

Biogeography, changing climates, and niche evolution

David B. Wake^{a,b,1}, Elizabeth A. Hadly^c, and David D. Ackerly^{a,d}

^aDepartment of Integrative Biology, ^bMuseum of Vertebrate Zoology, and ^dJepson Herbarium, University of California, Berkeley, CA 94720; and ^cDepartment of Biology, Stanford University, Stanford, CA 94305

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Modern concepts central to current studies of biogeography, changing climates and evolution of ecological niches were born approximately a hundred years ago. In 1908, the Regents of the University of California established the Museum of Vertebrate Zoology at Berkeley, in accordance with the wishes of Annie M. Alexander (1867–1950). Alexander conceived the institution and selected its first Director, Joseph Grinnell (1877–1939), a well known naturalist who had received his Ph.D. at Stanford University and was then teaching at the Throop Institute in Pasadena (later the California Institute of Technology). Grinnell, who founded the Museum in late 1908, meticulously adhered to the principles laid down by Alexander (1). Alexander would provide the funding and inspiration and Grinnell would do the intellectual and practical work to establish the institution and set it on a trajectory. The Museum quickly became known for its studies of terrestrial vertebrates, conducted in the framework of what we would recognize today as ecology and evolution. The founders were self-conscious of their roles from the beginning. They had no illusions that the work they set out to do would be easy or soon accomplished, if ever. Grinnell (2) set the course:

It will be observed, then, that our efforts are not merely to accumulate as great a mass of animal remains as possible. On the contrary, we are expending even more time than would be required for the collection of the specimens alone, in rendering what we do obtain as permanently valuable as we know how, to the ecologist as well as the systematist. It is quite probable that the facts of distribution, life history, and economic status may finally prove to be of more far-reaching value, than whatever information is obtainable exclusively from the specimens themselves.

At this point I wish to emphasize what I believe will ultimately prove to be the greatest value of our museum. This value will not, however, be realized until the lapse of many years, possibly a century, assuming that our material is safely preserved. And this is that the student of the

future will have access to the original record of faunal conditions in California and the west wherever we now work.

These ideas were prophetic, and have a special poignancy at this time, when the impact of global climate change is evident and when we realize how much we rely on records from the past, such as those meticulously kept by Grinnell, his students, coworkers and successors. A century has now elapsed since the Museum was founded, and we were stimulated by Joseph Grinnell's words to take stock of our current understandings of the relationships between geography, climate, and the distribution and ecological niche dimensions of organisms in an ecological and evolutionary context, using modern methods and approaches.

In this issue contributions are presented from an Arthur M. Sackler Colloquium of the National Academy of Sciences, held in Irvine, CA, December 11–13, 2008, in celebration of the Centennial of the Museum of Vertebrate Zoology at the University of California at Berkeley and with the spirit of Grinnell's contributions in mind. The colloquium was focused on issues central to Grinnell and his colleagues one hundred years ago: biogeography, niche evolution and changing climates (or, more generally, environments, for Grinnell focused much attention on human-induced impacts on the California environment). Grinnell was a pioneer in studying geographic variation within and between species, in focusing on the relationships between geography, ecology and the distribution of organisms, and especially in the formulation of the ecological niche concept (3). These are all current issues in modern science, and recent years have witnessed the emergence of new scientific challenges, conceptual frameworks, and analytic techniques, all of which were on display at the colloquium.

The colloquium took place at a propitious time, celebrating both the centennial of the Museum of Vertebrate Zoology and the sesquicentennial of the publication of Darwin's *Origin of Species* on November 24, 1859 (Table 1). Moreover, 2009 is also the 150th anniversary of the death of Alexander von Humboldt (1769–1859), a monumental

figure in the history of science who wrote extensively about the relationships of climate and vegetation. As a result of his studies of Volcán Chimborazo in Ecuador, von Humboldt appears to have been the first well known scientist to discuss the zonation of vegetation along an altitudinal transect and to develop a concept of life zones (4). von Humboldt's work deeply influenced C. Hart Merriam who recalled, shortly before his death, his father handing him a volume of Humboldt's "Views of Nature", where he found early inspiration for his work on species distributions (5). Merriam's classic study of the San Francisco Mountains in Northern Arizona and his biological survey of Mt. Shasta led to the development of his highly influential life zone concept (6). Merriam recognized 12 life zones in the United States and mapped them, noting that on altitudinal transects (e.g., from the Sonoran Desert to Humphrey's Peak) one would pass through as many as six life zones. Groups of species of plants and vertebrates were associated with each zone, and thus the zone itself became predictive. Grinnell was strongly influenced by this approach, and it became a hallmark of his subsequent research, especially evident in his famous studies of Yosemite National Park (7), and throughout his life he made regular emendations to his life zone map of California. Although life zones became increasingly controversial through time, attempts to adapt the life zone approach to modern understandings were made by several authors, notably Holdridge (8). Holdridge's life zones, based on integration of biotemperatures, precipitation, and potential evapotranspiration, were used by many researchers, especially in the

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¹To whom correspondence should be addressed. E-mail: wakelab@berkeley.edu.

Table 1. Early milestones and anniversaries related to the history of the niche concept in biogeography, ecology, and evolution

Year	Milestone
1805	First publication of von Humboldt's Volcan Chimborazo vegetation figure
1859	May 6: Death of Alexander von Humboldt (1769–1859) Nov. 24: Publication of Darwin's <i>Origin of Species</i>
1908	Founding of UC Museum of Vertebrate Zoology (Grinnell and Alexander)
1910	First published use of "niche" in ecological context (11)
1917	Publication of Grinnell's "The niche-relationships of the California thrasher"
1927	Publication of Elton's "Animal Ecology"
1936	Publication of Gause's "The Struggle for Existence"
1944	Publication of Simpson's "Tempo and Mode in Evolution"
1957	Publication of G.E. Hutchinson's "Concluding Remarks"

New World tropics and life zone maps were produced for several countries (e.g., refs. 9 and 10).

In parallel with his work on life zones, Grinnell pioneered the analysis of individual species distributions in relation to their biotic and abiotic requirements in his 1917 article "The niche-relationships of the California thrasher" (3). Although the term "niche" had previously appeared in print in its ecological context (11), Grinnell's article is appropriately credited with the introduction of the niche concept into general use in ecology (12). Grinnell apparently first explicitly referred to niches in his 1913 doctoral dissertation, cited in a 1914 monograph dealing with the Lower Colorado River region (13). Griesemer (14) says that the term "niche" first appeared in Grinnell and Swarth (15), a publication dealing with the vertebrate fauna of the San Jacinto Mountains. He guesses that the term probably emerged from discussions among active groups of students at Stanford, who were attracted by David Starr Jordan and inspired by the life zone concept of Merriam. Grinnell greatly admired Merriam, whose concepts were a significant influence on the development of his work. Grinnell's idea that each species occupies its own niche goes back to Darwin as a core concept, and Grinnell explicitly dealt with the issue of competitive exclusion in 1904 (16). By 1917, when Grinnell used the word "niche" in an article title (3), the term was in wide informal use. Grinnell concluded, "It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships," which led Leibold (17, p. 288) to observe:

Since that was one of the first uses of the term niche and one of the first statements of this principle, one wonders how much theoretical work was being developed outside of print by Grinnell and his collaborators.

Some insight into this conjecture is derived from the field notes of Grinnell's graduate student Walter P. Taylor, who was conducting field research in the Yosemite region in early December, 1914 (notes on file, Museum of Vertebrate Zoology, University of California, Berkeley, CA). Following routine observations for December 11, 1914, Taylor wrote a separate section headed "The Ecological Niche." These are musings, obviously stimulated by time in the field with Grinnell since mid-November. After a brief introduction Taylor observes

It seems to refer, as usage has it, to different habitats in the same locality, as for instance, in the case of birds, different states of foliage, or different kinds of brush.

He continued for 4 pages, stating at one point:

But the ordinary sense in which the term ecological niche is used refers to that critical something which is seized upon by one species, and by which it keeps its hold even in a locality where related species are living.

Taylor concludes:

Put in another way, the continued existence of a species in a locality where related species are living depends upon the critical differences, slight or large, in the totality of requirements of each.

These notes, written a decade after Grinnell's first formal conceptualization of niches and competitive exclusion, although without using those terms, suggest that "ecological niche" was a term already in circulation and a topic of debate and discussion among graduate students of the day.

An apparently independently developed concept of the ecological niche is attributed to Elton (18), who either was unaware of Grinnell or chose not to cite him (see ref. 19). Griesemer (14) sum-

marized the similarities and differences between the conceptualizations. Elton wanted to develop a coherent account of dynamics of interactions in communities, such as food chains, cycles of abundance, and the like; he was less concerned with individual species than was Grinnell. Grinnell's niche was seen as more habitat-oriented than Elton's, which was seen as more function-oriented, but both saw the niche as a place or role that a species occupies in the environment rather than as a property of the species itself, a view more associated with Hutchinson (ref. 20; see also refs. 21 and 22). The main difference between Grinnell and Elton identified by Griesemer is the issue of whether more than one species can occupy a niche, the difference stemming ultimately from Grinnell's systematic perspective and Elton's more functional one. In a concise and forceful overview, Udvardy (23) argued that there was no essential difference between Grinnell and Elton in conceptualizing the niche, but that Grinnell's formulation was earlier and broader. Furthermore, he credits Grinnell with the concept of competitive exclusion, which he calls "Grinnell's axiom." Hardin (24) agreed that Grinnell deserved credit, despite the fact that competitive exclusion was widely referred to as "Gause's principle" by that time (1960); he proposed the term "competitive exclusion principle" to extricate the terminology from its uncertain historical genesis.

G. Evelyn Hutchinson, in his famous "Concluding Remarks" article (25), formalized the niche concept as a set of niche axes defining an "N-dimensional hypervolume" within which a species could maintain a viable population. Hutchinson's concept of the niche as an abstract set of environmental axes closely mirrors Grinnell's original presentation, although he did not cite Grinnell's article at this time. A critical distinction is that Hutchinson redefined the niche as a property of the species in relation to its environment (20). Hutchinson introduced the distinction between the fundamental niche, reflecting the abiotic requirements of a species, vs. the realized niche, the set of conditions occupied in the presence of competitors. Ellenberg, working independently on vegetation ecology in Central Europe, had also considered how species distributions along environmental gradients shift in response to competitors (26). It is not known (to us) how the work of Ellenberg and other European ecologists, and that of the "American school" of evolutionary ecology in the 50s and 60s, may have influenced each other. The subsequent history of the niche

concept, and its central yet at times reviled role in community ecology, has been discussed in some depth by several reviewers (refs. 12, 14, 19, 20, 27, and 28; see also refs. 21 and 22).

While ecologists were wrestling with the niche concept and its implications, paleontologists were tackling related problems, although not always using the same language. George Gaylord Simpson presaged discussions of niche conservatism by ecologists through his consideration of the “realized environmental hyperspace” (29). He viewed each point in “environmental hyperspace” as a unique combination of environmental variables, and argued that individuals within populations, populations within species, species within genera, and so on, will exhibit a slowly decreasing measure of similarity in the positions they occupy. Building on Hutchinson’s formulations, Valentine (30) wrote:

The species niche is one of the more important concepts in paleobiology. As employed here, the unqualified term niche subsumes the potential interactions of a species with all the factors of the environment, physical and biological. Since evolution is essentially an ecological process operating with genetic machinery, a good case can be made that the niche is the most fundamental single unit of evolution.

For practical purposes, implicit use of niche concepts and niche conservatism is the foundation of environmental reconstructions that rely on the fossil record. Key traits associated with the niche (distribution, morphology, relative abundances, etc.) were assumed to be conserved and the veracity of that assumption was upheld by practical results that followed. As early as the 1960s, paleontologists of the oil industry were essentially applying the concept in facies reconstruction based on the assumption that certain assemblages of fossil marine organisms represented particular environments that were associated with oil-bearing strata. Transfer functions, developed in detail for foraminiferal assemblages (31) and used for tree rings, pollen and diatoms, are empirically derived equations used to calculate quantitative estimates of paleoclimate, which are then tested against calibration datasets (32). Modern plant distributions and their associated abiotic environments are fundamental for hindcasting the climates of the past (33, 34), and associations of the environment with present mammalian geographic distributions have been used as a technique for

inferring terrestrial paleoclimates and paleocommunities (35). In the case of Quaternary plants and mammals, the niches of species have been inferred to remain “constant” over the time periods studied (usually the last million years or so).

The success of these applications depends on the relative constancy of niche relations over long periods of evolutionary time. In its strongest formulation this constancy is manifest as evolutionary stasis, the prolonged persistence of forms in the fossil record with negligible morphological change. The observation of stasis, and its implications for evolutionary biology, were the focus of Eldredge and Gould’s theory of punctuated equilibria (36, 37). Punctuated equilibria sparked a heated debate between population geneticists and paleontologists, and contributed to the integration of developmental biology and evolution (“evo-devo”) (38). Less appreciated was the role of ecological dynamics as a potential mechanism of stasis. As Eldredge wrote later (ref. 39):

[S]pecies tend to change locale—rather than anatomical features—in response to environmental change. As long as suitable habitat can be found, a species will move rather than stay put and adapt to new environmental regimes.

[W]e . . . have always emphasized that it is habitat tracking—stabilizing natural selection in the face of environmental change—that basically underlies stasis.

Habitat tracking, together with behavioral and phenotypic plasticity and the dynamics of species interactions, offer a variety of ecological factors that may help to resolve the observation of evolutionary stasis with the ubiquity of climate change and environmental heterogeneity (40, 41).

Researchers in comparative biology, focused primarily on extant taxa, have also had a long-standing interest in the similarities—and differences—among close relatives. Dating back to Darwin (42), comparisons between close relatives have played a critical role both to elucidate patterns of evolutionary change, and in mechanistic studies to “control” for the many features shared by relatives and isolate the importance of traits of interest. Clutton-Brock and Harvey (43), studying behavioral organization in primates, recognized that the similarities of close relatives also pose a statistical problem for the analysis of comparative data, as closely related and phenotypically similar species may not represent “independent data points”

with respect to adaptive hypotheses. Although this view has generated considerable debate, their work did represent a key step in the development of statistical comparative methods in phylogenetics. Harvey and Pagel (44), in their 1991 monograph, coined the term “phylogenetic niche conservatism”, referring to the role of ecological sorting processes as factors that would promote stabilizing selection and minimize niche evolution. They drew their concept from a brief passage by Grafen that outlined the same argument, acknowledging that it was “so natural that it cannot be original” (ref. 45, p. 143). There has subsequently been a lively debate regarding the definition, significance and mechanisms of niche conservatism, with no immediate resolution in sight (40, 46–48). Currently, the integration of phylogenetic comparative methods and statistical niche models is opening up a new era of insight into niche evolution and its relationship to diversification and biogeography (49–51).

In recent years, the niche concept has come full circle and returned to play an important role in biogeography, particularly in regards to the impacts of climate change (52–54). Geographical distributions of species in relation to underlying climate gradients have received renewed attention, particularly as the foundation for what are variously termed “species distribution models”, “climatic niche models”, or “statistical niche models” (55). These models draw on a variety of statistical methods to model species geographic distributions in relation to large-scale climatic and topographic variables (56). Predictions of species responses to climate change are then derived by combining the models with outputs from global circulation models that project changes in spatial patterns of temperature, precipitation, and associated climate variables. A critical and unresolved issue in the use of predictive models is the extent to which dispersal limitation will constrain short-term (i.e., century-scale) range shifts (57). However this problem is resolved, the models still offer one of the most powerful approaches to project potential impacts of climate change on biodiversity.

In this Sackler Colloquium, we sought a wide array of perspectives on the niche concept, and its role in ecology, evolution, and climate change biology. We intentionally intermixed topics, juxtaposing paleontology with conservation, and conceptual reviews with case studies. Most of the talks from the colloquium are represented by papers in this Special Issue. The result, we hope, is an intellectually diverse yet inter-

twined series of papers that will illuminate current advances at the intersection of ecology, evolution and biogeography.

The Colloquium opened with a contribution from the "Grinnell Project," a series of studies by personnel associated with the Museum of Vertebrate Zoology to resurvey original study sites laid out by Grinnell in the early part of the last century. The ambitious project is stimulated by Grinnell's prediction that the value of his team's research might not be fully appreciated for a century. The first publication from the project focused on mammals (58), and showed that although some species in the Sierra Nevada (Yosemite National Park) had similar elevational distributional patterns as in the past, others had undergone major shifts in distribution. Tingley et al. (59) found that many species of birds have also experienced changes in distributional patterns. Bird communities were studied along four elevational gradients in the Sierra Nevada, including 82 species and 53 separate localities. Species tracked changes in the geographical distribution of their climatic niches through time. These results suggest that climatic niche modeling may prove useful in predicting the distribution of birds under different models of climate change.

Several authors addressed issues related to conceptualization of niches and some historical perspectives. An advantage of the flurry of activity in discussions of niche conservatism is the multiple perspectives afforded by workers from many fields. The disadvantage is that concepts of the niche may not always align, which confuses the discussion. Soberón and Nakamura (22) focus specifically on discriminating between fundamental, potential, and realized niches to clarify exactly what is conserved. The distinctions between the Hutchinsonian "response niche" and the Grinnellian "impact niche" are timely because they have received relatively little attention and figure prominently in whether we view niches as conserved or not. Using a mathematical approach, Soberón and Nakamura also examine the fundamental differences in niche modeling algorithms that use presence data versus those that also rely on absence data. They conclude that clearly defined terminology and explicit treatment of the underlying variables in niche conservatism will do much to integrate this field. Colwell and Rangel (21) explore how Hutchinson's niche concept differed from earlier conceptions. Whereas Grinnell and Elton saw niches as elements of environments, Hutchinson attributed them to species. They identify Hutchinson's term biotope with a formal separation of physical place from environment and argue

that his duality (niche vs. biotope) established many elements of the modern approach to classifying and mapping environments, modeling species distributions under different climate models, and in general contributed greatly to broader dimensions of modern studies of niches. Holt (55) follows with an investigation of the demographic basis of the Hutchinsonian niche, emphasizing that under certain circumstances, possibly more widespread than currently recognized, conditions allowing population growth from low density can differ from the conditions under which an established population can maintain itself. Holt's work also provides an important link between microevolutionary processes and larger macroevolutionary patterns.

Few workers use physical principles to model persistence in environments. Porter and Kearney (60) apply an ecophysiological approach to explicitly model the thermal niche of an endothermic ellipsoid organism. From first principles of physics, they quantify how shape, size and body insulation (e.g., mammalian fur) affect metabolism in variable environments and test this against field and laboratory data. Their data show the power of biophysical models for combining functional traits with environmental data to recapitulate observed gradients in body size and suggest this as a fruitful area of further research. For example, recent exciting research combines ecophysiological models with population dynamics (see ref. 61).

From the outset, niche theory has played a central role in community ecology. The mechanisms underlying community composition and phylogenetic diversity are the subject of the study by Graham et al. (62) comparing 189 hummingbird communities in Ecuador. A robust phylogenetic hypothesis is used to assess how species and phylogenetic lineages change along environmental (e.g., elevational) gradients and biogeographic barriers. At lower elevations there is less phylogenetic clustering than at higher elevations, in accord with ideas that competition is more important in the lowlands and environmental filtering in the uplands, where coexistence of close relatives is found. Their study provides insight into the pattern of faunal buildup in a biotically rich and complex region. Community assemblage is also the focus of Okie and Brown (63), who examine the effects of rising sea level and concomitant creation of islands in the Sunda Shelf region. They show how the original mammal fauna of this region has been disassembled on islands of differing size and complexity following the late Pleistocene

events. Diversity is inferred to have dropped throughout the islands. Okie and Brown propose that unique mammalian traits, including body size and niche characteristics such as habitat and food requirements, played a role in extinction probability.

Jackson et al. (64) apply niche concepts to long-term ecological dynamics, emphasizing some simple yet surprising implications of climate variability nested across temporal scales. They illustrate that contrasting conditions for establishment and persistence can generate an "ecological ratchet," with episodic dynamics of range expansion and contraction (see related discussion in ref. 55). They further discuss several sources of uncertainty in the application of correlative niche models to the problem of future climate change, including the complex dynamics of climate change, the importance of the regeneration niche, and historical contingencies that can alter dynamic response of ecological systems.

Several papers address aspects of niche evolution, from small scale population level dynamics at range edges, to macroevolutionary patterns evident in comparative data and the fossil record. Processes operating at the margin of the geographic ranges will attract increasing attention as the magnitude of climate change becomes more evident to biologists. Angert (65) conducted field studies of the demography of two species of closely related monkey-flowers (*Mimulus*) in the Sierra Nevada of California, focusing especially on populations at the margins of geographic ranges. Central and marginal populations showed striking differences within species but there were also differences between species. One species had less productive populations at lower elevational marginal regions whereas both displayed higher fecundity and population growth in the upper elevational marginal regions. Recent climate changes are thought to have shifted climatic envelopes in the direction of higher elevations.

The study of niche evolution is an important focus of comparative biology, integrating ecological diversity and phylogenetic history. Ackerly (48) presents a simple extension of the theory of independent contrasts to measure rates of trait diversification, focusing on plant traits that are associated with growth and regeneration strategies. Comparisons among clades reveal >100-fold differences in rates of trait diversification, with higher rates on Hawaiian island clades compared with continental clades from California and the North Temperate flora. This approach could be ap-

plied widely across other groups, as comparative data and time-calibrated phylogenies become available.

Hadly and colleagues (41) examine patterns in the range size of mammal genera in North America from the late Pleistocene through the late Holocene, comparing distributions in the fossil and modern record. They find remarkable stability in range size within genera through time, despite the glacial-deglacial transition, extinction of species within the genus or how many species are included in the genus. They suggest that different processes may influence niche conservatism at higher taxonomic levels, positing that intrinsic traits are more important at higher levels and environmental controls may play more of a role at the species level. Using range size as a proxy for the realized niche, they propose a “genus niche” and underscore the importance of maintaining a genus pool for conservation of North American mammalian communities.

Across the broadest spatiotemporal perspective, Vieites et al. (51) apply an innovative use of the niche to explore how environmental tolerances of salamanders, which are thought to be prime examples of organisms with phylogenetically conserved niches, have evolved since mid-Tertiary times. They calculate the environmental niche space of species in the family Salamandridae in the northern hemisphere and use these data to propose the environmental niches of the lineage. The study examines methods and shows the promise of current approaches while at the same time indicates some of the daunting problems remaining.

The final set of papers examines applications of niche theory in climate change and conservation biology. Zimmerman and colleagues (66) consider the importance of climatic extremes in shaping distributions of tree species along climate gradients in Switzerland. Incorporation of climatic extremes (i.e., interannual variability) offers a modest but significant improvement in fitting distributions to climate data, and especially helps to correct marginal areas where over and under-prediction problems arise. Given the clear physiological impacts of climate extremes, they suggest several reasons why niche models based on climate averages may perform as well as they do. Wiens et al. (67) implement two species distribution models on a fine geographic scale to predict the future distribution of bird species in California by 2070 (also see 68). Of the 60 species they model, a majority show a reduction in geographic distribution within California. As a practical exercise, Wiens et al. compare and contrast these models and discuss implications to managers of the differences between them. They are mindful of the uncertainties and assumptions inherent in species distribution models and future projections, but stress the urgency of action despite them. The world is changing at a pace perhaps faster than our ability to model biotic response with our traditional standards of statistical rigor.

Niche theory has a variety of applications in conservation and restoration biology, beyond the current focus on climate change. Using patterns of abundance and distribution in Australian Wet Tropic vertebrate species, Williams

et al. (69) investigate the relative size of the niche. Counter to prevailing wisdom (70), they find that narrowly distributed species confined to the rainforest have high local abundances. They posit that persistence of restricted species is possible when intrinsic demographic traits permit high local abundance. Their results challenge the paradigm that geographically restricted species have a greater extinction probability than do widely distributed species.

In the following pages, a rich array of contributions to our modern understanding of the relationship between organisms and species, their ecological niches, and biogeography is presented. Although the integration of these topics has been a century-long goal, we have a sense of rapid progress during the last decade, and especially at the present time. In this era of rapid climate change, new ways of thinking are essential as we confront the reality of impacts on organisms and their distribution through space and time. If even a fraction of the projected changes are realized, the changes we face are truly frightening and the world of 2100 may be drastically transformed from its present state.

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- Stein, B. R. (2001) *On Her Own Terms: Annie Montague Alexander and the Rise of Science in the American West* (Univ of California Press, Berkeley, CA).
- Grinnell, J. (1910) The methods and uses of a research museum. *Popular Science* 163–169.
- Grinnell J. (1917) The niche-relationships of the California thrasher. *The Auk* 34:427–433.
- von Humboldt A. (1805) *Geographie des Plantes Equinoxiales*. in *Essai sur la Geographie des Plantes*, eds von Humboldt A, Bonpland A (Chez Levrault, Schoell et compagnie, Paris).
- Sachs A. (2006) *The Humboldt Current: Nineteenth Century Exploration and the Roots of American Environmentalism* (Viking, New York).
- Merriam CH (1890) Results of a biological survey of the San Francisco Mountain Region and desert of the Little Colorado, Arizona. 1. General results, with special reference to the geographical and vertical distribution of species. *North Am Fauna* 3:1–34.
- Grinnell J, Storer TI (1924) *Animal Life in the Yosemite: An Account of the Mammals, Birds, Reptiles, and Amphibians in a Cross-Section of the Sierra Nevada* (Univ of California Press, Berkeley).
- Holdridge LR (1967) *Life Zone Ecology* (Tropical Science Center, San Jose, Costa Rica).
- Tosi JA (1960) *Zonas de Vida Natural en el Peru, Moria Explicativa sobre el Mapa Ecologico de Peru. Bot. Tec. No. 5, Zona Andina Proy. 30. Programa de Coop. Tecn.* (Instituto Interamericano de Ciencias Agricola, Lima, Peru).
- Tosi JA (1969) *Ecological Map of Costa Rica* (Tropical Science Center, San Jose, Costa Rica).
- Johnson RH (1910) *Determinate Evolution in the Color Pattern of the Lady-Beetles. Publication No. 122* (Carnegie Institute of Washington, Washington, DC).
- Chase J, Leibold M (2003) *Ecological Niches: Linking Classical and Contemporary Approaches* (Univ of Chicago Press, Chicago).
- Grinnell J (1914) An account of the mammals and birds of the Lower Colorado Valley with special reference to the distributional problems presented. *Univ Cal Publ Zool* 12:51–294.
- Griesemer JR (1992) In *Keywords in evolutionary biology*, eds Keller EF, Lloyd EA (Harvard Univ Press, Cambridge, MA), pp 231–240.
- Grinnell J, Swarth H (1913) An account of the birds and mammals of the San Jacinto area of Southern California. *Univ Cal Publ Zool* 10:197–406.
- Grinnell J (1904) The origin and distribution of the chestnut-backed chickadee. *The Auk* 21:364–379.
- Leibold, M (2002) In *Life on Earth: An Encyclopedia of Biodiversity, Ecology, and Evolution*, eds Eldredge N (ABC-CLIO, Santa Barbara, CA), Vol. 1, pp 287–291.
- Elton CS (1927) *Animal Ecology* (Sidgwick and Jackson, London).
- Hutchinson GE (1978) *An Introduction to Population Ecology* (Yale Univ Press, New Haven, CT).
- Colwell RK (1992) In *Keywords in Evolutionary Biology*, eds Keller EF, Lloyd EA (Harvard Univ Press, Cambridge, MA), pp 241–248.
- Colwell RK, Rangel TF (2009) Hutchinson's duality: The once and future niche. *Proc Natl Acad Sci USA* 106:19651–19658.
- Soberón J, Nakamura M (2009) Niches and distributional areas: Concepts, methods, and assumptions. *Proc Natl Acad Sci USA* 106:19644–19650.
- Udvardy MDF (1959) Notes on the edological concepts of habitat, biotope and niche. *Ecology* 40:725–728.
- Hardin G (1960) The competitive exclusion principle. *Science* 131:1292–1297.
- Hutchinson G (1957) Concluding remarks. *Cold Spring Harbor Symp Quant Biol* 22: 415–427.
- Ellenberg H (1953) Physiologisches und ökologisches Verhalten derselben Pflanzenarten. *Berichte der Deutschen botanischen Gesellschaft* 65:351–362.
- Whittaker RH, Levin SA, Root RB (1973) Niche, habitat, and ecotope. *Amer Nat* 107:321–338.
- McIntosh RP (1985) *The Background of Ecology: Concept and Theory* (Cambridge Univ Press, Cambridge, UK).
- Simpson GG (1944) *Tempo and Mode in Evolution* (Columbia Univ Press, New York).

30. Valentine JW (1969) Niche diversity and niche size patterns in marine fossils. *Paleobiology* 43:905–915.
31. Imbrie I, Kipp NG (1971) In *The Late Cenozoic Glacial Ages*, ed Turekian K (Yale Univ Press, New Haven, CT), pp 71–181.
32. CLIMAP (1981) *Seasonal Reconstructions of the Earth's Surface at the Last Glacial Maximum in Map Series, Technical Report MC-36* (Geological Society of America, Boulder, CO).
33. COHMAP (1988) Climatic changes of the last 18,000 years: Observations and model simulations. *Science* 241:1043–1052.
34. Tiffney BH, Manchester SR (2001) The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *Int J Plant Sci* 162:53–517.
35. Graham RW (1984) Paleoenvironmental implications of the Quaternary distribution of the Eastern Chipmunk (*Tamias striatus*) in central Texas. *Quat Res* 21:111–114.
36. Eldredge N (1971) The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25:156–167.
37. Eldredge N, Gould SJ (1972) In *Models in paleobiology*, ed Schopf TJM (Freeman, Cooper and Co., San Francisco), pp 82–115.
38. Wake DB, Roth G, Wake MH (1983) On the problem of stasis in organismal evolution. *J Theor Biol* 101:211–224.
39. Eldredge N (1995) *Reinventing Darwin: The Great Debate at the High Table of Evolutionary Theory* (John Wiley, New York).
40. Ackerly DD (2003) Community assembly, niche conservatism and adaptive evolution in changing environments. *Int J Plant Sci* 164:S165–S184.
41. Hadly EA, Spaeth PA, Li C (2009) Niche conservatism above the species level. *Proc Natl Acad Sci USA* 106:19707–19714.
42. Ridley M (1992) Darwin sound on comparative method. *TREE* 7:37.
43. Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *J Zool* 183:1–39.
44. Harvey PH, Pagel M (1991) *The Comparative Method in Evolutionary Biology* (Oxford Univ Press, Oxford).
45. Grafen A (1989) The phylogenetic regression. *Phil Trans Roy Soc London Ser B* 326:119–157.
46. Wiens JJ, Graham CH (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Ann Rev Ecol Syst* 36:519–539.
47. Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol Lett* 11:995–1003.
48. Ackerly D (2009) Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. *Proc Natl Acad Sci USA* 106:19699–19706.
49. Yesson C, Culham A (2006) Phyloclimatic modeling: Combining phylogenetics and bioclimatic modeling. *Syst Biol* 55:785–802.
50. Evans MK, Smith S, Flynn R, Donoghue M (2009) Climate, niche evolution, and diversification of the “birdcage” evening primroses (*Denothera*, Sections *Anogra* and *Kleinia*). *Amer Nat* 173:225–240.
51. Vietes DR, Nieto-Román S, Wake DB (2009) Reconstruction of the climate envelopes of salamanders and their evolution through time. *Proc Natl Acad Sci USA* 106:19715–19722.
52. Austin MP, Nicholls AO, Margules CR (1990) Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecol Monogr* 60:161–177.
53. Peterson AT, et al. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* 416:626–629.
54. Thuiller W (2003) BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. *Glob Change Biol* 9:1353–1362.
55. Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proc Natl Acad Sci USA* 106:19659–19665.
56. Elith J, Leathwick JR (2009) Species distribution models: Ecological explanation and prediction across space and time. *Ann Rev Ecol Syst* 40:677–697.
57. Loarie SR, et al. (2008) Climate change and the future of California's endemic flora. *PLoS ONE* 3:e2502.
58. Moritz C, et al. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264.
59. Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian niche through a century of climate change. *Proc Natl Acad Sci USA* 106:19637–19643.
60. Porter W, Kearney M (2009) Size, shape and the thermal niche of endotherms. *Proc Natl Acad Sci USA* 106:19666–19672.
61. Buckley LB (2007) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Amer Nat* 171:E1–E19.
62. Graham CH, Parra JL, Rahbek C, McGuire JA (2009) Phylogenetic community structure in tropical hummingbird communities. *Proc Natl Acad Sci USA* 106:19673–19678.
63. Okie JG, Brown JH (2009) Niches, body sizes, and the disassembly of mammal communities on the Sunda Shelf islands. *Proc Natl Acad Sci USA* 106:19679–19684.
64. Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proc Natl Acad Sci USA* 106:19685–19692.
65. Angert AL (2009) The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proc Natl Acad Sci USA* 106:19693–19698.
66. Zimmerman NE, et al. (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proc Natl Acad Sci USA* 106:19723–19728.
67. Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proc Natl Acad Sci USA* 106:19729–19736.
68. Stralberg D, et al. (2009) Re-shuffling of species with climate disruption: A no-analog future for California birds? *PLoS ONE* 4:e6825–e6825.
69. Williams SE, et al. (2009) Ecological specialization and population size in a biodiversity hotspot: How rare species avoid extinction. *Proc Natl Acad Sci USA* 106:19737–19741.
70. Rabinowitz D (1981) In *The Biological Aspects of Rare Plant Conservation*, ed Synge H (John Wiley & Sons, Chichester, UK), pp 205–217.