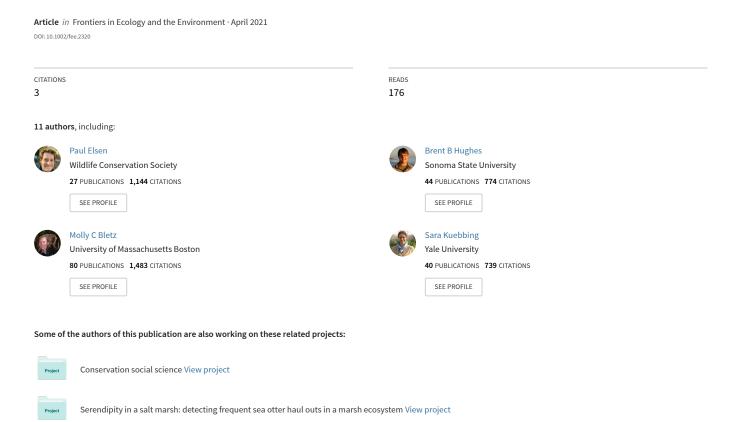
Trends in ecology and conservation over eight decades



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Trends in ecology and conservation over eight decades

Sean C Anderson^{1*}, Paul R Elsen^{2,3†}, Brent B Hughes^{4†}, Rebecca K Tonietto^{5†}, Molly C Bletz⁶, David A Gill⁷, Meredith A Holgerson^{8‡}, Sara E Kuebbing⁹, Caitlin McDonough MacKenzie¹⁰, Mariah H Meek¹¹, and Diogo Veríssimo^{12,13}

The fields of ecology and conservation have evolved rapidly over the past century. Synthesizing larger trends in these disciplines remains a challenge yet is critical to bridging subdisciplines, guiding research, and informing educational frameworks. Here, we provide what we believe is the largest full-text culturomic analysis of ecology and conservation journals, covering 80 years, 52 journals, and half a billion words. Our analysis illuminates the boom-and-bust of ecological hypotheses and theories; the adoption of statistical, genetic, and social-science approaches; and the domination of terms that have emerged in recent decades (eg *climate change, invasive species, ecosystem services, meta-analysis*, and *supplementary material*, which largely replaced *unpublished data*). We track the evolution of ecology from a largely descriptive field focused on natural history and observational studies to a more data-driven, multidisciplinary field focused on applied environmental issues. Overall, our analysis highlights the increasing breadth of the field, illustrating that there is room for more diversity of ecologists and conservationists today than ever before.

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The fields of ecology and conservation have undergone rapid growth since the discipline-specific journal *Ecology* was first published over a century ago (eg Reiners *et al.* 2017; Kim *et al.* 2018). Today, hundreds of ecology journals

In a nutshell:

- We analyzed the full text (over half a billion words) of papers published in 52 ecology and conservation journals to assess how the fields have changed over the past eight decades
- Many common terms today, including climate change, phylogenetics, and biodiversity, were coined only in recent decades, whereas several terms common in the early 1900s, such as agriculture and cell biology terms, are used only rarely today
- Ecology and conservation have broadened from local field studies to include global issues, and increasingly feature advanced statistical modeling
- Conservation science is one of the fastest growing subdisciplines, demonstrating the growing valuation of human dimensions of ecology

¹Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, Canada *(sean.anderson@dfo-mpo.gc.ca); ²Department of Environmental Science, Policy, and Management, University of California–Berkeley, Berkeley, CA; ³Wildlife Conservation Society, Global Conservation Program, Bronx, NY; ⁴Department of Biology, Sonoma State University, Rohnert Park, CA; ⁵Department of Biology, University of Michigan–Flint, Flint, MI; ⁶Department of Biology, University of Massachusetts Boston, Boston, MA; ⁷Duke University Marine Laboratory, Nicholas School of the Environment, Duke University, Beaufort, NC; (continued on last page)

represent subdisciplines spanning in scope from theoretical to applied and in scale from genomes to ecosystems. Synthesizing larger trends within a rapidly growing and diversifying field of study can be challenging, yet broad overviews are critical for bridging subdisciplines (Margles *et al.* 2010; Staples *et al.* 2019), guiding new research, and informing funding directions and educational frameworks (McCallen *et al.* 2019).

The discipline of culturomics – the quantitative analysis of large bodies of text – offers a rich framework with which to track the evolution of a field through time (Michel *et al.* 2011; Ladle *et al.* 2016). Word use in the published literature can serve as a proxy for tracking realized versus perceived importance of fundamental concepts and terms. This approach has been applied to smaller subsets of the ecological literature, notably a century of titles and abstracts in the journal *Ecology* (Kim *et al.* 2018), automated content analysis of titles and abstracts in top ecology journals (eg McCallen *et al.* 2019), and specific research questions for certain regions or taxa (eg Beale 2018).

Here, we build on previous analyses (eg Carmel et al. 2013; Hintzen et al. 2019; McCallen et al. 2019) with the first full-text analysis of ecology and conservation journals over eight decades, encompassing 52 journals, 131,533 articles, and over half a billion words. Our analysis extends McCallen et al. (2019) by five decades, and our full-text approach lets us investigate topics that would not appear in titles or abstracts. We analyze the JSTOR full-text corpus from 1930–2010 – the period of time with the most robust journal coverage in the JSTOR database – for all journals that regularly publish ecological or conservation papers and are not regionally or taxonomically exclusive (see WebPanel 1 for Methods). We searched the corpus for specific "n-grams", which are sequences of terms separated by a space. For example, biogeography is a

1-gram and *body size* is a 2-gram (hereafter, we denote *n*-gram terms in italics). We standardized *n*-gram frequency by total words per year published across all included journals and analyzed trends over time for a selection of *n*-grams. We derived our *n*-gram selection through both algorithmic and hand-curated approaches: (1) drawing on the most frequent and rapidly growing/declining *n*-grams in various decades and (2) developing logical groupings of terms that fall under key ecology and conservation themes (WebPanel 1).

Results

Broad trends in popularity

Between 1930 and 2020, the most commonly used 1- and 2-grams in ecology shifted from fundamental- to more applied-ecology terms (Figure 1, a–d; WebFigures 8–16). Of the nine 1-grams that were most common in the 1940s, only the top three – *species*, *plant*, and *area* – remained the same in the 2000s. However, the remaining most-common 1-grams in the 1940s (eg *time*, *water*, *number*) and nearly all top-nine 2-grams from that era (eg *oxygen consumption*, *soil moisture*) declined in use over time (Figure 1, a and

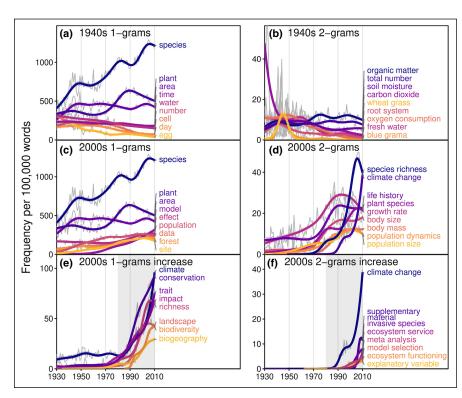


Figure 1. Top n-grams from the 1940s and 2000s. (a–d) Top nine 1-gram nouns and 2-gram nouns or adjectives from the 1940s and 2000s. Labels refer to "lemmas" or root words. For example, the 1-grams "plant" and "plants" were combined and labeled as "plant". (e–f) Most rapidly increasing 1-gram nouns and 2-gram nouns or adjectives from 1980 to 2010 (denoted by the gray-shaded rectangle). Light gray trend lines indicate frequency of the n-gram per 100,000 words. Dark colored trend lines and associated shaded ribbons represent generalized additive model fits with \pm 1 standard error (SE, 68%) confidence intervals (CI) (see Methods in WebPanel 1). n-grams are labeled in the same order as the trend lines and are connected via a thin straight gray line.

b), whereas many of the most popular 2-grams in the 2000s barely appeared in the corpus until after 1970 (Figure 1d). By far, the *n*-grams with the greatest rise in use over time were *climate* and *climate change* (Figure 1, e–f; eg Li *et al.* 2011; Scheffers *et al.* 2016; Staples *et al.* 2019). The 1- and 2-grams with the most rapid increases from 1980–2010 reflected a strong trend toward applied ecological research (eg *conservation*, *impact*, *biodiversity*, *ecosystem service*, *invasive species*; Figure 1, e and f).

Changes in popular terms from the 1940s to the 2000s reflected both shifts in science culture and changing societal needs. In the 1940s, popular terms such as *time*, *number*, and *day* (Figure 1a) referenced descriptive data. Popular datarelated terms in the modern era included *model*, *effect*, and *data* (Figure 1c). This shift likely represented both a replacement of terminology and a transition from a descriptive discipline to a more quantitative one (Ríos-Saldaña *et al.* 2018). Popular terms in the 1940s included *blue grama* (*Bouteloua gracilis*) and *wheat grass* (*Agropyron* spp) (Figure 1b), which likely had greater importance during and after the Dust Bowl drought experienced in the North American prairies in the 1930s (Worster 2004). This focus on agricultural research – in

an era that culminated in the formation of the Food and Agriculture Organization of the UN (Yates 1946) – was supported by other 2-grams from the 1940s, such as *organic matter*, *soil moisture*, and *fresh water* (Figure 1b).

We examined trends in 2-gram terms associated with scales in ecology (species, population, community, and ecosystem) by using a fill-in-the-blank algorithmic approach (Figure 2, leftmost and central columns). We found that species richness and plant species were the dominant adjective and noun uses of the term *species* (Figure 2, a and b). The term native rose in popularity around 2000 to become the third most common term preceding species as of 2010 (Figure 2b). As an adjective, the term population was primarily associated with size, growth, dynamics, and density, with population growth following approximately exponential growth itself (Figure 2d). Conversely, natural population was the dominant noun form of population, but was surpassed by human population as of 2010 (Figure 2e). Ecologists wrote about community structure and community composition more than any other adjective form of community and about plant communities, within our corpus, over three times more often than other community forms (Figure 2, g and h). The term ecosystem existed as a noun long before it was used as an adjective starting around 1970 (Figure 2, j and k). As a noun, ecosystem was most commonly associated with forest,

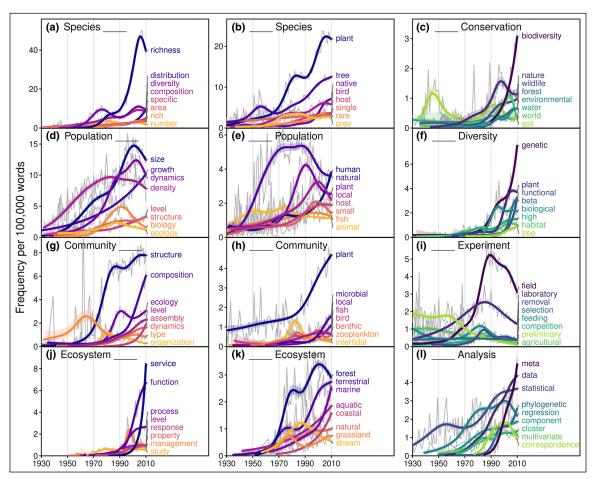


Figure 2. Top fill-in-the-blank 2-gram phrases. Each panel shows the top eight 2-gram terms where the blank in the panel label is filled in by the noun or adjective indicated beside each trend; for example, in (a), "Species ______" with the term "richness" corresponds to "species richness". The top *n*-grams are defined based on summing the occurrences throughout the entire time period, thereby weighting recent years more heavily. Panels in the leftmost and central columns (orange to blue colors) correspond to levels of ecological scale, whereas panels in the rightmost column (green to blue colors) refer to four selected concepts of interest to ecology and conservation. Panel I contains nine terms given that *cluster* and *multivariate* tied for the eighth position.

terrestrial, and marine, with the latter seeing an uptick after 2000 (Figure 2k). As an adjective, ecosystem service and ecosystem function were the dominant 2-grams (Figure 2j), with the former showing a rapid increase after the UN Millennium Ecosystem Assessment championed the concept in the early 2000s (MA 2005).

Using the same fill-in-the-blank approach, we examined adjectives associated with conservation, diversity, experiment, and analysis (Figure 2, rightmost column). Biodiversity conservation did not appear until the mid-1980s in our corpus (the term biodiversity was not coined until 1985; Wilson 1988) (Figure 1e) but by 2010 was being used more than twice as often as the next most common conservation term, nature conservation (Figure 2c). Genetic diversity ascended in the early 1990s to make genetic the dominant adjective associated with diversity (Figure 2f). References to field and laboratory experiment peaked around 1990 and declined thereafter (Figure 2i). Statistical, the only top adjective associated with analysis that appeared in the corpus in the 1930s, continued to grow in usage as of 2010 (Figure 2l); however,

data analysis, which did not appear until 1950, surpassed statistical analysis around 2000 (Figure 2l). Meta-analysis, which first appeared in the late 1980s in our corpus, became the most common adjective associated with analysis as of 2010 (Figure 2l).

Ecological scale and community ecology

From the onset, ecologists and conservation biologists studied organisms at the species level, reflected by the frequent mention and sustained growth of *species* in the corpus over time (Figure 3a; WebFigure 3). Although reference to the *cellular* level was initially the next most common, interest within the field of ecology then transitioned to *populations*, followed by *communities* and *ecosystems* (Figure 3b). It is perhaps unsurprising that *ecosystem* was the least common term given that it is also the youngest scale; while the term *ecosystem* was first described by Tansley (1935), ecosystem ecology was not formalized until Odum (1953). The way in which populations and communities are studied appears to have changed over time.

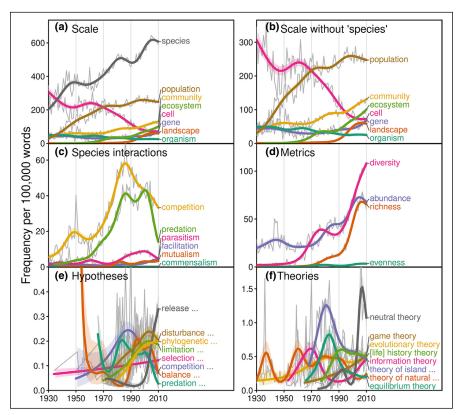


Figure 3. Community ecology and ecological hypothesis and theory n-grams from 1930 to 2010. Curated sets of n-grams related to selected themes. Light gray trend lines indicate frequency of the n-gram per 100,000 words. Dark colored trend lines and associated shaded ribbons represent generalized additive model fits with \pm 1 SE (68%) CI (see Methods in WebPanel 1). Note that in this and subsequent figures, the n-gram labels sometimes refer to multiple underlying related n-grams. For example, mutualism refers to multiple n-grams, including mutualism and mutualistic interaction. Panel (b) is the same as (a), but with the 1-gram species removed to allow better visualization of the remaining terms. Panels (e) and (f) are based on the same algorithm used in Figure 2 to find the top eight n-grams for "blank hypothesis" and "theory of blank" or "blank theory".

Lotka-Volterra models emerged in the 1920s (Lotka 1920; Volterra 1928) and functional response models in the 1950s (Holling 1959) to examine competition and predator-prey dynamics; competition and predation were the interactions most commonly included in the corpus (Figure 3c). Yet, both competition and predation experienced steep declines in use after the 1980s and early 2000s, respectively (Figure 3c), perhaps reflecting that initial models, while simple, marked the beginning of ecology moving beyond one or two species to explain more complex community dynamics, such as food-web structure and ecological niche modeling. To that end, the 2000s saw a revival of nicherelated terms (eg ecological niche, niche model, niche conservatism, niche breadth) after a long decline from a previous peak in the 1970s (WebFigure 5).

Perhaps the clearest example of terminology evolution was with ecological hypotheses and theories (Figure 3, e and f). We examined the top eight ecological hypotheses and theories using the fill-in-the-blank approach from Figure 2. We found no dominant hypothesis but a number of changing

patterns around the hypotheses related to predicting biodiversity. For example, one of the earliest hypotheses stemming from Darwin's finches was the *competition hypoth*esis, which peaked in the 1980s and was surpassed by the intermediate disturbance hypothesis (Figure 3e; Connell 1978). Yet the intermediate disturbance hypothesis itself peaked in the early 2000s, perhaps due to later critiques (Figure 3e; Fox 2013). Population and community ecologists may now favor asking what drives biodiversity. Indeed, metrics of diversity, which incorporate both abundance and richness, have increased in use since 1990 (Figure 3d). In terms of theories, 2-grams with large historical peaks included the theory of natural selection, the theory of island biogeography, and equilibrium theory (Figure 3f). By 2010, neutral theory (Hubbell 2001), game theory, and evolutionary theory were the most frequently referenced theories, although all were declining in frequency of use (Figure 3f).

Conservation and applied ecology

Terms related to *conservation* and applied ecology represented some of the fastest growing *n*-grams in modern ecology (Figure 1e). *Conservation* as a field originated alongside the formation of the Society for Conservation Biology in 1985 (Meine *et al.* 2006), prior to which the term *preservation* was used as frequently (Figure 4a; WebFigure 4). Ecologists increasingly studied major threats to biodi-

versity loss: habitat loss, invasive species, pollution, overexploitation, and climate change (Figure 4b). Despite overexploitation being considered one of the most prevalent causes of species extinctions (eg Díaz et al. 2019), the term itself received relatively little attention in our corpus (Figure 4b), although frequencies of terms associated with specific modes of exploitation (eg hunting, fishing, and logging) all grew steadily (Figure 4e). Up until the early 1990s, pollution was the leading term in the context of threats to biodiversity; its use peaked in the mid-1970s (Figure 4b). Frequencies of the term ozone, typically associated with studies of pollution, displayed a trend similar to that of pollution, but with a lag of approximately 15 years (Figure 4c) and peaked in frequency around 1985 with the announcement of an ozone hole over Antarctica (Farman et al. 1985). The term pollution was then surpassed by climate change and subsequently by invasive species, two terms that as of 2010 vastly outweighed all other threats in their frequency of use (Figure 4b) and two of the top three fastest growing terms in all of ecology (Figure 1f).

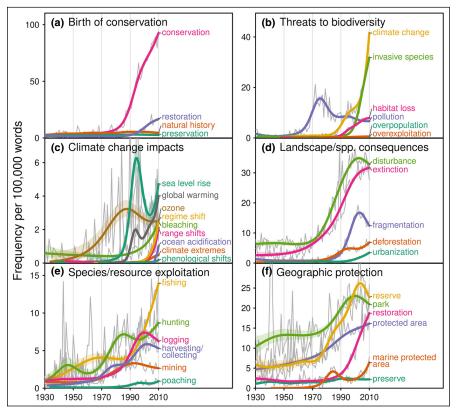


Figure 4. Conservation and applied ecology n-grams from 1930 to 2010. Details are otherwise the same as for Figure 3.

A multitude of concepts originated alongside the proliferation of studies of climate change, habitat loss, and overexploitation (Figure 4, c-e). For example, terms related to climate change, such as ocean acidification, range shifts, and climate extremes saw sharp upticks after the mid-2000s (Figure 4c). Other concepts exhibited more complex patterns. For example, sea-level rise spiked in frequency in the mid-1990s, declined in frequency by 2000, but then increased thereafter (Figure 4c). Fragmentation rose sharply following the common use of the related term habitat loss around 1990, but its use was in decline after about 2000 (Figure 4d). In terms of modes of species exploitation and resource extraction, fishing was the leading term as of 2010, followed by hunting and logging (Figure 4e). Historically, hunting and fishing exchanged positions of dominance every decade (Figure 4e). Modes of exploitation of non-animal resources, such as logging, harvesting, and mining, were consistently discussed less frequently than modes of animal exploitation (Figure 4e).

The concept of protection has long been a pillar of biodiversity conservation (eg Watson et al. 2014). Until roughly 2000, park was the most commonly used term related to forms of geographic protection (Figure 4f). References to protected areas have increased steadily since 1930, with the growth in marine protected areas displaying a similar pattern but lagging by several decades (Figure 4f). These patterns of usage

approximately mirrored the growth rate of actual protected terrestrial and marine areas globally (Watson et al. 2014). Many of the key forms of geographic protection, including parks, reserves, protected areas, and preserves, predated the frequent usage of the term conservation (Figure 4, a and f), although this could be due in part to several of these terms also frequently being used as verbs.

Statistics and data analysis

Ecology has increasingly become a data- and model-centric discipline (Figures 1 and 5; WebFigure 6). Regression, an overarching encompassing many statistical approaches, saw continued and rapid growth in use since the 1950s, approaching correlation by 2005 (Figure 5a). References to ANOVA and t tests both peaked around 2000, while mentions of generalized linear models (GLMs) steadily increased in frequency, surpassing t tests in 2004 (Figure 5a). In terms of how such models were fit, least-squares, formerly the dominant paradigm, was rapidly surpassed by Bayesian, maximum likelihood, and information theoretic (AIC) terms around 2000; as of 2010, the term Bayesian was used over twice as often as maximum likelihood

(Figure 5b). The Markov chain Monte Carlo sampling method (MCMC) first appears in the corpus in 1994 (Thompson 1994), 24 years after Hastings (1970) initially described the concept. Combined with modern computing power, MCMC has been responsible for much of the boom in applied Bayesian data analysis (Gelman et al. 2014).

Such statistical approaches and paradigms have been associated with endless debates about the role of hypothesis testing in ecology (eg Quinn and Dunham 1983; Burnham and Anderson 2002). To that end, use of the phrase null hypothesis peaked in the 1980s, and the phrase significant difference peaked around 1990 and declined thereafter (Figure 5c). The associated terms P value and confidence interval appeared in approximately equal frequency as of 2010 (Figure 5c), although both are often referred to by abbreviations missed in our corpus (eg "P =" or "CI"). Power analysis remained rarely used as of 2010 despite numerous calls for its increased use (eg Nakagawa and Cuthill 2007; Smith et al. 2011). The increased frequency of so many dataand model-centric terms, along with the advent of online publishing, coincided with the meteoric rise of supplementary material n-grams since around 2000 - the 2-gram itself had the second most rapid increase across all 2-grams from 2000-2010 (Figure 1f) - and a concomitant decline in unpublished data and personal communication (Figure 5d; WebFigure 6; Federer et al. 2018).

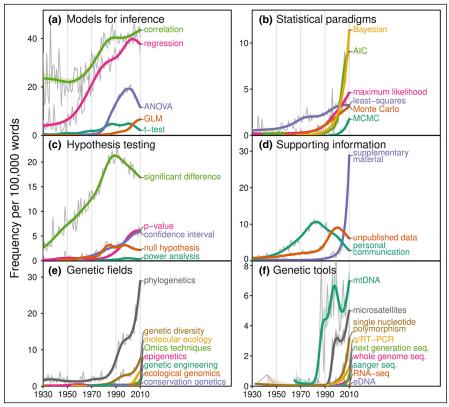


Figure 5. Data analysis, statistical methods, and genetics *n*-grams from 1930 to 2010. Details are otherwise the same as for Figure 3. ANOVA: analysis of variance, GLM: generalized linear model, AIC: Akaike information criterion, MCMC: Markov chain Monte Carlo, mtDNA: mitochondrial DNA, q/RT-PCR: quantitative reverse transcription polymerase chain reaction, eDNA: environmental DNA.

Genetics

The focus on genetics in ecology-related research increased markedly over the past several decades (Figure 2f; Figure 5, e and f; WebFigure 6). Phylogenetics remained the most referenced genetics term from 1930 to 2010 and increased in use after the late 1980s (Figure 5e). By 2010, phylogenetic was the fourth most common adjective associated with analysis (Figure 21) and the third most common adjective associated with hypothesis (Figure 3e). A strong interest in genetic variation and diversity began to emerge in the ecological literature in the 1980s, with the terms genetic variation, gene flow, and evolutionary biology all appearing in the top 144 2-grams for the years 1980-1999 (WebFigure 15) and genetic diversity showing up in the 2000-2010 range (WebFigure 16). In terms of genetics tools, microsatellites and mtDNA (mitochondrial DNA) were the most commonly referenced terms as of 2010, but next-generation sequencing (Sanger et al. 1977) nearly overtook microsatellites, and may have done so since 2010. We also saw an increase in sequencing-based approaches to studying genetic diversity, particularly a rise in references to single nucleotide polymorphisms (Figure 5f). Since 2010, there has likely been a continued increase in references to next-generation sequencing given that it is now

widely adopted in both macro- and microecological research of many species and communities – not just model systems (Andrews *et al.* 2016).

Social sciences

Over the past several decades, ecologists have paid increasing attention to the human dimensions of ecology (Figure 6; WebFigure 7; Bennett et al. 2017). Since the 1990s, references to market or community-based maninterventions gained agement traction - particularly environmental certification programs and payment for ecosystem services schemes, such as the Reducing Emissions from Deforestation and Forest Degradation (REDD) program (Figure 6a). We also observed an increased focus on human wellbeing (Figure 6b), with a spike of references to human health in the 1970s and more recently an overall growth in references to poverty, food security, and overall human wellbeing since the 1990s. This trend is paralleled by the rise in frequency of the terms ecosystem service and ecosystem function (Figure 2j), two terms that explicitly focus on ecological processes based on the benefits they impart to humans. Given the increased focus on the human dimensions of conservation over the past few decades (Bennett et al. 2017), it makes sense that methods involving interviews

and *questionnaires* would become more common (Figure 6c). Ecology is only just beginning to acknowledge different ways of knowing; however, qualitative methods, such as *focus groups*, *ethnography*, or *participant observation*, remain scarcely referenced, supporting the assertion that ecology and conservation continue to rely primarily on quantitative approaches (Figure 6c; Moon *et al.* 2016). Parallel to the increased focus on human well-being since the 1970s, we observed an increased frequency of *n*-grams related to *stake-holders*, *local communities*, and *Indigenous people* (Figure 6d).

Discussion

The ecology and conservation lexicons have expanded and evolved considerably over the past 80 years. The most frequently used terms in the 1930s were derived from the breadth of disciplines that inspired early ecologists, but by the 2000s had been largely replaced by terms that reflected the emergence of a data-driven scientific field focused mainly on applied environmental issues. The turnover in terminology demonstrates how ecologists and conservationists have embraced many newly coined terms (eg biodiversity, climate change, meta-analysis) that did

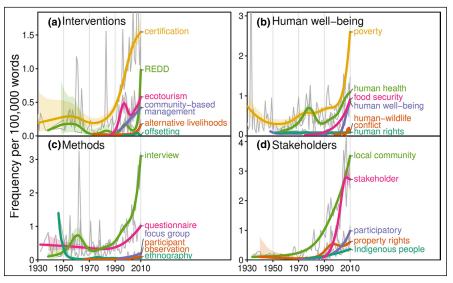


Figure 6. Social-science *n*-grams relevant to ecology from 1930 to 2010. Details are otherwise the same as for Figure 3. REDD: Reducing Emissions from Deforestation and Forest Degradation.

not exist in the early 20th century and signifies the evolution of ecology and conservation into fully independent research disciplines. Our results illustrate that ecologists and conservationists are working on increasingly complex and specialized topics at broader spatial scales (Estes *et al.* 2018) and higher levels of taxonomic and hierarchical organization (Kim *et al.* 2018), and are increasingly incorporating the human dimensions of conservation (Bennett *et al.* 2017).

There has been a shift in how ecologists and conservationists describe analytical techniques, demonstrating the evolution of ecological research into a more quantitative and data-driven field of study (Figures 1 and 5). In particular, ecologists and conservationists have adopted many statistical paradigms (eg Bayesian, AIC, and MCMC) and genetic analytical techniques (eg phylogenetics and omics) over the past three decades. The increased use of these terms highlights the importance of advanced training in statistics, genetic techniques, and computer programming. This shift toward analytical techniques does not appear to have come about at the expense of natural history (Figure 4a) - a loss that has been mourned and debated (Tewksbury et al. 2014; Able 2016; Barrows et al. 2016). Instead, our results suggest there is room for both natural history and rigorous quantitative analysis. In terms of preparing students to publish their work, our results reinforce the call to refocus ecological statistical education from declining recipe-based approaches (eg ANOVAs) to probability theory, programming, and simulation-based approaches (eg McElreath 2015).

There are caveats to consider when interpreting our results. First, our analysis tracks frequency of term use in the ecological and conservation literature, but frequency does not necessarily correspond to the importance of related concepts to the field. For example, some terms may be

commonly mentioned in paper introductions but appear less often as the core topic of research. Other terms, such as conservation, are linked to journal titles like Conservation Biology and appear in the bibliographic section of some papers. Second, the journals included in the corpus are not a random sample across the field of ecology. Our corpus excluded several prominent journals that do not focus solely on ecological or conservation research (eg Science, Nature) as well as taxonomic-specific journals (eg American Journal of Botany, Journal of Wildlife Management), which were intentionally omitted to reduce taxonomic bias (WebPanel 1). Third, the quality of the corpus improved through time - data from the earlier years in our analysis were based on much smaller sample sizes than more recent data (WebFigures 1 and 2), and the data from the earlier years are mostly based on optical

character recognition, a process in which scanned PDF files are converted into text, at times with errors.

Conclusions

Our analyses allow ecologists and conservationists to reflect on the past, present, and future of their field. Within eight decades, the field has evolved from focusing on natural history and observational field studies to a multidisciplinary field more applied and quantitative in scope. Undoubtedly, ecology and conservation have and will continue to grow and adopt approaches developed elsewhere, such as analyses of increasingly large datasets and the use of deep learning (Christin et al. 2019). These new tools will empower researchers to answer questions that were previously unanswerable and create niches for more types of ecologists and conservationists. Yet, while quantitative and meta-analysis-style research (this paper included) are valuable (Osenberg et al. 1999), if ecology wishes to maintain its natural-history and fundamental-science roots, the field needs to prioritize such a focus through research funding bodies and educational curricula. As we see it, elements of ecology today are almost unrecognizable from the field 90 years ago; only time will tell if this rate of evolution will continue, leaving ecologists in 2100 with a similar sentiment.

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References

- Able KW. 2016. Natural history: an approach whose time has come, passed, and needs to be resurrected. *ICES J Mar Sci* 73: 2150–55.
- Andrews KR, Good JM, Miller MR, et al. 2016. Harnessing the power of RADseq for ecological and evolutionary genomics. *Nat Rev Genet* 17: 81–92.
- Barrows CW, Murphy-Mariscal ML, and Hernandez RR. 2016. At a crossroads: the nature of natural history in the twenty-first century. *BioScience* **66**: 592–99.
- Beale CM. 2018. Trends and themes in African ornithology. *Ostrich* 89: 99–108.
- Bennett NJ, Roth R, Klain SC, et al. 2017. Mainstreaming the social sciences in conservation. Conserv Biol 31: 56–66.
- Burnham KP and Anderson DR. 2002. Model selection and multimodel inference: a practical information–theoretic approach, 2nd edn. New York, NY: Springer.
- Carmel Y, Kent R, Bar-Massada A, *et al.* 2013. Trends in ecological research during the last three decades a systematic review. *PLoS ONE* 8: e59813.
- Christin S, Hervet É, and Lecomte N. 2019. Applications for deep learning in ecology. *Methods Ecol Evol* **10**: 1632–44.
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–10.
- Díaz S, Settele J, and Brondizio ES, *et al.* (Eds). 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany: IPBES.
- Estes L, Elsen PR, Treuer T, et al. 2018. The spatial and temporal domains of modern ecology. *Nature Ecol Evol* 2: 819–26.
- Farman JC, Gardiner BG, and Shanklin JD. 1985. Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature* **315**: 207–10.
- Federer LM, Belter CW, Joubert DJ, et al. 2018. Data sharing in PLoS ONE: an analysis of data availability statements. PLoS ONE 13: e0194768.
- Fox JW. 2013. The intermediate disturbance hypothesis should be abandoned. *Trends Ecol Evol* **28**: 86–92.
- Gelman A, Carlin JB, Stern HS, *et al.* 2014. Bayesian data analysis. Boca Raton, FL: Chapman & Hall.
- Hastings WK. 1970. Monte Carlo sampling methods using Markov chains and their applications. *Biometrika* 57: 97–109.
- Hintzen RE, Papadopoulou M, Mounce R, *et al.* 2019. Relationship between conservation biology and ecology shown through machine reading of 32,000 articles. *Conserv Biol* **34**: 721–32.
- Holling CS. 1959. Some characteristics of simple types of predation and parasitism. *Can Entomol* **91**: 385–98.

Hubbell SP. 2001. The unified neutral theory of biodiversity and biogeography. Princeton, NJ: Princeton University Press.

- Kim JY, Joo G-J, and Do Y. 2018. Through 100 years of Ecological Society of America publications: development of ecological research topics and scientific collaborations. *Ecosphere* 9: e02109.
- Ladle RJ, Correia RA, Do Y, et al. 2016. Conservation culturomics. Front Ecol Environ 14: 269–75.
- Li J, Wang M-H, and Ho Y-S. 2011. Trends in research on global climate change: a Science Citation Index Expanded-based analysis. *Global Planet Change* 77: 13–20.
- Lotka AJ. 1920. Analytical note on certain rhythmic relations in organic systems. *P Natl Acad Sci USA* **6**: 410–15.
- MA (Millennium Ecosystem Assessment). 2005. Ecosystems and human well-being: synthesis. Washington, DC: Island Press.
- Margles SW, Peterson RB, Ervin J, and Kaplin BA. 2010. Conservation without borders: building communication and action across disciplinary boundaries for effective conservation. *J Environ Manage* **45**: 1–4.
- McCallen E, Knott J, Nunez-Mir G, et al. 2019. Trends in ecology: shifts in ecological research themes over the past four decades. Front Ecol Environ 17: 109–16.
- McElreath R. 2015. Statistical rethinking: a Bayesian course with examples in R and Stan. London, UK: Chapman and Hall/CRC.
- Meine C, Soulé M, and Noss RF. 2006. "A mission-driven discipline": the growth of conservation biology. *Conserv Biol* **20**: 631–51.
- Michel J-B, Shen YK, Aiden AP, et al. 2011. Quantitative analysis of culture using millions of digitized books. *Science* **331**: 176–82.
- Moon K, Brewer TD, Januchowski-Hartley SR, *et al.* 2016. A guideline to improve qualitative social science publishing in ecology and conservation journals. *Ecol Soc* **21**: art17.
- Nakagawa S and Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev* 82: 591–605.
- Odum EP. 1953. Fundamentals of ecology. Philadelphia, PA: Saunders.
- Osenberg CW, Sarnelle O, Cooper SD, and Holt RD. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* **80**: 1105–17.
- Quinn JF and Dunham AE. 1983. On hypothesis testing in ecology and evolution. *Am Nat* **122**: 602–17.
- Reiners WA, Lockwood JA, Reiners DS, and Prager SD. 2017. 100 years of ecology: what are our concepts and are they useful? *Ecol Monogr* 87: 260–77.
- Ríos-Saldaña CA, Delibes-Mateos M, and Ferreira CC. 2018. Are fieldwork studies being relegated to second place in conservation science? *Global Ecol Conserv* 14: e00389.
- Sanger F, Nicklen S, and Coulson AR. 1977. DNA sequencing with chain-terminating inhibitors. *P Natl Acad Sci USA* **74**: 5463–67.
- Scheffers BR, Meester LD, Bridge TCL, *et al.* 2016. The broad footprint of climate change from genes to biomes to people. *Science* **354**: aaf7671.
- Smith DR, Hardy ICW, and Gammell MP. 2011. Power rangers: no improvement in the statistical power of analyses published in *Animal Behaviour*. *Anim Behav* 81: 347–52.

- Staples TL, Dwyer JM, Wainwright CE, and Mayfield MM. 2019. Applied ecological research is on the rise but connectivity barriers persist between four major subfields. J Appl Ecol 56: 1492–98.
- Tansley AG. 1935. The use and abuse of vegetational concepts and terms. Ecology 16: 284-307.
- Tewksbury JJ, Anderson JGT, Bakker JD, et al. 2014. Natural history's place in science and society. *BioScience* **64**: 300–10.
- Thompson EA. 1994. Monte Carlo likelihood in the genetic mapping of complex traits. *Philos T Roy Soc B* **344**: 345–51.
- Volterra V. 1928. Variations and fluctuations of the number of individuals in animal species living together. ICES J Mar Sci 3: 3–51.
- Watson JEM, Dudley N, Segan DB, and Hockings M. 2014. The performance and potential of protected areas. Nature 515:
- Wilson EO. 1988. Biodiversity. Washington, DC: National Academy Press.
- Worster D. 2004. Dust Bowl: the Southern Plains in the 1930s. Oxford, UK: Oxford University Press.
- Yates PL. 1946. Food and Agriculture Organization of the United Nations. J Farm Econ 28: 54-70.

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⁸Department of Biology and Department of Environmental Studies, St Olaf College, Northfield, MN; *current address: Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY; ⁹Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA; ¹⁰Climate Change Institute, University of Maine, Orono, ME; 11 Deptartment of Integrative Biology, AgBio Research, and the Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI; ¹²Department of Zoology, University of Oxford, Oxford, UK; ¹³Institute for Conservation Research, San Diego Zoo Global, Escondido, CA; †these authors contributed equally to this work