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RAMON MARGALEF PRIZE LECTURE OF 2015

Intrinsic and extrinsic influences on ecological communities

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Summary. Ecologists and evolutionary biologists have sought to understand geographic variation in the diversity of species ever since the great natural history explorations of the 19th Century and the subsequent development of ecology and evolution as scientific disciplines. Early insights, beginning with Darwin and Wallace, focused on the role of competition in limiting species coexistence within communities, but ecologists have gradually shifted to a more regional perspective that includes the processes of species production and extinction within regions. Recent observations, including the evolutionary lability of distribution and abundance, and the absence of a clear signal of competition impacts on populations of close relatives, suggest that coevolutionary relationships between pathogens and their hosts might be responsible for observed variation in distribution and abundance, and also drive the diversification of species within regions. Margalef's emphasis on observing nature closely, and paying attention to the implications of patterns for underlying processes, had a strong influence on me as a graduate student 50 years ago, and continues to be valid. [**Contrib Sci** 12(1):27-34 (2016)]

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Even before the great explorations of Alexander von Humboldt (1769–1859), Charles Darwin (1809–1882), Alfred Russel Wallace (1823–1913), and others during the 19th century, biologists were aware of the tremendous diversity of species in tropical environments compared to environments within temperate and boreal latitudes. Modern species inventories show that life tends to be most varied where the climate is warm and wet, and in mountainous areas in any climate zone [13,55]. Yet ecologists and evolutionary biologists continue to debate the underlying causes of these consistent patterns in species richness. The origin of diversity lies in the production of new species through various mechanisms of speciation, which for the most part require the initial spatial separation of diverging populations, that is, the allopatric model of species formation. In this sense, speciation is a regional process and no doubt depends on the history and

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geography of a region, whether a continent or a large body of water. While speciation builds diversity, extinction diminishes the species richness of a region, often leaving little evidence of the past for biologists and paleontologists. Both speciation and extinction influence species richness, but controls on the rates of these processes are poorly understood. In particular, biologists have argued over whether present-day diversity represents a steady-state balance between speciation and extinction, as in the regulation of population size when births exactly replace births; alternatively, species richness tends to increase with time, barring catastrophic extinction, and diversity reflects the age of a taxon or region [7]. Also at issue is whether any steady-state in diversity would represent a regional limit to species reflecting the interaction of populations with the geographic heterogeneity of a region, or local limits to species coexistence set by competition for resources and other interactions between populations at a particular location.

Contemporary biologists have puzzled over the "problem" of species richness for decades, and although both the data on species distributions and evolutionary relationships, and our ability to analyze those data, have increased dramatically in recent years, general consensus about the meaning of patterns in species richness continues to elude us. In his seminal paper in the journal *American Naturalist* in 1963, entitled "On certain unifying principles in ecology," Ramon Margalef (1963) pointed out that "Ecologists have been reluctant to place their observations and their findings in the frame of a general theory. … A certain effort should be made in constructing a general frame of reference, even though some of the speculation may be dangerous or misleading." [27]. This paper appeared during my first year as a graduate student with Robert MacArthur at the University of Pennsylvania, and I remember it having a dramatic effect, as did Margalef's insights placing ecological systems in the context of cybernetics [28].

Ecologists and evolutionary biologists are not lacking in hypotheses concerning diversity patterns, particularly the dominant latitudinal gradient in species richness [11,32,34], however distinguishing among explanations has been problematic. In particular, we have in recent years lost track of many of the natural history insights that motivated earlier generations of biologists and molded their thinking. In his writings, Margalef frequently emphasized the intrinsic value of natural history and of observing nature with an open mind. As I hope to show here, simply paying attention to patterns in nature can still provide valuable insights into the processes that have shaped the contemporary natural world.

Competition and ecological communities

Contemporary ecological thinking, particularly concerning the dominant influence of competition among populations on the species richness of natural communities, has its roots in the early development of the theory of evolution. The economist Thomas Malthus (1798), in his *Essay on the Principle of Population* [25] famously emphasized that competition for food resources would limit the human population. Charles Darwin (1859) was greatly impressed by Malthus's theory and incorporated competition as the primary driver of diversification in the formation of new species, for example: "And we have seen … that it is the most closely-allied forms … [which] generally come into the severest competition with each other; consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them." [3]. This strongly ecological principal was quickly assimilated into thinking about the relationships among species. For example, the American ornithologist Joseph Grinnell (1904), who later gave the word 'niche' its ecological meaning, pointed out that "Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other; the one longest exposed to local conditions, and hence best fitted, though ever so slightly, will survive, to the exclusion of any less favored would-be invader" [10, p. 377].

This idea of competitive 'exclusion' was soon given an experimental foundation by the pioneering studies of Tansley (1917) [61] on closely related species of bedstraw (*Galium*) and of Gause (1934) [8] on competition in *Paramecium* in the context of the developing mathematical theory of population interactions by Lotka, Volterra, and others [18]. By the mid-20th century, community ecologists had concluded that membership in local ecological communities, as well as geographic distribution within regions, is constrained by interactions between species [15,16, 20]. Robert MacArthur, in his doctoral dissertation under the direction of Hutchinson, asked how five superficially similar species of warblers (Aves: *Parulidae*) could coexist in the spruce forests of his native New England. His field observations showed that each species foraged in a different part of the spruce trees—one in the open branches at the top of the tree, another among the foliage at the base of the tree, and so on. Observations of this kind led to the idea that species could coexist only by partitioning resources in such a way as to reduce competition between them. Formal mathematical theory based on com-

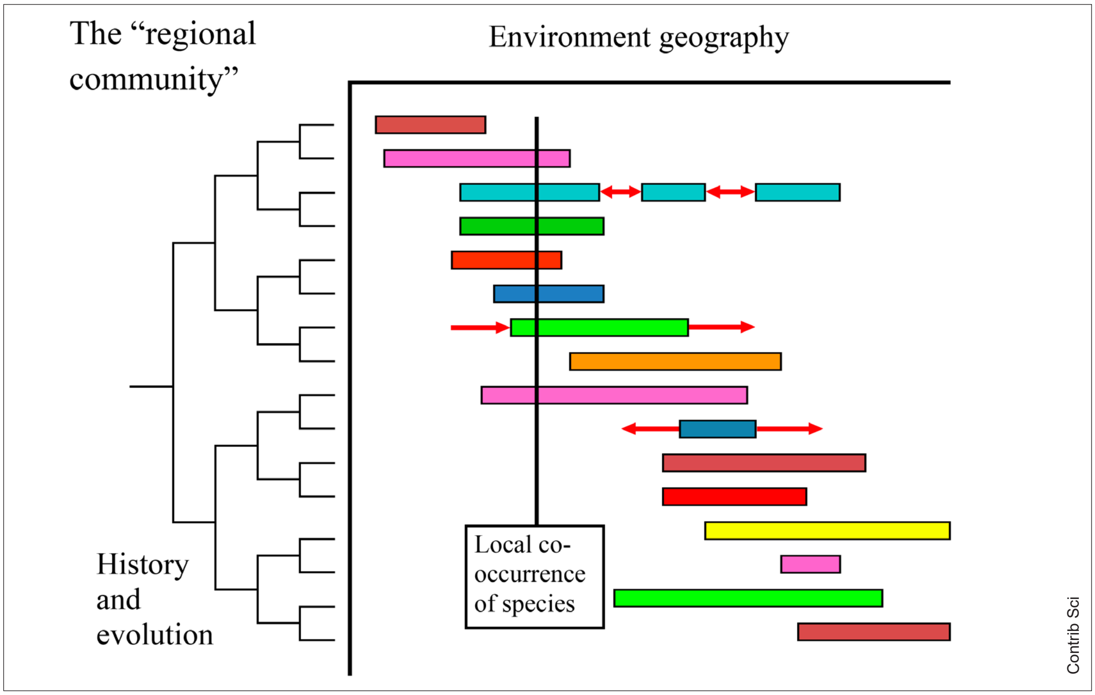


Fig. 1. A diagrammatic representation of the origin and distribution of species within a region, emphasizing the connection between regional processes and local assemblages of species and the dynamic nature of diversity and distributions on both evolutionary and ecological time scales.

petition equations supported the view that species richness is limited by competitive interactions among species for limited resources [24,29,62,63], reflecting the earlier insights of Darwin and Wallace, the latter of whom wrote "If a continent is fully stocked with animals, ..., then, so long as no change takes place, no new species will arise" [64].

If species richness were limited by competition and other local interactions between populations, then variation in species richness might be explained by the influence of physical characteristics of the environment—climate and soils—on the outcome of these interactions. This insight led to many analyses of the relationship between species diversity and climate and other variables [9,14]. A more recent example of such an analysis was that of Holger Kreft and Walter Jetz [19], who related plant species richness in hundreds of local floras to climate, while also investigating whether these relationships differed among regions. Seventy percent of the variation in species richness could be related statistically to local characteristics, particularly potential evapotranspiration (PET, a measure of the thermal energy of the environment) and number of wet days during the year. Except for the well-known elevated species richness of the Cape Region of South Africa, no region effects were identified—evidently species richness patterns were shaped by variation in local conditions.

Local and regional contributions to diversity

One of the apparent contradictions in the development of ecological theory during the middle of the 20th century was the emphasis on local conditions to explain patterns species richness in continental regions, and the emphasis on regional characteristics (area and distance to sources of colonists) to explain variation in species richness on islands [22,23]. Recently, many ecologists have been finding that regional characteristics do appear to influence, sometimes to a considerable extent, both regional and local diversity [52]. For example, mangrove forests have developed in essentially identical shallow marine environments throughout tropical regions of the world, but differ greatly in both regional and local numbers of species, being far more diverse in Australasia and the Indo West Pacific region than in the Atlantic and Caribbean regions [50,53]. The species richness of temperate forests, existing under similar climates and sharing many of the same genera of trees, increases from Europe to eastern North America and to eastern Asia [21]. This variation is quite generally related to the extinction of European species caused by climate cooling during the late Tertiary [57,58] and to regional influences on species formation contrasted between eastern Asia and eastern North America [35].

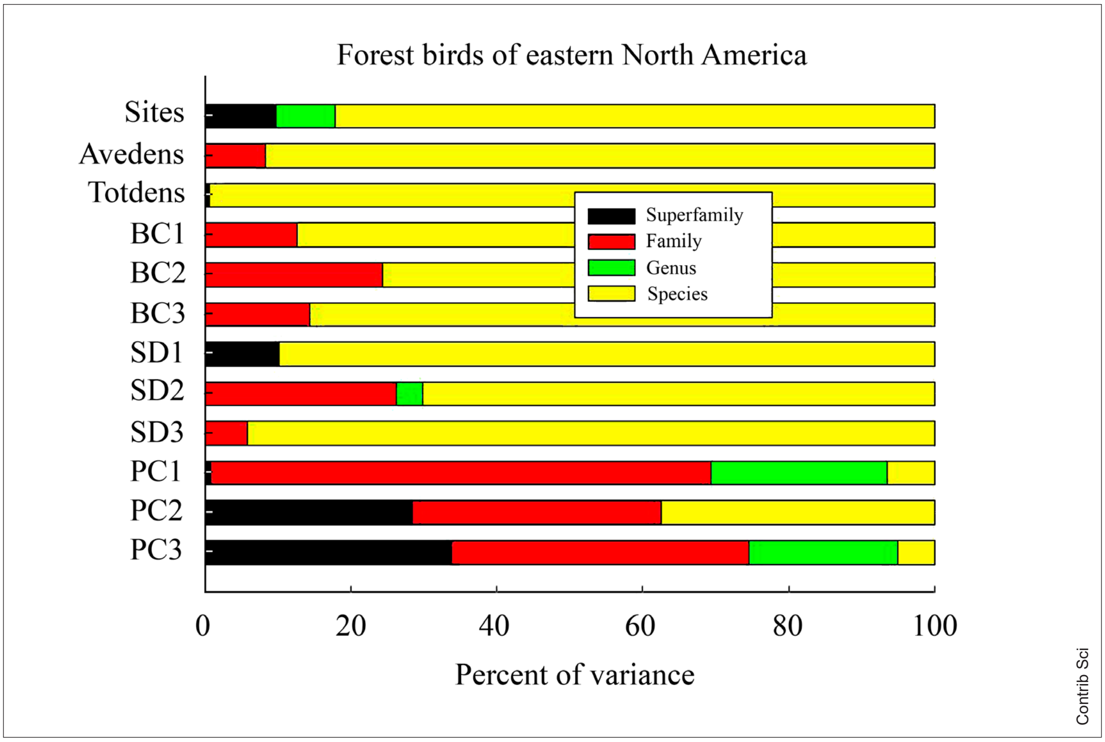


Fig. 2. The distribution of variance in population traits of forest birds of eastern North America. The yellow portion of the bar represents the proportion of the variance that represents differences between closely related species (i.e., in the same genus). The lowest three bars represent morphological variation, which exhibits the expected evolutionary conservatism represented by differences in measurements among higher taxa (green [genus], red and black [family and above]). The upper nine bars describe variation in population abundance, extent, and distribution. After [43].

Broad considerations of regional variation in species diversity, independent of differences in climate and other local conditions, have led me to adopt a regional concept of the ecological community that embraces interactions between populations over their entire distributions [37,38,42]. This idea is illustrated in Fig. 1, where regional and historical processes of species formation and extinction establish the overall diversity of a region, within which distributions are sorted out through interactions of populations over the entire area. A certain number of species will occur at any given point within the region—the local diversity—but their presence or absence at a particular place will depend on processes influencing population growth and the dispersal of individuals throughout the region. At any given time, a population might be expanding or contracting, which occasionally creates the isolated populations that can lead to independent evolution and formation of new species, and connects population processes to regional diversity.

At any given time, some species are widespread and abundant within a region, while others are rare and locally distributed. This variation is undoubtedly related to the particular adaptations of a species that determine its relationship to the physical environment, and also to other species that might be food resources, competitors, predators, or pathogens. These adaptations are difficult to characterize because the relationships of any particular species are complex. However, we can learn something about the nature of traits that influence a species' distribution and abundance by asking whether close relatives have similar population characteristics, which would therefore reflect shared adaptations inherited from a recent common ancestor. We can answer this question simply by conducting a hierarchically nested analysis of variance in distribution and abundance, as shown in Fig. 2 for forest birds of eastern North America. The result is that, in contrast to conservative morphological adaptations, distribution and abundance are evolutionarily very labile traits, with most of the variation reflecting differences between close relatives. That is, population characteristics appear to be unrelated to adaptations shared by close relatives.

One implication of this signal of extreme lability is that variation in distribution and abundance of populations must be influenced by highly species-specific factors. As I will emphasize below, I believe that the primary candidates

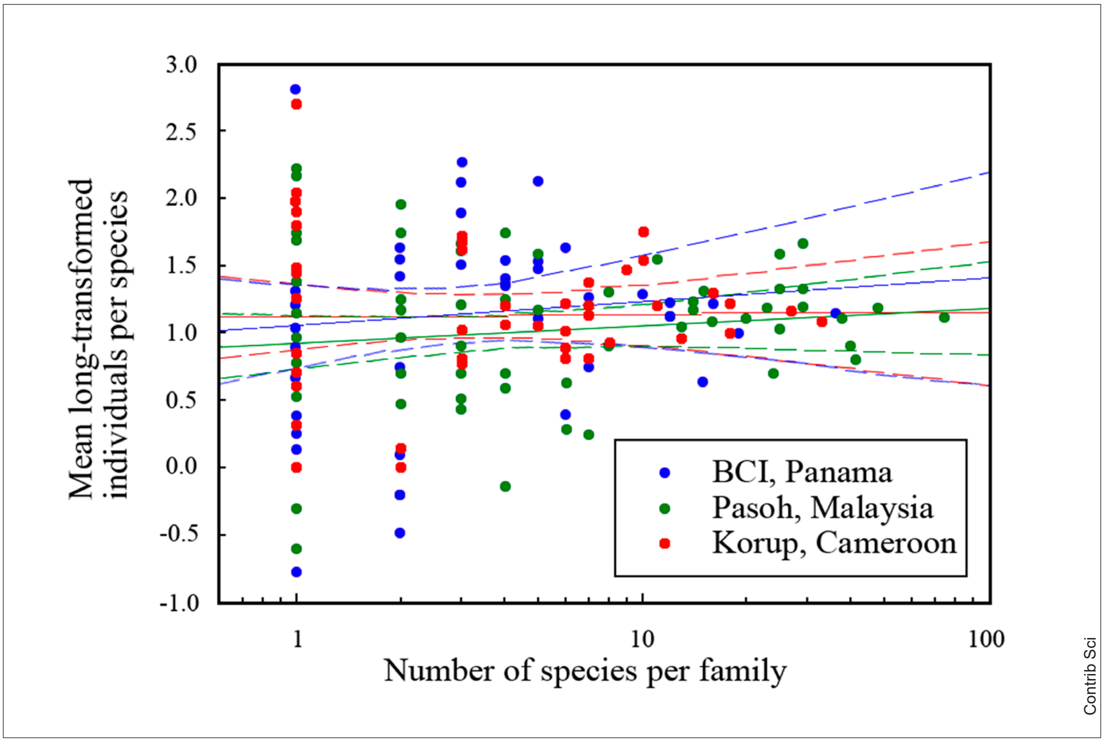


Fig. 3. The average abundance of a species of tree is not negatively influenced by the number of species belonging to the same family in 50-hectare forest plots in central Panama, Malaysia, and Cameroon. Data are from the Smithsonian ForestGEO project [www.forestgeo.si.edu]. After [43].

are specialized pathogens. This simple insight is very much in line with Margalef's admonition to learn from nature, that is, to let the patterns in nature suggest their underlying causes.

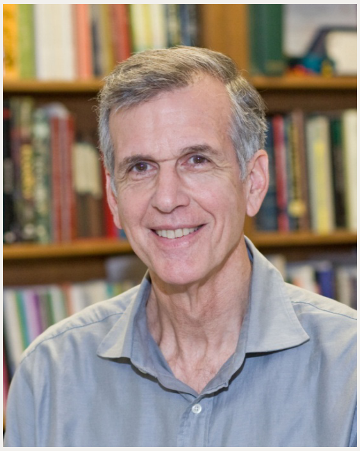
Testing the population effects of competition

Darwin's insight that "…it is the most closely-allied forms … [which] generally come into the severest competition with each other…" suggests a test for the influence of competition on local abundance. If this were true, we would expect the local abundance of a particular species to be depressed by the presence of close relatives in the same location. This hypothesis can be tested simply by relating the average abundance or density of species within a taxonomic group (say, a genus or a family) to the number of co-occurring species in that same taxon [39,41,44]. An example, based on the abundances of forest tree species in 50-ha plots in Panama, Cameroon, and Malaysia (Fig. 3), shows no impact on the local abundance of individual species from the presence in the forest of other closely-related taxa. I have observed such an absence of population impact from potentially close competitors in many tests of this type with a variety of organisms—trees, birds, butterflies. These results have led me to question, not that competition is a potent force in ecological systems, but rather that competition is primarily responsible for variation in the distribution and abundance in species.

These observations could be reconciled if ecological systems were more closely aligned with Steve Hubbell's [12] view of species being on a competitively level playing field, in which no one species has an advantage over another, but rather births and deaths in populations are completely random and occur at similar rates across all species. This is not the place to argue the merits of neutral theory in ecology. However, aligning ecological systems more closely with Hubbell's concept, and further removed from the competition-dominated concepts developed during the middle of the last century, allows small differences in population productivity to cause large variations in population abundance and distribution, which are then largely independent of particular functional traits.

Pathogens and the generation of diversity

My view that variation in distribution and abundance is related to the effects of specialized pathogens comes from work begun as a graduate student, and which has continued to the present, on the biogeography of birds in the West Indies [41]. Based on the varied distributions of species across the islands, it was clear to me and my long-time collaborator George W. Cox, that the range of one species might be expanding while that of a related, ecologically similar species might be contracting at the same time [47]. Such individualistic patterns argued against common causes, such as climate variation, and instead suggest specialized agents such as predators or, more likely, pathogens. Later phylogeographic work with Eldredge Bermingham at the Smithsonian Tropical Research Institute [45,46] confirmed that the so-called "taxon cycle" stages identified from geographic distributions and taxonomic differentiation of island populations indeed represented a temporal sequence, and that related species could be in different stages of this cycle at any given time. It is a small step to recognize that similar expansion and contraction cycles in continental biotas could ultimately drive species production within large regions.



About the author

Robert E. Ricklefs received his Ph.D. in Biology by the University of Pennsylvania in 1967. He developed his career as Assistant Professor and Professor of Biology at the University of Pennsylvania until 1995, when he gained the position of Curator's Professor of the Department of Biology at the University of Missouri-St. Louis. His research has been focused mainly in the evolutionary ecology and on diversity in ecological systems, with a special interest on birds as elements to explain the pathways of diversification. He has been awarded with several prizes, among them the William Brewster Memorial Award (1982), the Pacific Seabird Group's Lifetime Achievement Award (2003), the Margaret Morse Nice Medal (2003) and the Cooper Ornithological Society's Loye and Alden Miller Research Award. Since 2009 he is also a member of the National Academy of Sciences of the United States of America.

The potential impacts of pathogens on host distribution and abundance are well established by the detrimental effects of many introduced parasites and diseases on native host populations [1,2,17,26,33,40,56]. These effects are often species-specific. Pathogens and their hosts exert selective pressure on each other, either to increase virulence and contagion on the part of the pathogen, or to increase resistance to, and tolerance of, infection on the part of the host. This creates what has been referred to as a coevolutionary arms race between host and pathogen which, depending on the appearance of mutations that might shift the balance in the host-pathogen interaction, would lead to phases of expansion and contraction [4,5,36]. From the standpoint of the regional community, host-pathogen evolutionary dynamics seem capable of driving variation in distribution and abundance, which, interacting with the regional landscape, also might drive the large-scale processes that determine rates of species production and extinction.

Regardless of how causes(s) of variation in species richness over the surface of the earth and its waters are ultimately resolved, it is clear that discovery continues to depend on direct observation of nature—the natural history that Ramon Margalef found so important to the development of his own insights. Host-pathogen coevolution might not be the key to understanding patterns in species richness, but contemplating this perspective has led me to pursue new research on the haemosporidian (malaria) parasites of birds [6,30,31,48,49,51,54,59,60] that may yet contribute new insights into global patterns of diversity.

Acknowledgments. My research and insights into community ecology owe much to collaborators, students, and funding sources over the years. George W. Cox, Roger Latham, and Eldredge Bermingham have been wonderful colleagues; many students and postdoctoral fellows have contributed to the work in the West Indies and on avian malaria, including Irby Lovette, Steve Latta, Sylvia Fallon, Diana Outlaw, Maria Svensson-Coelho, Matt Medeiros, Vincenzo Ellis, and Leticia Soares; several organizations and agencies have generously funded parts of the research, including the National Geographic Society, Waitt Foundation, National Science Foundation, and the Curators of the University of Missouri. I am deeply honored by the Margalef Prize and humbled to be in the company of previous recipients. I am also grateful for the wonderful hospitality shown me by the Margalef prize committee, colleagues at the University of Barcelona, and members of the Margalef family.

Competing interest. None declared.

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Premi
RAMON
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Scientists awarded the Ramon Margalef Prize for Ecology (2005–2015)

The Autonomous Government of Catalonia created the Ramon Margalef Award for Ecology to honor the memory of the Catalan scientist Ramon Margalef (1919–2004), one of the main thinkers and scholars of ecology as a holistic science. His contributions were decisive to the creation of modern ecology. This international award recognizes those people around the world who have also made outstanding contributions to the development of the science of ecology. More information can be obtained at [www.gencat.cat/premiramonmargalef]. Since the 2010 Prize, all lectures given by the awardees are published in Contributions to Science [www.cat-science.cat].

Year	Winner	Main topic of research	Country
2005	Paul Dayton	Population and community ecology, mostly in benthic environments.	USA
2006	John Lawton	Dynamics of populations and communities, impact of global changes in organism populations and communities.	UK
2007	Harold A. Mooney	Plant physiological ecology and phenomena affecting global changes, such as ecological invasions, the loss of diversity and the degradation of ecosystems.	USA
2008	Daniel Pauly	Study of the decline of fish stocks and the ecosystems' response to human pressure.	France
2009	Paul R. Ehrlich	Population and human over-population.	USA
2010	Simon A. Levin	Mathematical modeling and empirical studies on the understanding of macroscopic patterns of ecosystems and biological diversities.	USA
2011	Juan Carlos Castilla	Marine ecology, mostly rocky ecosystems and their sustainability.	Chile
2012	Daniel Simberloff	Invasive species and their impact in the loss of diversity.	USA
2013	Sallie W. Chisholm	Biological oceanography and marine ecology, mostly for the studies in the understanding of the dominant photosynthetic organisms in the ocean and the microbiology of the oceans from a revolutionary new perspective.	USA
2014	David Tilman	Ecosystem functioning, biodiversity and protection of endangered species.	USA
2015	Robert E. Ricklefs	Intrinsic and extrinsic influences on ecological communities.	USA