Trends in ecology: shifts in ecological research themes over the past four decades

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As ecology enters a critical era, more comprehensive studies are needed to improve our understanding of the key themes, major trends, and potential gaps within the discipline. However, as the number of published scientific papers continues to grow, tracking the ever-expanding body of work becomes increasingly challenging. To identify trends in ecological research, we used recently developed machine learning techniques to perform an automated content analysis on over 84,841 articles published in 33 top-ranked scientific journals over the past four decades. We detected a clear decline in the relative frequency of classical theoretical research, and increases in data-intensive research at both micro- and macroscales and on anthropogenic themes. Scattered around the periphery of the expanding thematic space, themes such as microbial ecology, genetics, biogeochemistry, and management and policy have all increased in relative frequency. New educational and research frameworks, as well as funding priorities, should incorporate these contemporary themes so that the field of ecology can better address societal challenges.

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Ecology has grown dramatically as a discipline over the past 100 years from a subdiscipline of biology into its own discipline with many subdisciplines (Kingsland 2005; Ayres 2012). The goal of ecology is to understand the relationships between organisms and their environment, and to use these relationships to help address various complex and challenging environmental problems (Figure 1). As with any expanding scientific field, ecology has evolved from a focus on a central set of core principles into multiple lines of subdiscipline-specific inquiry, resulting in a flourishing of ecological literature (WebFigure 1). Ecologists have periodically assessed the important concepts (Cherrett 1989; Reiners *et al.* 2017), questions (Sutherland *et al.* 2013), and themes (Thompson *et al.* 2001) in ecology to understand the trajectory of the field and to evaluate the societal relevance of the discipline. Comprehensive assessments provide an overview of the intellectual structure of the field, present a framework for pedagogical development and curriculum design, offer guidance for new research directions, and can sometimes help identify paradigm shifts in the science.

In a nutshell:

- Ecology has experienced rapid growth over the past four decades, propelled largely by advancements in technology, availability of big data, and a new awareness of the connections between human and natural systems
- By analyzing a large body of ecological literature, we show that ecology has expanded beyond classical-, plant-, and population-oriented themes to cover anthropogenic and more contemporary, data-rich, micro- and macroscale themes
- The increased availability of complex data and advances in technological and analytical capabilities have expanded ecology from a classical theoretical discipline to a data-driven, multidisciplinary science focused on applying ecological knowledge to real-world problems

Previous attempts to determine and define these key concepts, questions, and themes have relied on tools such as literature reviews, professional surveys, and synthesized information in textbooks. Surveys of professionals in the field offer insight into what the scientific community perceives as important (Reiners *et al.* 2017), but may not convey the topics that are actually being addressed in current research (perceived versus realized importance). Literature reviews, on the other hand, can provide useful syntheses of a body of research. However, it is impossible for a single researcher to keep up with the rapidly growing amount of available literature, making it increasingly difficult to see the overarching picture of ecology. Moreover, the selection of studies to be included in such reviews is prone to unintended human biases, even when selection procedures are established ahead of time (Murtaugh 2002).

The development of automated content analysis (ACA) has given researchers the means to review vast amounts of literature in a more data-driven, unbiased manner. ACA is an innovative method for qualitative and quantitative text mining that uses text parsing and machine learning to identify the main concepts and themes discussed within a body of literature (Nunez-Mir *et al.* 2016). ACA methods have been applied for reviews in forestry (Nunez-Mir *et al.* 2015, 2017) and other fields (Chen and Bouvain 2009; Cretchley *et al.* 2010; Travaglia *et al.* 2011), but not to describe the overarching themes across the entire discipline of ecology. We contend that ACA can provide the systematic, data-driven analyses across time that are

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Figure 1. Examples of grand challenges of ecological importance: (a) conservation of threatened species, (b) urbanization and expanding socioecological interactions, (c) population growth, and (d) protection of degraded ecosystems.

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required to gain a better understanding of the major themes, gaps, and trends in ecological research.

Taking advantage of the wealth of knowledge contained in "big literature" (Nunez-Mir *et al.* 2016), we analyzed trends in ecological research by performing an ACA on a total of 84,841 ecological articles published in the top 30 ecology journals (ranked by impact factor) and three prominent multidisciplinary journals between 1980 and 2016. We addressed three questions: (1) what are the main themes in the published ecology literature over the past four decades?, (2) how has the appearance of each of these themes changed in frequency over time?, and (3) which themes are over- or underrepresented in primary research articles versus review articles?

Methods

Data analyzed

We collected data from articles appearing in the 30 top-ranked ecology journals as well as ecology-related articles from three well-known, high-impact, multidisciplinary journals. We selected the top 30 journals classified under the subject "ecology" in the Institute for Scientific Information (ISI) Web of Knowledge citation reports based on their 5-year impact factor as of 2014 (*Proceedings of the Royal Society B* was ranked in the top 30, but we excluded it from our analysis because it contains a large proportion of general biology [ie non-ecology] literature). We also collected ecology-related article abstracts from three multidisciplinary journals, specifically *Nature*, *Proceedings of the National Academy of Sciences of the United States of America* (*PNAS*), and *Science*, by including articles classified in the "ecology" category in the ISI Web of Science research database. Because abstracts of articles published prior to 1980 are often unavailable in electronic form, we limited our analysis to papers published between 1980 and 2016. We used the Scopus database to download the title, author keywords, year of publication, and abstracts of all available research articles and reviews meeting our criteria. There were noticeable discrepancies in the continuity of the data from Scopus for certain journals and years; in such cases, the ISI Web of Science research database was used to obtain the missing information. A total of 84,841 article abstracts, titles, and author keywords (82,670 from the 30 ecology journals and

2171 from the three high-impact multidisciplinary journals) were downloaded from the two databases in February of 2017. A full list of the journals is available in WebTable 1, and a full list of the articles is available at www.doi.org/10.4231/R7KD1W40.

Content analysis

We used ACA to synthesize and analyze the titles, author keywords, and abstracts in our dataset. ACA is an innovative text-mining and machine learning approach for qualitative and quantitative synthesis of literature that uses a group of algorithms and probabilistic models to discover the underlying topics within a body of literature in the form of "concepts", or families of words that appear together and are strongly correlated (Alexa and Zuell 2000; Smith and Humphreys 2006; Krippendorff 2012). We conducted our ACA using Leximancer software (v4; Leximancer Pty Ltd; Brisbane, Australia) to identify important concepts in the literature through the discovery of concept seeds (words that occur frequently in the literature) and to build a concept thesaurus (ie a group of words that forms a concept) for each of the concept seeds. Leximancer uses an iterative, bootstrapping, machine learning algorithm that finds words that co-occur frequently with the concept seed word and infrequently elsewhere, and classifies text segments in the literature with the concepts identified and defined in the previous stages (Smith 2003; Smith and Humphreys 2006; Stockwell *et al.* 2009).

For the purposes of this study, we initially set the program to identify the top 1000 concepts discussed in the literature. We narrowed the list by removing concepts that were uninformative (eg "suggested", "different") or related to scientific writing style (eg "results"), leaving us with a total of 547 concepts. A full list of concepts and their occurrence and co-occurrence frequency can be found at www.doi.org/10.4231/R7KD1W40.

Identification of themes

To identify emerging patterns and trends, we grouped the identified concepts into commonly occurring ecological themes based on their co-occurrence frequency in the text. Following row normalization, we used Ward's minimum variance clustering based on a Bray-Curtis distance matrix to create a dendrogram of concept relatedness, which was then divided into 50 groups to serve as a guide; however, we used our own judgment to merge and divide suggested groups into meaningful themes (see WebFigure 2 for an example dendrogram). In addition, we removed certain concepts that resulted in non-meaningful themes, such as experimental design (eg "field", "laboratory"), proper nouns (eg "Africa", "North America"), organism groups below kingdom (eg "insect", "mammal"), and taxon (eg "genus", "species"). A list of concepts excluded from our analyses can be found in WebTable 2. Ultimately, we refined the list to 415 concepts grouped into 46 ecological themes for further analysis (WebTable 3).

To calculate theme frequencies, we used the compound concepts setting in Leximancer. Concepts within the same theme were joined with a Boolean OR statement, and Leximancer re-tagged all of the literature with the new compound concept themes. This eliminated the possibility of double-counting concepts in text segments that were composed of multiple concepts within the same theme. After themes were identified and counted in all of the titles, author keywords, and abstracts, we used the occurrence data to map ecological thematic space, examine temporal trends, and make rank comparisons between primary and review articles.

Thematic space

To understand how themes co-occur with one another, we first created a matrix of the relative abundance of each theme in each journal. Ideally, we would have liked to use the full co-occurrence matrix of themes of individual abstracts, but this can bias ordinations toward overall theme abundance rather than co-occurrence. We utilized a normalized journal-by-theme matrix to reduce the effects of unequal sampling (eg differences in publication rate, years of publication, and abstract length) among journals, and then calculated the distance between journals using Bray-Curtis dissimilarity. We performed non-metric multidimensional scaling (NMDS) on the distance matrix to compare the similarity between the themes among journals. The NMDS scores were used for the themes to define the thematic space, with themes near the center of that space representing the core of ecology – those that are most connected with other concepts – and those around the periphery representing the frontiers of the field.

Temporal trends

To understand changes in thematic importance over time, we ranked themes by each decade based on concept frequency. Concept frequencies were highly overdispersed, and we therefore used ranks in all of our analyses. In order to keep our review succinct, we focused entirely on the trajectory of the 46 key themes identified in the thematic space. The temporal trends of the full list of concepts are available in WebTable 4, and an interactive visualization of the full list of concepts is available at https://feilab.shinyapps.io/Ecol_Concepts.

Comparison of article types

We compared concept theme rankings between primary research articles ($n = 78{,}786$) and review articles ($n = 6018$). We categorized text segments based on article type (original research or review), following the designation used by each journal, and used Leximancer to classify these text segments according to concept theme. We ranked themes in both bodies of literature and compared their rankings using

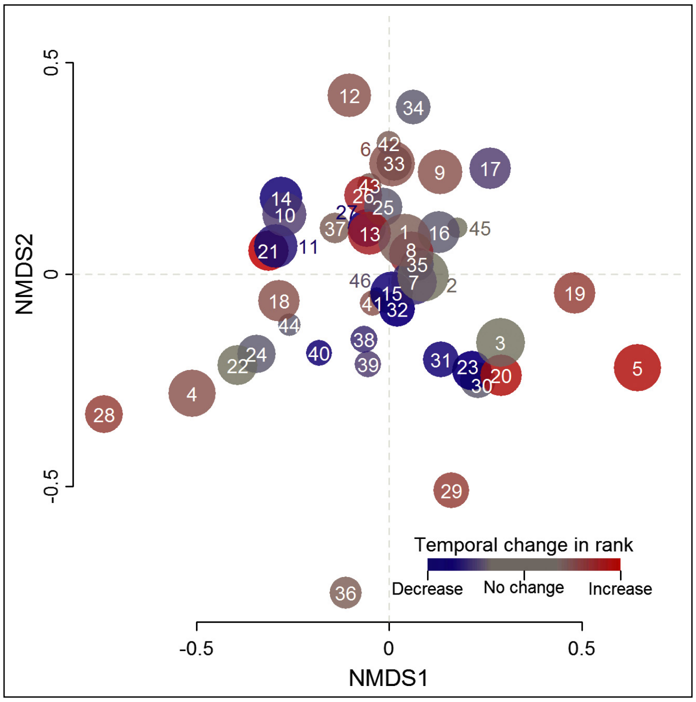

Figure 2. Relationship of major ecological themes based on 84,841 ecological article abstracts published between 1980 and 2016. List numbers correspond to the overall rank of the themes, with 1 = highest rank. Circle size is proportional to their occurrence frequencies in the analyzed literature; color corresponds to their temporal trends (red indicates increase in rank, blue indicates decrease in rank, and less color saturation indicates less change; see Figure 3 for rank changes). 1 – Modeling; 2 – Community processes; 3 – Behavior and sex; 4 – Biogeochemistry; 5 – Genetics; 6 – Landscape; 7 – Developmental; 8 – Community structure; 9 – Species distributions; 10 – Forests; 11 – Seasonal trends; 12 – Management and policy; 13 – Scales; 14 – Disturbance; 15 – Food webs; 16 – Movement; 17 – Paleoecology and biogeography; 18 – Physiography; 19 – Macroevolution; 20 – Traits; 21 – Climate change; 22 – Aquatic environment; 23 – Life history; 24 – Plant structure and productivity; 25 – Large-scale patterns; 26 – Anthropogenic; 27 – Survivorship; 28 – Gas flux; 29 – Cellular biology; 30 – Disease; 31 – Competition; 32 – Plant reproduction; 33 – Invasion; 34 – Conservation; 35 – Carrying capacity; 36 – Microbial ecology; 37 – Long-term trends; 38 – Herbivory; 39 – Stress; 40 – Plant physiology; 41 – Environmental patterns and processes; 42 – Population dynamics; 43 – Geospatial; 44 – Aquatic processes; 45 – Population demographics; 46 – Agronomy.

Spearman's rank correlation coefficient test. The use of theme rankings allowed us to compare bodies of literature of drastically different sizes. Statistical analyses were conducted in R 3.4.3 (R Core Team 2017) using the "vegan" package (Oksanen *et al.* 2018) for concept clustering and NMDS.

Results

Major themes in ecology

We identified 46 meaningful themes that ranged across temporal, spatial, and theoretical scales: from classical (eg food webs, life history) to contemporary (eg climate change, anthropogenic impacts), from microscale (eg cellular biology, microbial ecology) to macroscale (eg biogeography, long-term trends), and from theoretical (eg carrying capacity, competition) to applied (eg management and policy) (Figure 2). Across the study period, the most frequently occurring theme was modeling, followed by community processes, behavior and sex, biogeochemistry, and genetics.

Using the co-occurrence matrix of themes in the 33 journals included in this study, we mapped the thematic space of ecology. Classical themes such as food webs, developmental ecology, and community processes lie at the center of the thematic space (Figure 2). Toward the periphery are more contemporary themes like genetics, microbial ecology, and biogeochemistry, which were once considered separate disciplines but are now commonly incorporated into ecology. This trend reflects the growth of the discipline, demonstrating that ecology now encompasses a variety of subfields. Modeling, a tool applied in nearly every subdiscipline, has the highest frequency and is at the center of the thematic space. The dominance of modeling as the most prevalent concept theme may reflect recent advances in the complexity and diversity of statistical tools used to analyze newly available, complex datasets (Touchon and McCoy 2016; Courchamp and Bradshaw 2017). Community structure and community processes are both centrally located in the thematic space, which reflects that communities occur as ecological units across subdisciplines. Another noteworthy concept located near the center is scale, which was voted as the most important concept by ecologists in 2014 (Reiners *et al.* 2017). Temporal and spatial scale are inherent considerations in the design of any ecological study, and more explicit consideration and description of the scale at which ecological patterns and processes occur are becoming increasingly important (Jérôme 2013).

Temporal trends in key ecological themes

In general, the ranks (ie relative frequency of a theme in relationship to other themes) of classical themes decreased, whereas macroscale, microscale, and applied themes increased over time (Figure 3). Microscale themes (eg genetics, cellular biology, microbial ecology), macroscale themes (eg species distribution, climate change, macroevolution), and applied research (eg management and policy, anthropogenic impacts) are becoming more prevalent, as indicated by their increase in rank. Conversely, many classical ecology themes (eg carrying capacity, competition, developmental, disturbance, food webs, life history, seasonal trends, survivorship) and plant-related themes (eg forests, herbivory, plant physiology, plant reproduction, plant structure and productivity) that tend to focus on the local, individual, or population scale (eg life history, survivorship, competition) have fallen in ranking over the past four decades.

Rank comparisons between reviews and primary articles

Overall, there was strong agreement between the ranks of themes across different groups of literature (Spearman's

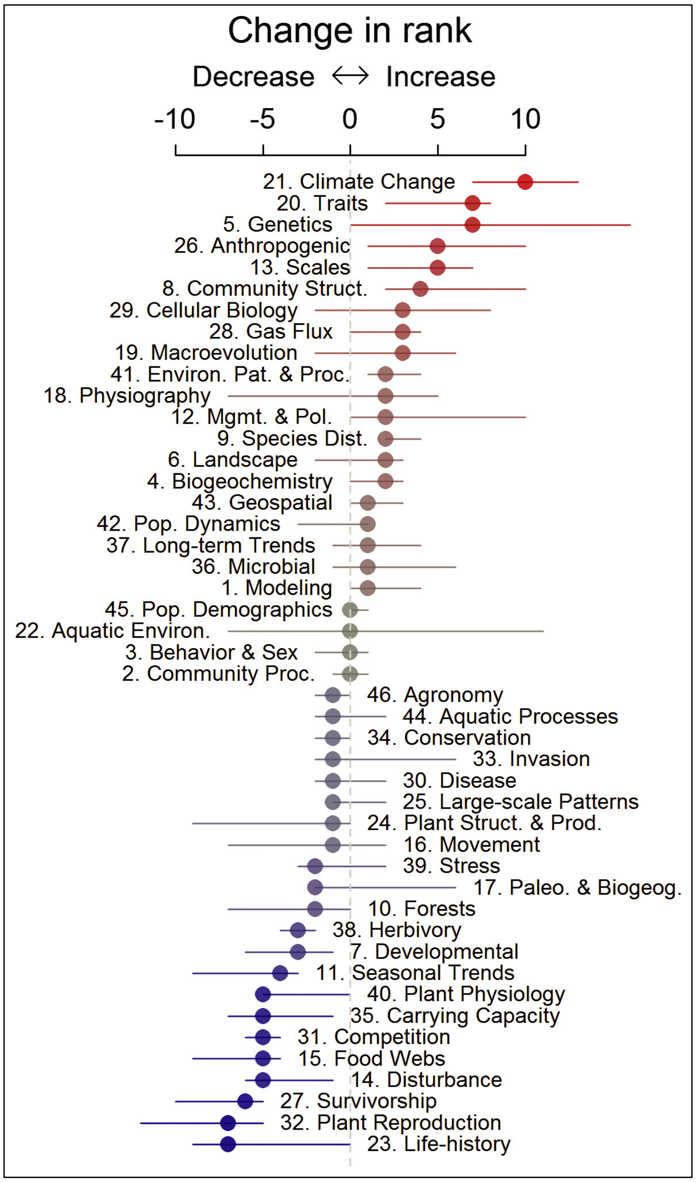

Figure 3. Change in rank over the study period for each of the 46 major themes. Each dot represents the median rank change between two consecutive decades (1980s to 1990s, 1990s to 2000s, and 2000s to 2010s); bars represent the maximum and minimum rank change between decades. See WebFigure 3 for decadal ranks.

$\rho = 0.83$, $P < 0.001$; Figure 4). We found that upward trending themes were much more likely to be above the 1:1 line (Figure 4), indicating that these upward trending themes were also reviewed more frequently. This suggests that synthesis efforts are more often dedicated to themes that are emerging in importance and popularity. In fact, the most frequently reviewed themes (eg anthropogenic impacts, long-term trends, invasion, traits) represent topics that have become a high priority during the past two decades for understanding ecological patterns and processes (Turner 1989; Murrell *et al.* 2001; Fridley *et al.* 2007). The least frequently reviewed themes were physiography and seasonal trends, which both represent local processes that are difficult to generalize across studies. Nonetheless, some infrequently reviewed topics, especially those that are upward trending (eg biogeochemistry, gas flux), could benefit from additional reviews and syntheses, as they are becoming more prevalent in ecological research.

Discussion

Over the past four decades, ecology has expanded from classical, plant-, and population-oriented themes to more contemporary microscale, macroscale, and anthropogenic themes. However, expanding to new research areas does not necessarily mean abandoning old ones, as they are the cornerstones of the ecological research and education that make up the conceptual center of the field (Reiners *et al.* 2017). Research density in scientific fields fluctuates over time as subfields and topics become saturated with knowledge, and researchers gravitate toward less explored areas (Milojević 2015).

The growth of macroscale and microscale themes is not surprising, as Thompson *et al.* (2001) anticipated the relative growth at both of these scales. The adoption of geospatial technologies along with the accumulation of large-scale ecological datasets has led to increased spatial extents in ecological studies, so that the upsurge of macroscale themes, such as species distribution, macroevolution, and environmental patterns and processes, was not unexpected. As the variation in the spatiotemporal scale of ecological studies increases, there will be a growing need for cross-scale understanding of ecological interactions (Thompson *et al.* 2001). Macrosystems ecology (Soranno and Schimel 2014; Fei *et al.* 2016), which emphasizes the interactions of biological, geophysical, and socioeconomic processes, pattern emergences, and scale dependencies, could very likely grow substantially in the near future, as the amount of research on many of the themes in this subdiscipline has increased in the recent past. At the microscale, we are seeing a rise in basic research as next-generation gene sequencing has made it possible to identify microbial and fungal taxonomic groups (Ekblom and Galindo 2010). Now that more advanced technologies are available, ecologists are striving to understand the role of these previously "hidden players" in ecological processes (Stapley *et al.* 2010).

Close attention should also be paid to the upward trends in evolutionary themes (genetics, cellular biology, macroevolution, and traits). Genetics has become a behemoth in the field, and is currently perched at the fifth highest rank overall, quickly rising from 27th place in the 1980s to the fourth highest rank in the most recent decade. Despite calls for a more explicit evolutionary framework in ecology (Thompson *et al.* 2001), evolutionary concepts are among the least valued of all concepts by ecologists (Reiners *et al.* 2017). Failure to emphasize genetics and evolution as central to ecology could lead to curriculum deficits among student ecologists (Brewer and Smith 2011), and much of the ecological literature may soon

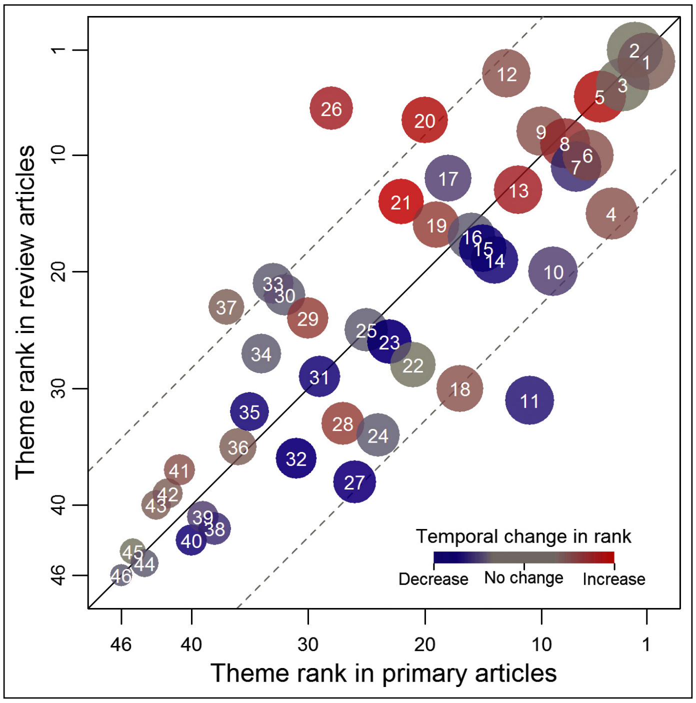

Figure 4. Relationship between ranks of ecological themes in abstracts in primary research articles and reviews articles. Dashed lines represent the 5th and 95th percentile in rank difference; list numbers correspond to the overall rank of the themes, with 1 = highest rank. Themes that are above the 1:1 line (solid line) were ranked higher in reviews, suggesting that they are discussed with higher relative frequency in review articles than original research articles. The opposite is true for those below the 1:1 line. Circle size is proportional to their occurrence frequencies in the analyzed literature; color corresponds to their temporal trends (red indicates increase in rank, blue indicates decrease in rank, and less color saturation indicates less change; see Figure 3 for rank changes). The numbering scheme in Figure 4 is identical to that described in the Figure 2 caption.

become incomprehensible in the absence of a basic understanding of genetics and evolution.

The increased focus on human-induced changes over the length of the study (eg anthropogenic impacts, climate change, species invasions) suggests that ecological research is increasingly embracing human dimensions (WebFigure 3). This shift in ecological focus has been noted previously (Palsson *et al.* 2013) and likely reflects the global influence of humans on the world's ecosystems (Gallagher and Carpenter 1997; Vitousek *et al.* 1997; Galli *et al.* 2012). The heavy focus on anthropogenic themes in turn reflects the increasing need to understand the role of human-influenced changes in complex ecological systems (Folke 2006). The relative increase in the theme of policy and management reflects a field that is trying to protect ecosystems in the face of global changes but also demonstrates a maturing discipline moving toward applied versus basic research.

The reduced emphasis on classical ecology themes and plant-based systems suggests that the field is diversifying in scope. It is not surprising that the relative rankings of these themes, which made up much of the main body of ecological research in the 1980s, have decreased over the past four decades. This is in part due to the inclusion of several newer journals that are subdiscipline specific or focused on more contemporary themes (see WebTable 1), thereby driving down the rank of classical themes. Yet the dominance of these classical themes is evident in earlier surveys of the British Ecological Society (Cherrett 1989) and the Ecological Society of America (Reiners *et al.* 2017) (WebTable 5), and this shift likely represents a true conceptual expansion in a maturing field. It is important to note, however, that these decreases in rank are not reductions in the overall amount of literature but rather declines in relative frequency. Both the total number of articles and the total frequency of each theme increased over time, suggesting that although they have become less dominant over the past four decades, classical ecology themes are still popular topics of study among ecologists.

There are some limitations to the data used in our analyses. First, authors are likely to emphasize the novelty of their research in the title and abstract, and classical themes, although present, might not be explicitly stated. We were also limited to analyzing text that is universally available via Web of Science and Scopus (ie abstracts, titles, and author keywords of journal articles only); this also restricted the temporal scope of our analysis, because literature published prior to the 1980s was largely unavailable in a digital format. However, using abstracts (rather than full articles) from years with an abundance of literature allowed us to reduce the bias associated with longer papers (ie higher theme frequency in longer papers) and low sample size (which may not be representative of the actual research being conducted during the earlier time periods). The ACA approach, although not without limitations, has, to the best of our knowledge, for the first time provided a means of using the massive literature across four decades to define and map the conceptual landscape of ecology, and to depict its temporal trends.

Conclusions

The results of our analysis suggest that ecological research is shifting toward fields that depend heavily on large, complex datasets and/or specialized technology. At the periphery of the thematic space and at the top of the theme ranks in the most recent decade are the frontiers of ecology, where technological advances (eg whole genome sequencing for genetics research, aerial and satellite-based sensors for monitoring Earth's ecosystems) and statistical improvements (eg Bayesian modeling, machine learning) have provided ecologists with the tools to rapidly generate new varieties of data in large volumes, and to analyze data in ways that were beyond the capacity of the computational and statistical capabilities of just a few decades ago. The availability of abundant complex data and advanced analytical capacity may have shifted ecology toward a new era of data-driven multidisciplinary science. Visualizing, describing, and analyzing patterns in data, rather than describing patterns in nature alone, have become important stepping stones for understanding underlying processes

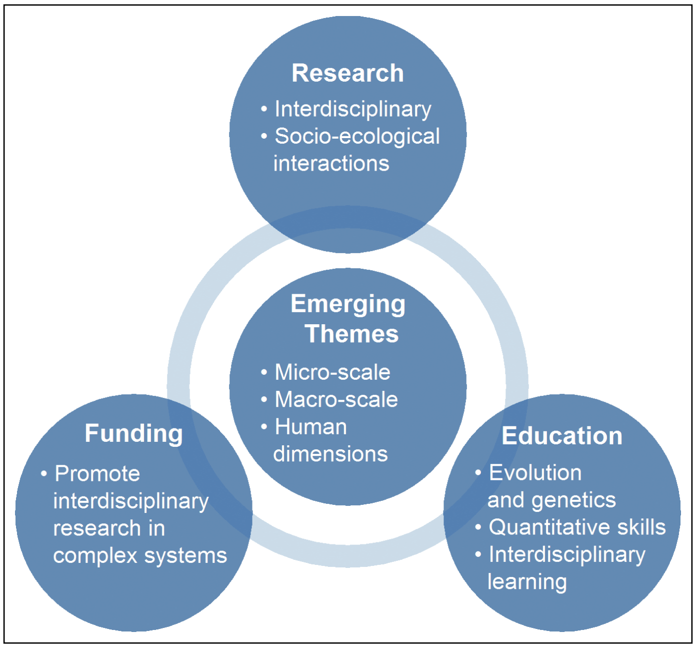

Figure 5. An integrated framework for the advancement of ecology in addressing global challenges. There is a need to incorporate emerging themes into research, funding, and education, and to utilize the outcomes to inform management of Earth's ecosystems.

and mechanisms (Grimm *et al.* 2017). Accordingly, these new technologies, data sources, and analytical techniques provide avenues for ecologists to further advance their science, and indicate areas that ecology students can pursue to better prepare themselves to be the next generation of ecologists.

Ultimately, one of the main purposes of science is to provide the necessary information to address challenges faced by our planet and humankind; therefore, as new challenges arise, boundary-pushing research can inform solutions to these problems. Although addressing societal challenges goes beyond science alone, stakeholders should facilitate the sustained growth in ecological research to aid the process of identifying novel solutions to these challenges (Figure 5). In particular, universities need to enhance students' knowledge base by providing more explicit training in (1) evolution, genetics, and related tools; (2) quantitative skills for analyzing complex data; and (3) interdisciplinary problem-solving skills, including human dimensions. Researchers meanwhile must (1) synthesize knowledge gained in these classical topics, while increasing original research at the frontiers; (2) adopt emerging technologies and analytical tools to facilitate discoveries; and (3) further incorporate human dimensions into ecological investigations. Funding agencies should promote and facilitate ecological research that considers the complexity and multidimensionality of our ecosystems (eg greater support for interdisciplinary programs, such as the US National Science Foundation's MacroSystems Biology, Rules of Life, and Coupled Natural and Human Systems programs, which aim to connect the many aspects of preserving Earth's ecosystems). Finally, the outcomes of all three of these entities – education, research, and funding – must be implemented through informed management of natural resources.

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Data availability

An occurrence and co-occurrence matrix of the original 547 concepts is available through the Purdue University Research Repository (www.doi.org/10.4231/R7KD1W40), and a Shiny app for interactive visualization of the full list of concepts is available at https://feilab.shinyapps.io/Ecol_Concepts.

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Supporting Information

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