Important roles of natural history in ecology

Charles BIRKELAND*

U.S. Geological Survey, Hawaii Cooperative Fishery Research Unit, Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, USA

* Corresponding author: C. Birkeland
E-mail: charlesb@hawaii.edu

Communicated by Makoto Tsuchiya

Abstract Natural history information is important for deciding the appropriateness of apparently proven theoretical models in particular cases, for interpreting controlled field experiments, for determining the ecological importance of individual species and the invasive potential of introduced species, for ground-truthing the extrinsic variables of ecological theory to evolutionary processes, for resolving unwarranted controversies into appropriate interpretations for different species, and for more effective and reliable management of resources. Manuscripts with natural history information are commonly devalued by reviewers of journals for functional and applied ecology, although they are still the foundation of journals for regional and evolutionary ecology. Gordon Orians concluded in 1962 that both functional ecology and evolutionary ecology are valid and useful, and it would be a mistake to construct ecological theory exclusively on either.

Keywords natural history, extrinsic variables, diversity, evolutionary ecology, functional ecology, management

Demotion of natural history

“Natural history” is the scientific study (more observational than experimental) of the adaptations of particular species, such as choice of diet, manner of reproduction, habitat, and especially, interactions with other species. With the accelerating global-scale effects of human activities such as climate change, lowering of ocean pH, severe overharvesting of resources, and with the potential for modern technology to assess large-scale phenomena with extrinsic variables (indices, ratios, and other metrics of groups of species), natural history has been moved to a lower status for acceptance in ecological journals.

Global-scale changes in ecosystem processes have compelled many ecologists to examine ecological processes with a “systems approach”. When initially drafting his book on “Ecology of coastal waters”, K.H. Mann considered trying to focus on large-scale ecological processes without mentioning the name of any plant or animal. The book eventually acquired a scattering of names of organisms, but they are incidental and the focus is on ecological processes. The complexity of coral reefs makes such a systems approach attractive. The April 2004 issue of Coral Reefs was devoted entirely to remote sensing of coral reefs, using sensors from satellites and aircraft to assess percent cover of living coral, percent coral bleaching, biomass of fleshy algae, substratum rugosity, transport of dissolved organic matter, fine-sediment transport, and other variables on a very large scale.

Perhaps one of the earliest direct assessments of extrinsic variables for coral reefs was reported in the classic
paper by Odum and Odum (1955). To determine the productivity of a coral reef at Enewetak, they measured the oxygen content of the water upstream and downstream, with the increase in oxygen during the day being a measure of the net primary production and the decrease in oxygen during the night being a measure of the total respiration of the community. Of course there are at least four kingdoms of algae contributing to the primary production and hundreds of species of microbes, algae, and animals contributing to the respiration. The contribution of each of these hundreds of species varies through time as a result of their respective diurnal shifts in activities. If the total respiration and primary production were estimated by adding the contributions of each of the species through their patterns of daily activities, the error variances would be compounded and the estimate would possibly be far from the true total value. The simple difference in oxygen content upstream and downstream integrates the effects of the entire community with extrinsic variables that can be quite accurate. A ratio of gross primary production to community respiration > 1 shows the reef community to be autotrophic (producing its own food) and < 1 shows the reef community to be heterotrophic (requiring food input).

Technology has also granted us an insight into the diversity of biological systems that we would never have obtained through examining individual species. It is estimated that less than one percent of bacteria can be cultured and individually examined (Gewin 2006). Of 52 phyla of bacteria found by 2003, only about half have any representatives that have ever been cultured (Rappé and Giovannoni 2003). The microbial diversity of the world’s oceans is being assessed on a global expedition by taking samples of seawater from a depth of about 5 ft, filtering the water to remove all but microbial DNA (Rusch et al. 2007). The DNA fragments are then amplified using polymerase chain reaction (PCR) and the resulting sequences are analyzed by computer algorithms that search for overlapping sequences to determine how they originally fit together into longer sequences. The numbers of species and phyla in the samples are then calculated by comparing the sample DNA to those from known microbial species. Venter et al. (2004) sampled the oligotrophic (“barren desert”) Sargasso Sea and the computer calculated about 1800 species from the DNA fragments. The species in samples from Long Island Sound overlapped with those from the relatively nearby Sargasso Sea by only one percent (Pennisi 2004) so the diversity in the world ocean must be immense. Although we may never know the nature of half the phyla of bacteria from which we are not able to culture a representative species, we will know of their existence through the DNA fragments. Diversity itself is often considered a key to ecosystem stability and services because it adds redundancy and thereby reliability to the ecological functioning of individual species (Naeem 1998).

In recent years, a number of books have focused on how the diversity of life and ecosystem processes are providing services that have sustained our civilization (e.g. Baskin 1997; Daily 1997). Functional ecology is now structured largely on extrinsic variables such as diversity, community heterotrophy, ecological efficiency, and others, i.e., variables that are made of ratios or indices that incorporate assessments of many individual organisms and usually many species. Journals that focus on functional and applied ecology tend to relegate manuscripts that contain natural history of individual species to regional journals (e.g. *Pacific Science*) or to journals of evolutionary ecology (e.g. *American Naturalist, Trends in Ecology and Evolution, BioScience*, etc). This essay will in no way deny the value of extrinsic variables of functional and applied ecology, but it will outline some of the important functions of natural history.

When I entered graduate school in the mid-1960s, one of the first pieces of advice I was given by Robert Paine was to be sure to know the natural history of the organisms, or I could misinterpret my data and experimental results. In those times, the importance of natural history was emphasized in the textbooks of ecology, especially evolutionary ecology (Pianka 1974), and in papers by modelers (e.g. Levins 1966) and analytical ecologists (e.g. Cohen 1968).

**Contributions of natural history to ecology**

**Determining the applicability of theoretical models**

Paul Dayton (1973) tested the quantitative predictions of a model by MacArthur and Levins (1967) of limiting
similarity in diet among competing members of a community. The model predicts that in a linear array of diets of three consumers, the diet of the species in between the other two cannot overlap with either more than 0.544. If the overlap exceeds this value, then the diet of the species in the center will converge towards the one with which it overlaps the most and only one of the two more closely overlapping species will survive the competition. Dayton gathered data from a number of different circumstances and found that the data did indeed fit the MacArthur–Levins model of limiting similarity for the three species through various conditions of overlap. However, natural history observations by Dayton showed that the central species, the sea anemone *Anthropleura xanthogrammica* depended on the two species of seastars to incidentally loosen the attachment of their respective prey so that wave action carries the prey into the grasp of the sessile anemone. The diet of the anemone converged with that of the seastar most common in the area nearest to it because the seastar that was most common provide the most food. The quantitative model of limiting similarity in competition was confirmed, but natural history observations showed that the process was dependence of one species on the other for provision of food rather than competition. As Dayton concluded, the right prediction was made, but for the wrong reason. On page 2 of Eric Pianka’s textbook on Evolutionary Ecology, the author states that “…there is certainly no substitute for a firm foundation in natural history. Models based on erroneous biological assumptions, no matter how elegant and elaborate, can hardly be expected to reflect nature accurately!”.

**Determining ecological importance of individual species**

In 2003, Peter Kareiva and Simon Levin compiled a book with 30 eminent ecologists as authors to examine the importance of species (Kareiva and Levin 2003). The chapters in the book explain how the natural history and thereby functional importance of individual species to the community changes with environmental context (Menge 2003), evolution (Palumbi 2003), and other perspectives. The biomass, abundance, proportion of community metabolism (perhaps measured by O$_2$ consumption or CO$_2$ release) or number of prey consumed are not necessarily the most reliable measures of the importance of a species in its community. Paine (1980, 1992) measured the comparative importance of individual species through per capita interaction strength. In his 1966 paper, Paine describes how a predatory gastropod *Thais* can kill more barnacles than does the predatory asteroid *Pisaster* in the area, yet *Thais* has no apparent effect on the diversity of the area because it drills and consumes its prey, leaving the “husks” or tests of the prey occupying the space (Paine 1966). Although *Pisaster* might eat fewer prey, its substantial effect on community structure is explained by the natural history observation (and confirmed my controlled manipulative field experimentation) that it removes a cluster of prey during high tide, clearing a patch, and carries the group of prey down to lower levels to consume during low tide periods. The patch cleared by predation sometimes weakens the solid mat structure of the prey population and allows wave action or drift logs to further

**Interpretation of controlled manipulative experiments**

Dayton (1973) also tested with experimental manipulation the hypothesis that competition limits the number of species sharing a simple resource. A simple resource on the rocky intertidal is space for attachment. The model predicts that when space is cleared by a disturbance, the number of species will initially increase with recruitment, but as space becomes filled, the number of species will decrease because of competition for space. Dayton cleared space and covered half the cleared spaces with predator exclusion cages. In all treatments and replicates, the predicted results were obtained and so the hypothesis was confirmed. However, natural history observations by Dayton found that in spaces that were not protected from predation, there was always an abundance of unused space and that some of the residents were eliminated by desiccation, predation or other disturbances and competition was not observed. So the controlled manipulated experiment confirmed the predicted outcome, but natural history observations indicated that in half the cases, the predictions were correct, but for the wrong reasons. Natural history observations can validate or correct the interpretations of controlled manipulative experiments. If the insight from natural history was available a priori, then the experimental design could have been modified accordingly.
erode the basal attachments from the side and expand the size of the patch, providing space for an added diverse assortment of species. In any case, it is the manner of predation rather than the number of prey taken that determines the major role of *Pisaster* in maintaining the diversity of the community.

Ecological theory considers the role of diversity per se. Diversity purportedly adds stability to ecosystem function and reliability to ecosystem services through species redundancy (Naeem 1998). With a greater number of species present, it is also more likely that species with the necessary functions are present. Theory notwithstanding, observations indicate that the resiliency of coral reef systems does not appear to be related to species diversity. Presentations at the 11th International Coral Reef Symposium generally reported that less diverse mid-ocean reefs were nonetheless resilient when subjected to numerous disturbances and factors of stress. Bermuda hosts only 22 species of coral. The waters of the north Atlantic have the greatest rate of atmospheric CO₂ uptake in the world (Sabine et al. 2004), and the rates of calcification of corals have been declining over the past 50 years (Cohen et al. 2008), yet the reef communities of Bermuda are more resilient (Murdoch et al. 2008) than those of the tropical western Atlantic (Gardner et al. 2003) even though the western Atlantic has about three times as many species of corals. Likewise, the reefs of the central Pacific (e.g. French Polynesia 119 species, Chevalier 1982) are less diverse than those of Japanese waters (410 species, Nishihira and Veron 1995), yet those such as in American Samoa (Birkeland et al. 2008), Fiji (Lovell and Sykes 2008) and Moorea (Adjeroud et al. 2008) have proven surprisingly resilient to disturbance and stress.

Although diversity per se does not seem to have the consistent effect on coral reef communities suggested by ecological theory, individual species with particular characteristics can have large-scale effects. Natural history characteristics of *Acanthaster planci* lead it to occasionally devastate many km² of coral communities while nine or ten other species of asteroids in the Pacific that prey upon corals are constrained by their own morphological traits (Birkeland and Lucas 1990). The crown-of-thorns seastar has the gifts of a morphology with large food-intake to biomass ratio as a juvenile that provides for rapid growth to maturity and an elastic disk-like structure in early reproductive years that allows for a broad range of available prey. Furthermore, the extraordinary fecundity of *A. planci* provides it with the capacity to capitalize rapidly when the larvae are fortunate and provided with a dense food supply for larvae. The natural history of the benthic phase of the life history of *A. planci* explains why it is the only corallivorous asteroid with an occasional major effect on the coral-reef community and the natural history of the larval phase provides for occasional increases in population size of up to six orders of magnitude.

The geographic-scale effects of a single species of herbivore *Diadema antillarum* in the Atlantic (Carpenter 1990) was recognized by its absence after the spread of a disease, in contrast to the effects of *Acanthaster planci* in the Pacific which was documented after its overwhelming presence (Birkeland and Lucas 1990) following a phytoplankton bloom which provided food for its larvae. A few large parrotfishes will excavate coral-reef substrata, while the same total biomass of more numerous smaller individuals will have negligible effect (Bruggemann et al. 1996).

Of 287 species of alien marine invertebrates that have probably permanently established themselves in Hawaii, quite a few have become widely distributed and abundant (Coles et al. 2006), but so far only four or five have a major influence on other Hawaiian marine life through forcing niche compression in particular indigenous species (Kahng and Grigg 2005; Zabin 2009) or simply having become overwhelmingly abundant and occupying space to the exclusion of indigenous species (Coles et al. 2006, Riegl et al. 2009). It is generally the case that alien or introduced species that have the natural history traits of being generalists, i.e., without constraining niche requirements, and with rapid maturation to sexual reproduction and high fecundity, are most likely to have potential to be invasive.

**Ground-truthing the extrinsic variables of ecological theory to evolutionary processes**

Lawrence Slobodkin was an exemplary scientist because he kept an open mind, recognizing and accepting how natural history characteristics of individual organisms can undermine years of work on ecological theory.
Slobodkin spend a number of years early in his career testing a hypothesis of constancy of maximum ecological efficiency (the steady state ratio of yield to food ingested) at around 10 percent. He did sets of experiments with *Daphnia* and again with *Hydra* that “were expensive and time consuming in the extreme” (Slobodkin 1961, 1962, 1964). At first, field data seemed to generally corroborate a relatively constant ecological efficiency. But with time it became apparent to him that ecological efficiency is not a constant; it varies substantially with the natural history of the species, e.g., whether it is a homeotherm or poikilotherm, whether it is a herbivore or a carnivore, whether it is fast-moving (hummingbird, shrew) or slow-moving (albatross, sloth), whether it is fecund or recently born.

More importantly, Slobodkin pointed out that there is a fundamental difference in extrinsic (ecological theory) variables such as ecological efficiency, diversity, and community autotrophy that characterize populations, communities or ecosystems and intrinsic (natural history) variables such as body size, fecundity, and other characteristics of individual species. The difference is that natural history traits can be acted upon directly by natural selection. Extrinsic variables such as ecological efficiency, diversity, topographic complexity, community stability cannot be directly maximized, minimized or otherwise directly influenced by natural selection (Slobodkin 1972). He admonished us to show, for any ecological theory based on extrinsic variables, how it can be related to intrinsic variables for individual organisms that can be acted upon by natural selection.

Slobodkin (1970) summarized findings presented at a fisheries symposium on marine food chains by warning that rather small inaccuracies in estimates of extrinsic variables can become orders of magnitude errors across trophic levels with serious practical consequences. Further, as admonished by Johannes (1998) for coral-reef fisheries, when requesting responsible management from local fishers, it is unrealistic to base regulations on extrinsic variables such as quotas or total catch, but they should be addressed in terms of intrinsic variables such as size of fish, reproductive activities, or protected areas (Slobodkin 1970; Johannes 1998). As with theoretical models and controlled manipulative experiments, fisheries models based on extrinsic variables should be frequently ground-truthed by natural history observations.

**Effective and reliable management of fisheries resources**

Natural history has also been more effective in handling applied ecological challenges such as resource management. Quantitative fisheries science has not been effective in sustaining marine fisheries (Pauly et al. 1998; Myers and Worm 2003). The scientific management of coral-reef fisheries has been particularly poor (Munro 1996), a consequence of the complexity of the multispecies system. In contrast, Pacific islanders have often been able to manage resources sustainably by establishing fishing practices based on the biology and natural history of the individual species (Johannes 1998). In some successful Pacific island fisheries managed by indigenous cultures, there are no quantitative restrictions on how many fish or other resource species can be taken or which gear can be used (other than prohibition of destructive practices, e.g., using dynamite or chlorine), but rather qualitative restrictions based on the natural history of the species, i.e., recognition of closure to fishing during the breeding season of the particular species (Titcomb 1972; Johannes 1998; Pacific American Foundation and Hui Malama O Mo’omomi 2001) or taking only intermediate-sized fish of a species, leaving the larger for effectively sustaining the resource by advantage of their fecundity and by allowing a complete array of sexes (Birkeland and Dayton 2005). Robert Johannes (1988) has already reviewed the need for dataless, adaptive, precautionary management.

**Resolving unnecessary ecological controversies**

Ecological controversies have endured for decades on theoretical issues such as whether population regulation is density-dependent (usually controlled by species interactions which change with population density such as competition or predation or disease) or density-independent (usually affected by changes or disturbances in the physical environment such as storms, heat-waves, droughts which are indiscriminant of population density). Gordon Orians pointed out in 1962 that the natural history of the different species and communities used as focus of studies by the two camps might automatically compel them towards their respective viewpoints. Birds were used as
examples by David Lack (1954) in promoting the influence of density-dependent processes. If the population density of birds was too great for the food supply, the birds laid fewer eggs or there was a lower survival of offspring, which led to density-dependent regulation of population size. Furthermore, birds are often territorial, which is an evolved intraspecific density-regulating behavior. Birds might be less vulnerable to fluctuations in weather because they are homeotherms. In contrast, agricultural insect pests were used as examples by Andrewartha and Birch (1954). The agricultural insect pests tended to be short-lived poikilotherms and more directly affected by seasonal changes in weather.

In explaining how the decades of controversies over whether the mechanisms of regulation of animal populations are density-dependent or density-independent were on a peripheral issue, Orians (1962) concluded that the deeper root of the dichotomy was a fundamental division of ecology into two major fields, functional ecology and evolutionary ecology. Natural history has been moved to a lower status for acceptance in ecological journals that focus more on systems ecology, applied ecology, ecosystem ecology, i.e., functional ecology. Journals that are focused on evolutionary ecology such as American Naturalist, Trends in Ecology and Evolution, BioScience, American Scientist, and others often examine adaptations and roles of individual species in systems, i.e., are rich in natural history. American Naturalist unabashedly has a regular section called “Natural History Miscellany” and many of the papers cited in this essay on the important roles of natural history in ecology are from American Naturalist (Dayton 2003). As Gordon Orians concluded in 1962, both functional ecology and evolutionary ecology are valid and useful, and it would be a mistake to construct ecological theory exclusively on either.

Acknowledgments

This essay is in recognition of Professor Kiyoshi Yama­zato who, in his studies of reproduction and species inter­actions of corals, always based his research on a solid foundation of natural history.

References


Received: 31 August 2009
Accepted: 13 October 2009

Ⓒ Japanese Coral Reef Society