focus that had important consequences for trophic ecology. Perhaps, because of this trophic focus, Elton's niche was less explicitly focused on competition than Grinnell had been, though Elton and Miller (1954) noted that the niche inherently served as the expected boundaries for competition. While much has been made of the difference in emphasis on impacts and requirements in the niches of Grinnell and Elton, both authors devoted at least some consideration to impacts and requirements. Despite these similarities, the differences in emphasis and the consequences of these emphases are striking: because Grinnell's discussions of niches largely presumed similar environmental conditions and communities, the spatial scale at which Grinnell considered niches was generally modest. Conversely, Elton's definition made fewer assumptions about the environment in which species were found and as such had a much broader spatial scale (e.g., one could be a predator in an ocean or in a grassland). Consequently, while Grinnell's niche lent itself to accentuating the taxonomic differences between similar communities, Elton's niche lent itself more to demonstrating the functional similarity of communities that were potentially very distinct taxonomically.

Hutchinson's niche: Hutchinson's niche existed in two forms: the fundamental niche, which represented the (multidimensional) environmental conditions in which a population could exist in the absence of ecological interactions, and the realized niche, which represented the conditions in which a population could exist in the presence of ecological interactions (Hutchinson 1957). As such, Hutchinson's niche was focused on the relationship between the environment and a population's fitness, and, unlike the niches of Grinnell or Elton, was quantifiable. A number of reviewers have noted that Hutchinson's niche in many ways echoed the Grinnellian niche's emphasis on habitat requirements (Leibold 1995), or that the two differed in that Hutchinson's niche was unambiguously a property of the organism, and not the community (Colwell 1992), but it is also worth pointing out that while Grinnell envisioned niches that had definite existence in the world, Hutchinson's niche existed in abstract environmental space that might, or might not, be represented in the actual environment (Holt 2009, Godsoe 2010).

communities in terms of the functional roles that the constituent species played. In contrast to the niches of Grinnell and Elton, Hutchinson's niche was less a property of the community than it was a property of a population (Colwell 1992, Griesemer 1992, Colwell and Rangel 2009), and it developed a formal relationship between an organism's fitness and environmental conditions.

Despite the apparent differences in the niches of Grinnell, Elton, and Hutchinson, the three definitions share the fundamental goal of providing a theoretical framework for the relationship between organisms and their environments. Each author highlighted different aspects of ecology in their definition, but all three shared the view that organisms relate to the environment differently and that a theoretical framework for organism-environment relations was essential to understanding ecological communities. The synthesis of these three definitions has led many contemporary ecologists to consider the niche to represent both a species' requirements of its environment and its impacts on the environment (Leibold 1995), resulting in a synthetic niche concept that describes not only where a given population can persist but also how other organisms in the community will be affected by it (e.g., Odling-Smee et al. 2003, Holt 2009).

Given the theoretical importance of the niche, it might not seem surprising that the concept has been adopted by many branches of ecology. Yet during the initial period of the niche's development, ecology was a strongly divided science, and its different streams such as plant ecology, limnology, and animal ecology had developed relatively independently of one another (Egerton 1976), with authors tending to focus their research on either animals or plants, but rarely both (Jax and Schwarz 2011). Grinnell and his colleagues were zoologists, and Elton an animal ecologist, and as a consequence, the ecological niche entered the world through the publications of animal researchers in an era when plant ecology was more developed (Shelford 1913). Given the disciplinary history of the niche, and its central role in ecology today, we wanted to examine how the niche spread in ecology and to investigate whether the conceptual integration that resulted from its broad adoption across ecology might be evident in citation patterns. Consequently, we performed a citation network analysis with the following goals:

(1). To map the historical spread of the niche in the ecological literature: when did new subdisciplines adopt the niche, and in what relation to its use in other subdisciplines?
(2). To determine what role the different niche definitions have played in the spread of the niche concept: how have different subdisciplines employed the different niche definitions, and is it possible that the existence of multiple definitions has aided the spread of the concept by providing variations that appealed to different research communities?
(3). To assess whether the development of the niche framework in ecology has led to an integrated body of literature (i.e., one in which citations between subdisciplines are as frequent as might be expected due to chance): has the adoption of a common conceptual framework been mirrored in the citation patterns of ecologists?

Materials and Methods

Citation network construction

To assess these questions, we searched the Web of Science (Web of Science Core Collection) for papers with the topic search term "niche*" published between 1900 and 1999, with data collection running from 18 June 2013 to 30 August 2013. Web of science topic searches return results that include the search term in the title, abstract, keywords, or Keywords Plus fields, but do not perform full-text searches, and as such should be regarded as a highly conservative estimate of the actual circulation of the niche in the ecological literature. As this search returned many results for the niche that used it in a nonecological sense, we made the decision to exclude these, including or excluding references based on their titles, and when titles were ambiguous by using other available information, including the keywords, the abstract, and the source publication. None of the papers that played an important role in defining the niche were returned by our search: Grinnell (1917) and Elton's textbook (Elton 1927) were not found in the Web of Science core collection, and neither Elton (1927) nor Hutchinson (1957) used "niche" in their title, nor did they provide

an abstract or keywords. Consequently, to address our questions, we manually added these records to the search results (with data collection on 24 February 2014) and refer to them hereafter as "key definitions." We constructed a network based on the citations between these records and used this network to evaluate our questions about the nature of the niche's spread, the importance of the three niche definitions, and the integrated nature of the ecological literature. Selection of relevant records was done in the Web of Science interface, and all subsequent manipulation, and analysis of records was done in R version 3.0.2 (R Core Team 2013) using the packages bibtex version 0.3-6 (Francois 2013), and igraph version 0.6.5-2 (Csardi and Nepusz 2006) (detailed methods in Appendix A).

Citation network analysis

To address our questions about the effects of the niche on the disciplinary structure of ecology, it was necessary to assign a subdiscipline to each record in our network, which we did by defining the target audience of the record (Ecological Archives, Supplement 1). Records without an associated journal (e.g., proceedings papers) were classified based on the associated book title, conference title, or the publication series if appropriate. Records published in journals were classified based on the title of the journal, and, if necessary, by using descriptions of the journal. For example, papers from *Canadian Journal of Zoology* were assumed to be directed at other zoologists and were sorted into the "Animal Science" subdiscipline, whereas those published in *Ecology*, which publishes on many aspects of ecology, were sorted into the "General ecology" subdiscipline.

To assess the relationship between the different niche definitions and the uptake of the niche by subdisciplines, we compared the identities of the subdisciplines citing each key definition and also analyzed whether citation of a given definition was subdiscipline dependent for the eight subdisciplines that cited all three definitions using a χ^2 test. We also examined the in-degree centrality of the different papers in our network, a measure of the importance of a paper determined by the number of citations it has received. To assess hypotheses about the integration of subdisciplines, we focused on the linkages between seven subdisciplines that played important roles in the formation of ecology (Egerton 1976): "Animal research" (a combination of the animal ecology and animal science subdisciplines), "plant research" (a combination of the plant ecology and plant science subdisciplines), limnology and oceanography, medicine, general ecology, agronomy, and conservation.

We used randomization (Quinn and Keough 2002) to test hypotheses about the integration of different subdisciplines, generally by retaining as much of the network structure as possible while randomizing the destination of citations. A detailed list of the null models and randomization methods used is available in Appendix B.

Results

The disciplinary spread of the niche

Our final dataset included 3687 records and demonstrated that the niche spread from early records in animal science and animal ecology into 41 subdisciplines over the course of the 20th century (including one record for which the subdiscipline was classified as "Other") (Fig. 1). For some of our subdisciplines, the niche remained a marginal concept, only returning a few records, but for the majority of our subdisciplines, it has clearly found acceptance, with 31 of the subdisciplines having more than 10 records and 18 subdisciplines having more than 50 (Table 1). The rate at which subdisciplines began using the niche was greatest in the 1970s–1980s (Fig. 1, Table 1), with 19 subdisciplines added in the years 1970–1979. The decade 1970–1979 was also the period at which the network was at its most cohesive, with the fewest number of network subcomponents scaled by the total number of vertices (Appendix C: Fig. C1), and half of the top 1% of papers in terms of citations received were published in the decade. In contrast to the rate at which subdisciplines adopted the niche, the number of records on the niche, the number of citations in the niche network, and the number of journals invoking the niche all had their greatest rates of increase in the 1990s (Fig. 1). Interestingly, most disciplines appeared in the niche citation network without reference to other

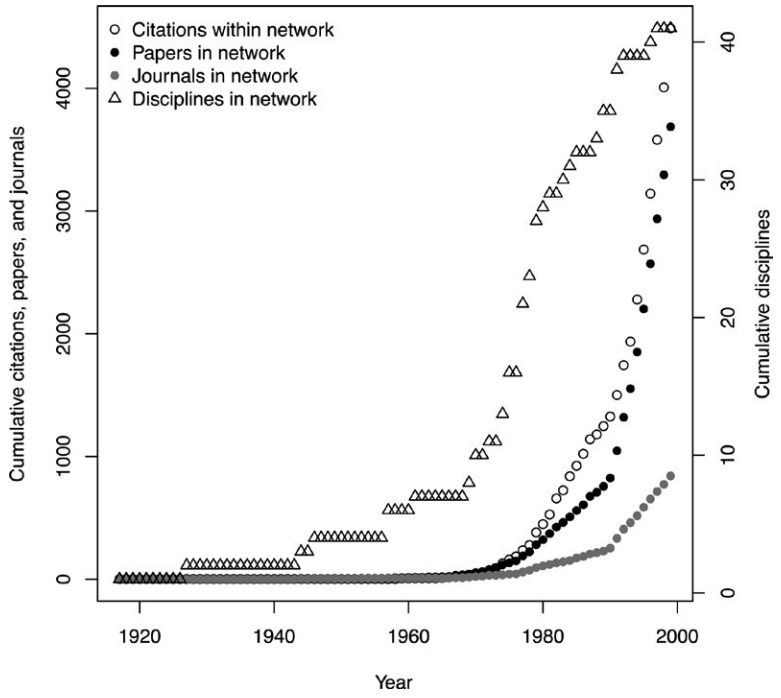

Fig. 1. Cumulative counts of citations, papers, journals, and disciplines within the network from 1917 to 1999.

papers in the network: in only 10 of our 41 subdisciplines did a paper published in the subdiscipline's first year cite another paper in the network. This tendency for disciplines to enter the network independently of papers already in the network was broadly paralleled by the overall structure of the network, where citations between papers were relatively rare and concentrated. There were a total of 4489 citations in the network, with individual papers giving as many as 21 citations and receiving as many as 201, but 0 was the median value for both citations to and from other papers in the network.

The impact of multiple niche definitions

We found little evidence that the number of niche definitions was important to the adoption of the niche by different subdisciplines. All three of the key definitions we included were within the top 1% of papers in terms of citations received, but Hutchinson (1957) received far more citations than the other two key definitions (Fig. 2)—indeed, Hutchinson (1957) was the most cited record in the entire network, surpassing its nearest competitor by 39 citations (Appendix C: Fig. C2).

A core of eight subdisciplines cited all three of our key definitions, and a number of disciplines cited two, one, or no definitions (Appendix C: Fig. C3, Table C1), but, key to our question about the effect of multiple definitions, all subdisciplines that cited a definition cited Hutchinson (1957), and none of the citations to Grinnell (1917) nor Elton (1927) in our network predate 1957. Furthermore, there was no significant relationship between the key definitions and the eight subdisciplines that cited all three definitions in terms of citation patterns ($\chi^2 = 14.26$, df = 14, $P = 0.43$).

The integration of the niche within ecological literature

Our results suggest that subdisciplines in the niche network were not generally strongly integrated with one another. There was marked heterogeneity in the number and identity of subdisciplines that each subdiscipline cited, and was cited by (Fig. 3). When we examined the number of citations in both directions between animal research, agronomy, limnology and oceanography,

Table 1. The number of papers and year of network entry for each subdiscipline in the network.

Subdiscipline	Paper count	Entry year
General ecology	639	1944
Animal science	551	1917
Limnology and oceanography	321	1961
Plant science	306	1974
Medicine	164	1970
Microbiology	149	1977
Evolutionary biology	138	1957
Entomology	135	1975
General biology	131	1970
Conservation	109	1969
Agronomy	108	1975
General science	103	1946
Theoretical biology	89	1957
Paleobiology	70	1978
Terrestrial ecosystems	62	1979
Animal ecology	55	1927
Parasitology	54	1983
Cell biology	52	1977
Anthropology	47	1972
Environmental science	47	1977
Primatology	42	1974
Geology	40	1979
Plant ecology	38	1977
Behavioral ecology	37	1977
Forestry	34	1988
Engineering	26	1979
Biogeography	25	1984
Microbial ecology	20	1985
Biotechnology	17	1992
Human ecology	14	1975
Veterinary science	14	1981
Scientific philosophy	9	1980
Education	7	1979
Climate change	7	1996
Interdisciplinary	6	1989
Landscape ecology	6	1989
Computer science	6	1991
Geography	5	1978
Law	2	1997
Economics	1	1991
Other	1	1991

medicine, plant research, general ecology, and conservation in the niche network, we found that the majority of interconnections between these subdisciplines were represented by significantly fewer citations than would be expected by chance (Table 2). For example, while the null expectation for connections between animal and plant research was roughly 153 citations, our network only had

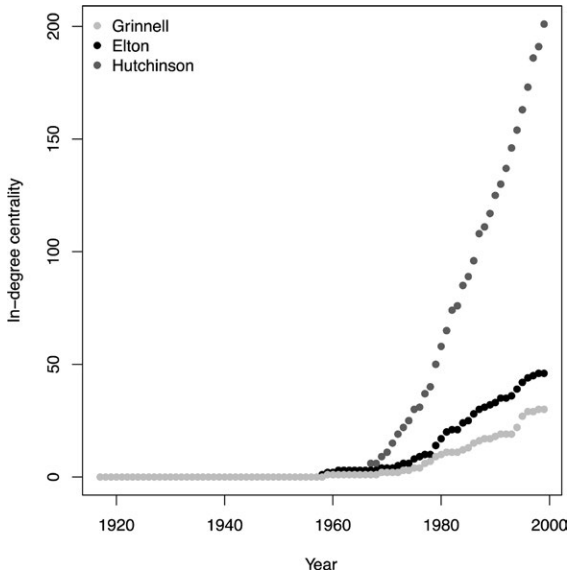

Fig. 2. The in-degree centrality of each key definition through time from 1917 to 1999.

11 (Appendix C: Fig. C4). In only one case, the link between animal research and general ecology was the connectivity between subdisciplines significantly stronger than the null expectation. Despite this underconnected network, there appeared to be a trend toward increasing citations between the animal and plant research subdisciplines toward the end of the 20th century, so we evaluated the citation patterns of records published from 1990 to 1999, but found only one change in the patterns of interconnections between subdisciplines from the whole network results: the connections between general ecology and conservation became significantly stronger than expected (Appendix C: Table C2). Whereas interconnections between subdisciplines revealed a trend toward less linkage than expected from a null model, citations within subdisciplines were either within the null expectation or significantly greater than expected by chance (Table 2; Appendix C: Table C2).

Discussion

The first goal of our paper was to document the spread of the ecological niche from animal researchers to other ecological subdisciplines and in particular to plant research. Perhaps not surprisingly, the first subdisciplines to take up

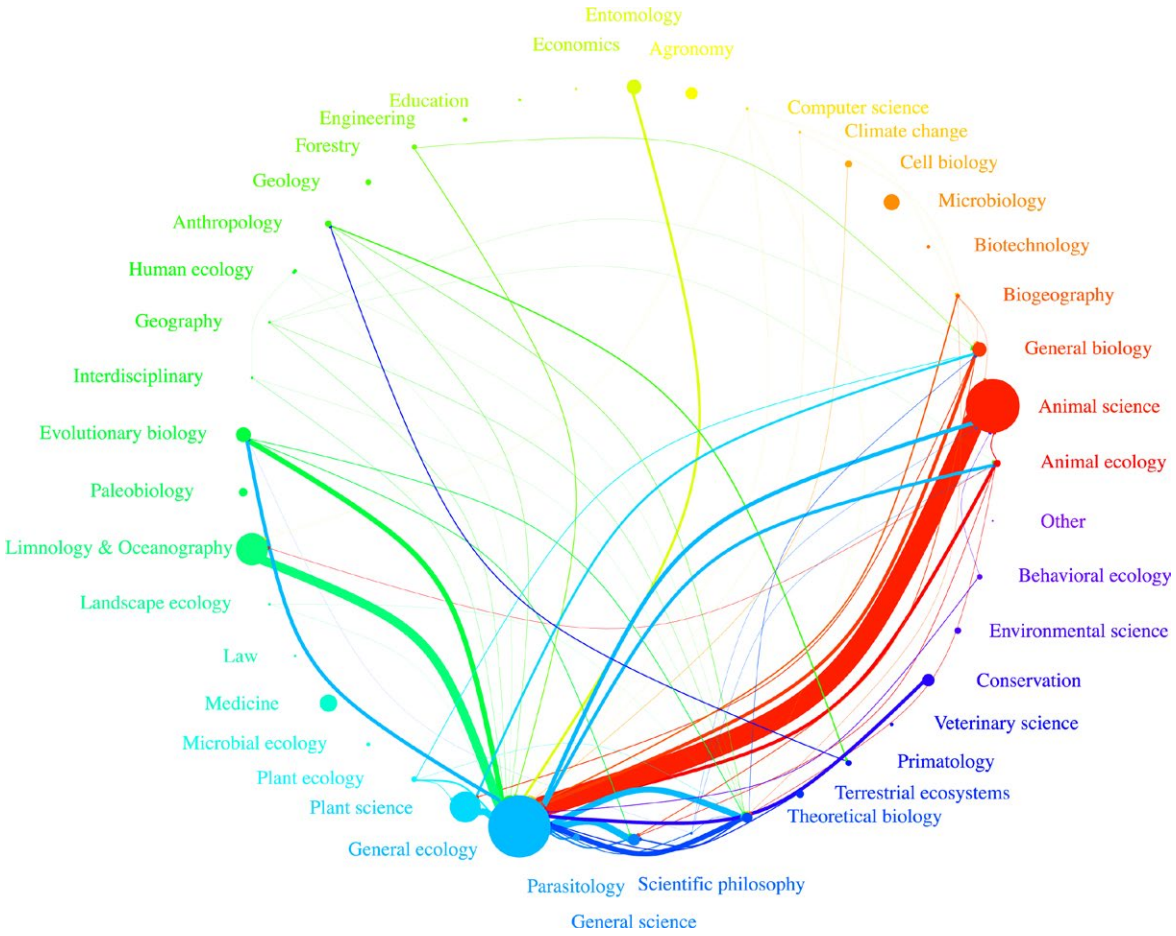

Fig. 3. A simplified representation of interdisciplinary niche network structure. The complete network has been simplified by the removal of weak links between subdisciplines (where the number of citations from one discipline to another is less than the total number of papers in the citing subdiscipline divided by 10). The sizes of vertices are scaled to the number of papers in each subdiscipline, and the width of the connecting lines is scaled to the number of citations issued from the citing subdiscipline to the recipient discipline. The vertices are color coded by their subdiscipline, and the links between them are color coded by the citing subdiscipline.

the niche in our network as it left animal research were the general ecology and general science subdisciplines, in papers concerning the ecology of animals. Subsequent spread followed in a number of subdisciplines that either had potentially broad taxonomic focus (e.g., evolutionary biology, theoretical biology, limnology and oceanography, conservation, general biology) or obvious associations with animal research (e.g., medicine, anthropology). The first plant research paper in our network appeared in 1974, but despite the relatively late adoption of the niche, combined plant research was the third subdiscipline in terms of records by the end of the 20th century, surpassing many subdisciplines that had preceded it in the network. The niche has clearly become an important concept for ecological researchers working with a variety of taxonomic groups and in a variety of ecosystems.

Despite our expectation that the existence of multiple niche definitions would play a role in attracting subdisciplines to the niche concept, this does not appear to have been the case: relative citation of the different niche definitions was not subdiscipline dependent for the subdisciplines that cited all three definitions, and only Hutchinson's definition had subdiscipline citations

Table 2. Comparison of realized and expected citations between the animal research (AR), agronomy, limnology and oceanography (L & O), medicine, plant research (PR), general ecology (GE), and conservation subdisciplines.

	AR	Agronomy	L & O	Medicine	PR	GE	Conservation
AR	†						
Agronomy	‡	†					
L & O	‡	†	*				
Medicine	‡	†	‡	†			
PR	‡	‡	‡	‡	*		
GE	*	‡	†	‡	†	*	
Conservation	†	†	‡	†	‡	†	*

* The observed citations were significantly higher than the null expectation.
‡ The observed citations were not significantly different from the null expectation.
† The realized citations were significantly less than the null expectation. Significance was determined after Holm correction for all tests in the table (Holm 1979) at $\alpha = 0.05$, n = 5000 randomizations for each cell. Raw P-values are available in Table C3.

unique to itself. Altogether these results suggest that only Hutchinson's niche has been truly essential for the disciplinary success of the niche, potentially because his definition was the most general, and possibly also because his definition was, in some ways, the most accessible. Grinnell's niche, while typically understood today as representing the environmental necessities of a species, was actually embedded in a sophisticated system for categorizing the distributions of both species and species assemblages that owed much to C. Hart Merriam (Merriam 1890, 1899, Wake et al. 2009) and classification systems used then in botany (Grinnell and Swarth 1913), which may have proved to be a barrier to ecologists not fluent in this work. Elton's niche, on the other hand, while descriptively simple, was initially communicated in a strongly animal-centric context, which may have dissuaded researchers not interested in animals (Hutchinson 1978). Furthermore, both Grinnell (1917) and Elton (1927) were explicitly targeted at researchers who worked with animals. Hutchinson's niche, while mathematically complex, was extremely general in its formulation and was published in a venue that had no taxonomic focus, and Hutchinson produced publications over his career that bridged the traditional animal-plant and terrestrial-aquatic divides (Hutchinson 1951, 1959, 1961). Of course, while Hutchinson's definition was wildly successful in terms of citations received from both papers and subdisciplines, part of its success may also be attributed to the fact that the niche was already a well-established concept by the time Hutchinson's definition was introduced.

It is worth noting that none of our key definitions cited each other, and the influence of the niche definitions on each other has a bit of a notorious history: Elton (1927) both cited and praised Grinnell and Storer (1924), which dealt with the niche, but insisted that his niche was developed independently of Grinnell's (Elton and Miller 1954), and Hutchinson, while a great admirer of Grinnell (Hutchinson 1978), and aware of Elton (1927) (e.g., Hutchinson 1951), cited neither when crafting his own definition. While these omissions have attracted attention from reviewers of the niche (Colwell and Rangel 2009), they do fit into the trend where the vast majority of the papers (and some subdisciplines) in our network did not cite a niche definition. The traditionally accepted initial use of the term by Johnson (1910) without an explicit definition suggests that the term would have been easily grasped by readers, and consequently, it is possible that later authors also felt that the term was intuitive, rather than novel, or possibly in such broad circulation that it needed no definition or external reference (Hutchinson 1978). Warming (1909), for example, used the niche (in translation) in a hybrid sense, retaining its nonecological meaning of a nook or cranny, but specifically referring to a cranny in the abstract space of nature.

We also showed that the years 1970–1979 formed a remarkable decade for the niche. During this period the rate of new subdisciplines adopting the niche was greatest, the cohesiveness of the network was at its peak, and it also was when the majority of well-cited papers in our network were published. This decade also coincided with

a turning point with respect to attitudes about competition, generality, and theory in ecology (Kingsland 1985, Cooper 2003, Slack 2010), which may have heralded an end to the greatest success of broad conceptual devices like the niche, which was strongly linked to competition by both Grinnell (Grinnell and Storer 1924) and Hutchinson (1957), and to some extent by Elton (Elton 1946, Elton and Miller 1954) also. After this period, as ecology moved into a phase of increasing interest in historical contingency and skepticism about the role of competition (e.g., Connor and Simberloff 1986), the rate at which new subdisciplines joined the network slowed down, and the network became more fragmented, despite the fact that the number of papers, journals, and citations in the network continued to grow exponentially.

Our analysis dealt with a network that was, by definition, conceptually integrated in that all the records included had a strong emphasis on the ecological niche. Given this conceptual unity, it is surprising that our analysis revealed a network that shows relatively little integration among the different subdisciplines that constitute it, specifically in terms of links between the animal research, agronomy, limnology, medicine, plant research, general ecology, and conservation subdisciplines. Such fragmentation may represent a limited potential for researchers to glean insights from other subdisciplines (e.g., if a lack of citation of inter-subdisciplinary research is reflective of a lack of consumption of the same) and makes the search for general principles more challenging (e.g., by limiting discussion of the differences or similarities between subdisciplines).

As with any study that attempts to ask broad questions about the literature, our analysis comes with a set of provisos and caveats. Our original search did not return any of our key definitions, a symptom of the way in which our search returned only a limited fraction of the papers published that address the ecological niche. Instead, the results returned were restricted to those papers in the Web of Science core collection that focused sufficiently on niche research to have "niche" in the title, keywords, Keywords Plus, or abstract. An obvious consequence of these limited results is that we have had to form conclusions based on a small subset of the total ecological literature invoking the niche, and as a result, there are potentially gaps in the network that obscured the transmission of the niche concept. On the other hand, by using only papers that were strongly focused on the niche, our dataset forms a more conservative estimate of conceptual unification, and thus, our expectation of a unified literary network was strong.

A number of decisions were made in preparing the data set: we had to decide which records used the niche in an ecologic sense, and we had to estimate the target audience of different publications, all while assuming that the subdiscipline of the paper was the same as that of its publication. The selection of relevant papers was usually straightforward, and given the strength of our trends, we doubt that any mistakes made are likely to have had strong effects on our results. The classification of subdisciplines was more complex, but we feel confident with our assignments, especially given the tendency for strong intradisciplinary citation. Of course, publications are unlikely to be exclusively read by one discipline, or publish exclusively on just one discipline's work, but authors do select publications for the audience they believe that the publication will reach, and publications select papers with the same consideration in mind. Consequently, we felt that classification based on publication source was a reasonable proxy for the subdiscipline of each of our records.

Our decision to limit our network to the 20th century has a number of consequences, in particular that later papers in the network had less time to accumulate citations. While it is possible that this could account for the remarkable success of papers from the 1970s, we do not believe this to be an artifact. Citation and paper count per year increased through time, such that the number of citations issued by 1999 papers, and the number of papers from 1999, accounted for over 10% of the total citations and papers, respectively. Given these numbers, almost any of the 2930 papers from the 1990s could have easily entered the top 1% of cited papers, but instead only two papers did. Indeed, when looking at how citations from papers published in 1999 were apportioned, while the majority went to papers from the 1990s, papers from the 1970s did better at attracting citations than those from the 1990s on a per paper basis. Our final caveat deals with the key definitions of the niche. While the Grinnellian, Eltonian, and Hutchinsonian niches were certainly the most important in terms of the development of the niche

concept (Wake et al. 2009), choosing a paper to represent them was somewhat subjective. We chose the paper for which their definitions are best known, but in all three cases, the authors had discussed niches in earlier papers (e.g., Grinnell and Swarth 1913, Elton 1924, Hutchinson 1944). These earlier papers were probably most problematic for Grinnell, who often discussed and employed the ecologic niche at greater length in lesser known papers than Grinnell (1917), especially Grinnell and Swarth (1913).

A number of questions about the niche's role in structuring ecology remain. While we have documented the spread of the niche, how the word was chosen by a number of prominent ecologists to represent a central concept in their discipline remains unclear. Cox (1980) has shown that the word was being used to refer to animal living spaces in English as early as the 18th century, and indeed the word has Latin roots that indicate a space for life. Still, a number of obvious competitors exist, for example *la station*, as used by de Candolle (1820). How the niche, a concept pioneered in animal ecology during a time of dominance by plant ecologists, spread so readily and came to be so important remains to be addressed, though Kingsland (1985) has noted that the transfer of concepts from animal to plant research in the 1960s played an important role in stimulating the latter. Our analysis also revealed a number of records using "niche" in a nonecological context that none the less retained an implicit emphasis on competition, and an in-depth semantic study of the word would no doubt be fascinating. We limited our analysis of the niche network to papers from the 20th century to highlight the era in which the niche was emerging, and to restrict the amount of data to what was manageable, but given the trend toward more citation between animal and plant research at the end of our data set it would be interesting to see whether current niche literature is more integrated. The timespan of our network also omits a number of subsequent developments in niche theory, such as Chesson (2000) and Hubbell (2001), and the question of how developments in theory after 1999 will affect the integration of niche literature remains unanswered. The question also remains of what factors maintained the lack of integration we observed in the 20th century literature despite conceptual unification. It is possible that, despite a common conceptual background, practical differences caused by taxonomy were sufficient to maintain the separation (e.g., Daubenmire 1968), or it could be that the niche was actually used in subtly different fashions in different subdisciplines or indeed that adherence to the concept was only marginal in some subdisciplines.

Ultimately, our research suggests that while ecology experienced increasing conceptual unification during the 20th century as many subdisciplines adopted the niche, the niche literature remained fragmented. Even from its earliest stages ecology has struggled with the extent to which it represented one or many disciplines (Kingsland 2005), and our analysis suggests that the emergence of a truly integrated discipline may be yet to come. Still, the niche has undeniably furnished a concept around which many of ecology's central questions have been organized, and the use of the niche continued to expand exponentially into the 21st century. Whether the niche has entered a codified space, as might be suggested by the centrality of papers from the 1970s in our network, or whether new innovations and definitions have the potential to radically alter the niche's form and use remains to be seen.

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Literature Cited

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