4 *Ecological Invariance and the Search for Generality in Ecology*

H. Ronald Pulliam and Nickolas M. Waser

Figure 4.0. The "Ipo Disciples" at work: field studies of scarlet gilia (*Ipomopsis aggregata*) in the Colorado Rocky Mountains. Photograph by Dennis Johns, 1981.

Abstract

Whereas the physical sciences seem to be characterized by universal constants and laws, which allow generalization from one system to another, it is questionable whether ecology enjoys any such invariants. The Hutchinsonian niche might be one ecological invariant, and it has been used as such in relating distribution and abundance of species to their niche requirements. On the other hand, ecologists are unsurprised to find variation in niche expression of a given species. We present two examples: geographic variation in tolerance to herbivory in the montane wildflower *Ipomopsis aggregata*, and geographic differences in the relationship between soil moisture and abundance of the understory herb *Polygonatum biflorum*. The first example illustrates the unfortunate possibility that perceived differences in niche expression derive from differences in method—"unfortunate" because it is difficult to detect unless researchers truly cooperate, and also because it can foster fruitless debate. Both examples illustrate two additional possibilities: that variable niche expression derives from location-specific differences in

the "realized" niche of a species, and that it derives from differences in the "fundamental" niche due to genetic differentiation within species. Deducing the contributions of these two factors is beyond our current ability. Instead we discuss how to explore such possibilities by challenging multiple working hypotheses with increasingly sophisticated knowledge of natural history derived from long-term place-based observation and experimentation. This approach is an alternative to more common "null-hypothesis testing," and we assert that it can lead to a depth of mechanistic understanding at which one does in fact reach a level of ecological invariance.

Introduction

> H e insisted that there is no Truth but only many truths; that Truth is not a colored bird to be chased . . . but a skeptical attitude toward life.
>
> *Sinclair Lewis (1925)*

> Consider the concept of niche.
> If I knew what it meant I'd be rich.
> Its dimensions are *n*
> And a knowledge of Zen
> Is essential to fathom the bitch!
>
> *Grant Cottam and David Parkhurst (unpublished, ca. 1969)*

Some sciences—especially physics and chemistry—are known for their invariant physical constants and general laws. Just look in the back of any standard textbook: Planck's constant is $h = 6.626069 \times 10^{-34}$ Js; Newton's constant of gravity is $G = 6.6743 \times 10^{-11}$ $m^3\ kg^{-1}\ s^{-2}$; the speed of light in a vacuum is $c = 299{,}792{,}458$ ms^{-1}. Furthermore, these constants can be used to quantify relationships among independent variables. For example, Newton's Law of Universal Gravitation states that the force with which one object attracts another is $F = G\frac{m_1 m_2}{r^2}$ where m_1 and m_2 are the masses of the two objects and r is the distance between them. Hence the physical sciences appear to enjoy laws, constants, and relationships—descriptions of the behavior of matter and energy—that apply universally, at least at macroscopic and nonrelativistic scales.

Does ecology have any similar universal laws or invariant constants, which allow us to generalize from one system to another, so as to predict a priori the behavior of systems that have not been studied? The exponential growth equation, $dN/dt = rN$, relating population growth rate (dN/dt) to population size (N), is sometimes called the Malthusian law (e.g., Gause 1934) and the parameter r is called the intrinsic rate of natural increase. But

measuring r at one place and time may reveal little to nothing about its value in another place or time.

Ecological invariants known as "scaling and power laws," that describe power relationships across species or across ecological systems, also have been well documented and explored (e.g., Charnov 1993, Brown et al. 2000, Marquet et al. 2005). For example, the number of species (S) in a given land area (A) can be expressed as the species-area relationship, $S = cA^z$ (MacArthur and Wilson 1963). This is a pretty good law (description of a system's behavior), as it has been shown to apply for both true oceanic islands and for habitat "islands" in a "sea" of other habitats. But the exponent (z) varies, usually between 0.20 and 0.35, so the law hardly qualifies as a universal constant. Furthermore, we are concerned here with invariance of another sort—in particular, with whether or not the relationships among species, or between species and environment, documented at one place can be generalized and applied to other places.

Let us carry our musings further. The fact that r varies across species is somewhat akin to different chemical elements having different atomic mass. It could also be argued that r is really more like weight than mass, inasmuch as it varies as a function of biological species and environment rather as weight varies as a function of chemical element and environment. A more apt physical analogy to the species-area relationship or the exponential growth equation might therefore be a model for the rate of a certain chemical reaction at standard temperature and pressure: the rate of reaction applies only for specific environmental conditions. So far, so good; it seems that ecological and physical laws have some similarities. However, much of the predictive power of modern physical chemistry comes from the ability to extrapolate from standard conditions to other conditions. Alas, in ecology, a careful measurement of the rate of increase of a species in one environment might provide little information about how the same species will perform in other environments.

Is the Fundamental Niche an Ecological Invariant?

The "niche" of a species has served as a central concept in ecology, and is another candidate for an ecological invariant. Early ecologists (Grinnell 1917, Elton 1927) used the word to refer to a "recess" in the environment that has the potential to support a species. In this view the niche is an attribute of the environment; niches can be empty or full, and more than one species might vie for the same niche. G. E. Hutchinson (1957) turned the concept on its head, defining the niche as the environmental requirements of a species; in this view species, not environments, have niches. Hutchinson defined the

"fundamental niche" of a species as an *n*-dimensional hypervolume, "every point in which corresponds to a state of the environment that would permit a species to exist indefinitely." Alternatively, the fundamental niche is the set of all environmental conditions for which the per capita population growth rate ($1/N\ dN/dt$) is greater than or equal to zero.

Is this mapping of fitness[1] on environment invariant? Standard texts often describe niche requirements as if they are fixed characteristics of species. In a typical example, *Bergey's Manual of Determinative Bacteriology* (Bergey et al. 1994) states that the bacterium *Norcardia farcinia* grows at temperatures between 20° and 40° C and at pH of from 6 to 10, and does best at 35° C and pH 7.5, but that *Treponema phagedenis* grows at temperatures of between 30° and 42° C and at pH of from 6.5 to 8, and does best at 37° C and pH 7. Should we treat such descriptions as invariants that determine the distribution and abundance of species in nature? This is commonly done, in fact, and has been done since the earliest days of ecology. For example, the distribution of trees along elevation and latitudinal gradients is often interpreted as a response to temperature and moisture requirements (e.g., Merriam 1890). In the southwestern United States, for example, Douglas fir (*Pseudotsuga menziesii*) is found at higher elevations where precipitation is high and temperatures are low, but descends to lower elevations in cool, moist canyons. The fixed relationship between climate and species distribution is a guiding principle of paleoecology, and is used extensively to reconstruct past climates.

In short, patterns in the distribution of terrestrial organisms (and analogous patterns in aquatic ecosystems) make sense in light of modern niche theory. The concept of fixed niche requirements provides a powerful tool for interpreting current distributions, reconstructing environmental conditions of past distributions, and predicting response to future conditions, including a changed global climate.

The Variable Niche

Although ecologists often treat the niche as an invariant, we also recognize that the observed niche may vary through space and time. Hutchinson himself distinguished between "fundamental" and "realized" niches. The fundamental niche characterizes the fundamental requirements of a species and, in this respect, might be thought of as invariant. The realized niche is molded by biotic interactions. Hutchinson argued that a species may be absent from a portion of its fundamental niche because it is displaced by competition from a superior competitor (figure 4.1). Imagine, for example, a laboratory study of the ability of a particular plant species to grow and reproduce. In a separate field study the species is present at low values of soil moisture but absent from wetter locations, even though it does well under

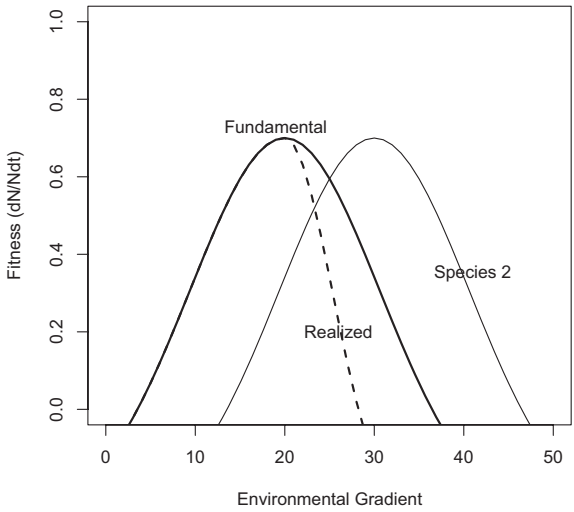

Figure 4.1. The realized niche may be a portion of the fundamental niche because a superior competitor (species 2) displaces the species from the rest of its fundamental niche.[2]

such conditions in the laboratory. Following Hutchinson, we postulate the presence of an unknown competitor that displaces the species from wetter locations. This seems akin to an astronomer postulating the presence of an unseen planet by observing some anomaly in the movement of a star.

The possibility of deducing the presence of a hitherto unknown competitor from the distribution of another species might lift the spirits of ecologists looking for generality and predictive power. Alas, there are other possible explanations for variable niche expression. For example, our plant might be able to resist fungal attack at low soil moisture, whereas the pathogen, not present in the laboratory studies, gains an upper hand in moister locations in nature. Indeed, ecological interactions are not limited to those that are antagonistic; mutualisms also might vary in space or time, leading to different observations of realized niches.[3]

Still other explanations are possible that may dash our hopes for the Hutchinsonian niche as an ecological invariant. Although it is not uncommon for ecologists to think typologically of a species, Charles Darwin introduced an alternative in chapter 2 of the *Origin of Species*: "No one supposes that all the individuals of the same species are cast in the same actual mold. These individual differences . . . afford materials for natural selection to act on and accumulate." If laboratory and field studies are done in different locations, they may compare genetically different entities within one species, the results of different histories of natural selection that have led to a different (in this example smaller) fundamental niche at one location than the other.

A Roadmap for What Follows

In what follows we present two examples of niche variability. First we consider the response of plants to a biotic dimension of the niche, the intensity of attack by herbivores. Reproduction of the wildflower *Ipomopsis aggregata* appears to respond differently to grazing by herbivores depending on geographic location. In most locations grazed plants suffer reduced flower and seed production, but in some locations grazing seems to *increase* fecundity. Tempting explanations include environmental or genetic differences that elicit different plant responses—that is, changes in realized or fundamental niches, respectively—but we cannot exclude the possibility that variable responses are artifacts of using different study methods. In the second example we explore why population density of the forest herb *Polygonatum biflorum* increases with increasing soil moisture at one site but declines in another. Since high population density is often taken as a reflection of suitable environmental conditions, we first consider this to be example of variable niche expression, but later raise the possibility that high density per se does not necessarily reflect suitable conditions. We end by recommending how ecologists can treat niche variability as an opportunity rather than a problem. We discuss some features of niche theory that reconcile the possibility of an invariant fundamental niche with a variable realized niche. More generally, we recommend ways in which place-based research, informed by knowledge of natural history, can contribute to an iterative process of model building that provides an alternative to classical "hypothesis testing" for gaining certainty about nature.

Variable Compensation by *Ipomopsis Aggregata* to Browsing of Inflorescences

Scarlet gilia, *Ipomopsis aggregata*, is an attractive wildflower common to mountains of western North America (Grant and Wilken 1986). Although often described as biennials, these plants are usually longer-lived semelparous perennials—that is, they flower once and die after spending multiple years (Waser et al. 2000) as vegetative rosettes of leaves. Flowers are both male, reproducing through export of pollen to other plants, and female, reproducing through import of pollen and setting of seeds. They are pollinated primarily by hummingbirds, but insects also play a role (Price et al. 2005). Throughout much of its geographic range, *I. aggregata* plants are browsed by ungulates (elk, *Cervus elaphus*, mule deer, *Odocoileus hemionus*, and/or white-tailed deer, *O. virginianus*) as they elongate their single flowering stalks. The usual response among surviving plants is to produce multiple

secondary flowering stalks on lateral stems, eventually yielding a replacement crop of flowers.

The simplest expectation is that the unlucky browsed plant might produce a fraction of the seeds it would have otherwise—better than nothing, but not compensating for the loss of female reproductive success represented by the original inflorescence. In 1987, however, Paige and Whitham reported that naturally browsed plants of *I. aggregata* subspecies *formosissima* in northern Arizona, as well as plants clipped experimentally to mimic browsing, actually overcompensated. Browsed and clipped plants flowered virtually synchronously with undamaged plants and achieved the same total inflorescence height but, because of their multiple inflorescences, produced on average 2.8 times as many flowers and 3.0 times as many fruits and seeds as undamaged plants (in turn, overcompensation by experimentally-clipped plants averaged 1.9 times as many flowers and 2.4 times as many fruits and seeds). In subsequent work, Paige and colleagues reported overcompensation in other subspecies (in particular, *I. aggregata* subspecies *aggregata* in Colorado; Paige 1999), and in male reproductive success (success in siring seeds on other plants) in *I. aggregata* (Gronemeyer et al. 1997) and its relative *I. arizonica* (Paige et al. 2001).[4]

Overcompensation to browsing was not without precedent (e.g., McNaughton 1983). Still, overcompensation in *Ipomopsis* met with excitement because of its apparent magnitude. Several investigators attempted to confirm the result, without success.[5] Bergelson and Crawley (1992a, 1992b) summarized results of an extensive survey across a large portion of the geographic range of *I. aggregata* encompassing several subspecies, including those studied by Paige and colleagues. In comparing both naturally browsed and experimentally clipped plants to controls, they found the opposite of the previous result: dramatic undercompensation to browsing, with controls achieving up to 7.5 times the average female reproductive success of damaged plants.

Response to browsing by ungulates can be thought of as an expression of part of the Hutchinsonian niche, especially as extended by Maguire (1973), because it represents the mapping of a fitness component onto a biotic niche axis (figure 4.2). Contemplate a niche axis of increasing intensity of browsing. At some point it is easy to imagine that $1/N\ dN/dt$ becomes negative—browsing of reproductive structures is so intense that a plant species cannot replace itself and, in the absence of immigration, will go locally extinct. This represents a condition outside of the fundamental niche. But in scarlet gilia one confronts the possibility that ungulate herbivory may increase fecundity, so that ungulates act not as enemies but as mutualists.[6] This is a reversal of niche relationships in that one expects the species to be absent in areas of high ungulate density at one location, but to be concentrated in such areas

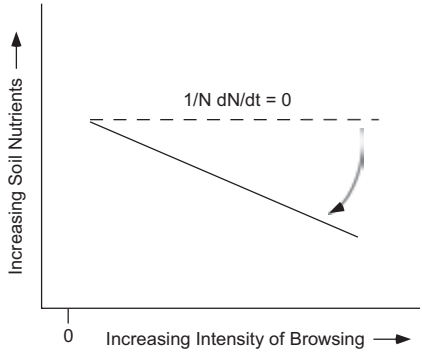

Figure 4.2. Hypothetical niche axes for *I. aggregata* in northern Arizona. If browsing by ungulates were absent, populations would achieve positive growth only if soil nutrients fell above the level indicated by the dashed line, which is therefore the zero-net-growth isocline (ZNGI) for this hypothetical situation. In fact, ungulate browsing does occur, and as browsing intensity increases, so does fecundity. Thus the actual ZNGI has a negative slope, as indicated by the solid line.

at another location. What could explain such variable niche expression, and what does it say about the niche as an ecological invariant? We return to this after the next section.

Variable Response of *Polygonatum Biflorum* to Soil Moisture

Polygonatum biflorum is a common understory herb in moist mid-elevation forests of the southeastern United States. Pulliam and coworkers have analyzed survival, growth, and reproduction of *P. biflorum* of this and several other species (Giladi 2006, Diez 2006, Diez and Pulliam 2007) in a region extending from the Whitehall Forest (<150 m elevation) in the Piedmont near Athens, Georgia, to the Coweeta Hydrologic Laboratory (750–1,500 m elevation) in the Blue Ridge Mountains of North Carolina. This represents a steep gradient in elevation, and thus in mean annual precipitation (≈120 cm at Whitehall, >180 cm at Coweeta) and temperature (16.5° C at Whitehall, <12° C at Coweeta). Plant populations at the southern end of the gradient typically experience a three- to six-month period during the summer when evaporation exceeds precipitation, whereas at higher elevations the period of moisture stress is shorter and less severe.

If the niche is an ecological invariant, we might expect the abundance of *P. biflorum* to be related to soil moisture in a consistent fashion. To explore this, Pulliam and coworkers marked individuals on six study grids at Coweeta and six at Whitehall. On each grid, soil moisture was measured throughout the growing season and the average was calculated. A prelimi-

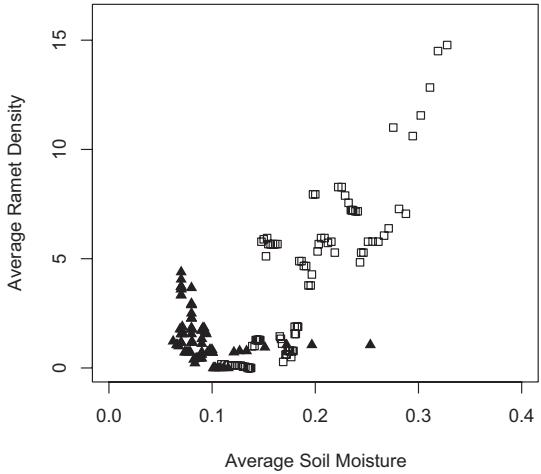

Figure 4.3. Relationships between *P. biflorum* ramet abundance and soil moisture at Coweeta (squares) and Whitehall (triangles). Average ramet abundance generally increased with increasing soil moisture at Coweeta, but not at Whitehall. The average ramet abundance shown is the nine-point running average with data arranged from the driest to moistest cell for each place.

nary look at the data (figure 4.3) suggests that *Polygonatum* abundance increases with moisture at Coweeta, and the opposite at Whitehall. We want to look behind this simple interpretation; in particular, we want to determine whether the relationship truly varies between the two locations approximately 100 km apart, and among grids separated by 0.5 to 2 km within each location. Our basic approach is to use a Bayesian "model selection" criterion to ask how the relationship varies between locations and among study grids within locations (box 4.1).

We anticipated an optimum moisture level, and expected that abundance might initially increase with increasing moisture and then eventually decrease. Parameter estimates from model 3a (box 4.1), the model that best fit the data, indeed suggest humped curves (figure 4.4) with intermediate moisture optima. But the overall trends were a decrease in abundance with increasing soil moisture at Whitehall and the opposite at Coweeta. We surmise that this is because none of the observed soil moisture values at Whitehall was less than 10%, so most observed abundances come from the descending right side of the Whitehall moisture curve. At Coweeta, only a few of the observed soil moisture values were above 35%, so most observed abundances come from the ascending left side of the Coweeta curve. The lack of observations in the lower part of the moisture curve at Whitehall may also partially explain the uncertainty about the parameter values for this location. Again, we return to these possibilities after the next section.

BOX 4.1. Analyzing responses of *Polygonatum biflorum* to soil moisture at two sites.

To compare the reactions to soil moisture of *Polygonatum biflorum* plants at Whitehall Forest, Georgia, and Coweeta, North Carolina, we used nested, hierarchical Bayesian models (Carlin and Louis 2000, Press 2003). Because we anticipated that abundance might initially increase with increasing moisture and then decrease, we included both first-order (moisture) and second-order (moisture-squared) terms in all models, and subsequently removed terms to see whether the model was improved without them. Bayesian regression analysis was performed with the WINBUGS statistical package (MRC Biostatistics Unit, Cambridge University, UK), with 30,000 iterations and a burn-in of 10,000 iterations.

The first set of models is nonhierarchical and assumes that regression coefficients relating density to moisture are the same at all sites:

$$D_{ijk} = \exp(a + b_1 M + b_2 M^2) + \varepsilon_{ijk}, \qquad \text{(model 1A)}$$

where D_{ijk} is the number of ramets on cell i of grid j at site k, a is the intercept, b_1 and b_2 are first- and second-order regression coefficients, and ε_{ijk} is the Poisson distributed error term. The second set of models is similar, but it allows the regression coefficients to vary between sites:

$$D_{ijk} = \exp(a_k + b_{1k} M + b_{2k} M^2) + \varepsilon_{ijk}, \qquad \text{(model 2A)}$$

where a_k, b_{1k}, and b_{2k} are the regression coefficients for place k. Finally, the third set is similar but allows each grid in each site to have a different intercept:

$$D_{ijk} = \exp(a_{jk} + b_{1jk} M + b_{2jk} M^2) + \varepsilon_{ijk}, \qquad \text{(model 3A)}$$

where a_{jk}, b_{1jk}, and b_{2jk} are the regression coefficients for grid j of place k. We also included a variant B of each model in which the moisture term is retained and the moisture-squared term is removed; and a variant C in which the moisture term is removed and the moisture-squared term is retained.

Bayesian regression models require specifying "prior distributions": probability distributions that represent the modeler's beliefs, based on previous studies or natural history intuition, about parameter values before new data are taken into account. Both the prior distributions and the data influence "posterior distributions" which specify the probability distribution for each parameter after the data have been considered. In the present case, we had no previous studies to inform the priors, so the resulting posterior distributions of the parameters were primarily determined by the data rather than by prior expectation.

Table 4.1 shows the results. In all cases the models were improved by retaining the regression coefficients for both moisture and moisture-squared, and allowing all coefficients to vary with place and grid. For the best model, 3a, all

BOX 4.1. *(continued)*

first-order (b_1) moisture coefficients (slopes) were significantly greater than zero at Coweeta, and all second-order (b_2) moisture-squared coefficients were significantly less than zero, indicating bell-shaped moisture curves. Whitehall showed the same trends, but most of the 95%-credible intervals for parameter values overlapped zero, indicating more uncertainty about the exact shape of the moisture curves than at Coweeta.

TABLE 4.1. Comparisons of nine models relating *P. biflorum* abundance to soil moisture. The models are compared using the Deviance Information Criterion (DIC), which takes into account the deviation of observations from model predictions and the effective number of parameters (pD) in each model (Spiegelhalter et al. 2002). DIC is similar to the non-Bayesian Akaike's Information Criterion (AIC) inasmuch as a lower DIC implies a more parsimonious model.

Model	*pD*	*DIC*
1a. $D_{ijk} = \exp(a + b_1M + b_2M^2) + e_{ijk}$	3.1	1935.8
1b. $D_{ijk} = \exp(a + bM) + e_{ijk}$	2.0	2035.2
1c. $D_{ijk} = \exp(a + bM^2) + \varepsilon_{ijk}$	2.0	2130.2
2a. $D_{ijk} = \exp(a_k + b_{1k}M + b_{2k}M^2) + \varepsilon_{ijk}$	5.3	1852.8
2b. $D_{ijk} = \exp(a_k + b_kM) + \varepsilon_{ijk}$	3.9	1884.6
2c. $D_{ijk} = \exp(a_k + b_kM^2) + \varepsilon_{ijk}$	3.9	1911.8
3a. $D_{ijk} = \exp(a_{jk} + b_{1jk}M + b_{2jk}M^2) + \varepsilon_{ijk}$	23.4	902.1
3b. $D_{ijk} = \exp(a_{jk} + b_{jk}M) + \varepsilon_{ijk}$	17.4	950.8
3c. $D_{ijk} = \exp(a_{jk} + b_{jk}M^2) + \varepsilon_{ijk}$	19.3	954.3

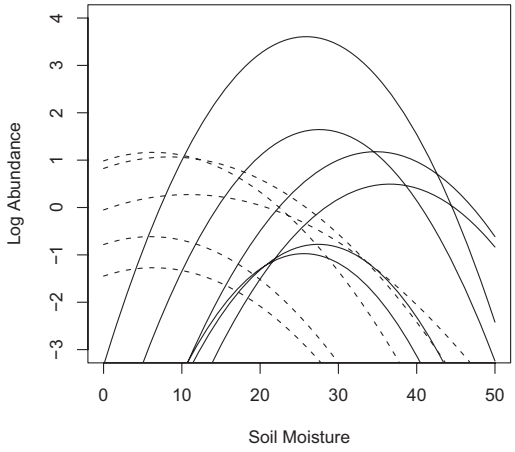

Figure 4.4. Moisture curves for *P. biflorum* abundance, drawn using the mean parameter estimates for model 3a (box 4.1). The six curves to the left (dashed lines) are for study grids at Whitehall, and the six curves to the right (solid lines) are for grids at Coweeta. The *y* axis is the natural log of abundance, allowing all values to fit on the same graph.

Possible General Reasons for Variable Niche Expression

We can imagine several hypotheses to explain an observation of variable niche expression (box 4.2). Our immediate goal is not to choose among these hypotheses, but to show for both examples given above that there are several explanations consistent with niche theory.

Different methods

Compensation to browsing in I. *aggregata* exemplifies the possibility that apparent differences in niche expression simply derive from different approaches used in different times or locations. Indeed, much discussion of this system in the literature has focused on differences in methodology. In responding to Bergelson and Crawley (1992a), Paige (1994) pointed to details of method, such as the precise method of mimicking browsing with experimental clipping, as critical to the results obtained. Bergelson et al. (1996) and Juenger and Bergelson (1997) copied as best they could the methods used by Paige, and still obtained undercompensation. Still, it is impossible to rule out subtle differences in method. For example, it may be that early reports of overcompensation failed to distinguish browsed individuals from those damaged during the years of vegetative growth that precede the flowering year. Vegetative damage can produce a multi-stalked flowering architecture resembling that of browsed plants, but it affects fitness in different ways—by lowering survival and delaying flowering (Brody et al. 2007). A team that confirmed the remains of a central inflorescence before assigning a plant as "browsed" might arrive at a very different accounting of fitness than a team that unknowingly included plants damaged in vegetative stage.

We can be much more confident that geographic differences in the *Polygonatum* system are not due to differences in method. All measurements in this case were done with the same method by the same investigators. The alert reader may see a potential flaw, since local abundance of *Polygonatum* may depend on additional soil properties that might vary between sites (just as it may depend on site-to-site variation along unmeasured biotic niche axes: e.g., abundance of a competitor). However, Pulliam and coworkers analyzed soil properties and found broad overlap between Coweeta and Whitehall, rather than differences that might explain the different *Polygonatum* abundance patterns.

Variation in the realized niche

Although the fundamental niche might be invariant, its realized expression may vary. In the *Ipomopsis* example, it is easy to erect location-specific

BOX 4.2. Three reasons for variable niche expression

1. Different methods
Apparent variation in niche expression may simply reflect different methods used by different investigators. Most ecological studies are done in a short time in one location by a single investigator. Each investigator chooses methods that he or she thinks appropriate for the question at hand. Often niche measurement, *per se*, is not a primary aim, and standardization of methodology may be given lower priority than cost and convenience. When a similar study is done by another investigator, different methods may lead to different results. The final outcome may be a contentious and futile debate in the literature, with each investigator defending his or her methods and results.[7]

2. Variation in the realized niche
Under this hypothesis, observed differences in niche expression are real, not an artifact of method. Even if the fundamental niche is invariant, its expression is likely to vary with ecological context: we may be looking at different realized niches, i.e., different parts of the fundamental niche. To see if this is so, we need to recognize other factors that vary across time and space, and to explore the possibility that they are responsible for differences in niche expression.

3. Variation in the fundamental niche
Finally, we can imagine that variable niche expression reflects genetic variation in the fundamental niche. Such variation seems especially likely over larger spatial or temporal scales. A species is not monolithic; rather it can be thought of as a cluster in phenotype space, corresponding to a cluster in genotype space.[8] If natural selection or other agents of genetic change produce geographic races or subspecies with different fundamental niches, then we expect variable niche expression.

hypotheses for the reversal of the relationship between browsing and fitness. Sharaf and Price (2004) showed that most of the undercompensation at the Rocky Mountain Biological Laboratory (RMBL) in Colorado was due to direct loss of biomass to browsers, rather than to indirect changes in pollination success resulting from delayed flowering. Furthermore, Campbell and Halama (1993) reported that flower production at the RMBL was limited by availability of water and nutrients. Combining these results suggests that compensation might be limited in dry, nutrient-poor soils. In northern Arizona, where most reports of overcompensation arose, the growing season is longer and warmer than at the RMBL. Assuming that the Arizona soils are relatively rich in nutrients (Whitham et al. 1991), and that summer rains

provide adequate moisture to mobilize these nutrients, one can imagine that browsers open the possibility for plants to use new nutrients (rather than those stored in roots) to produce more flowers than could be produced on a single original inflorescence. Furthermore, in Arizona the southward migration of hummingbirds may span a longer period than in Colorado (e.g., Calder 1987). Under such combined conditions, browsing might push plants into a region of the fundamental niche of lower fitness in Colorado but of higher fitness in Arizona (figure 4.2). Evaluating this scenario—or others that can be erected to explain location-specific tolerance to browsing without invoking change in the fundamental niche (see Aarssen 1995 for examples)—requires an understanding of mechanism beyond that presented in most of the papers we have cited. The study by Sharaf and Price (2004) exemplifies the value of peeling back the onion of natural history sufficiently to understand mechanism, a point to which we will return.

Pulliam and coworkers are exploring several alternative hypotheses for possible differences in the realized niche of *Polygonatum*. One of these (figure 4.5a) assumes that population density of the species is not an adequate measure of fitness. On average, Whitehall is drier than Coweeta. Suppose that asexual reproduction (cloning), which is common in this species, is more likely in drier soils, resulting in a secondary peak in ramet abundance (but not fitness) under dry conditions. Higher cloning frequency at Whitehall, for which there is some evidence, might then explain the bimodal pattern of densities in figures 4.3 and 4.4. A second hypothesis (figure 4.5b) assumes that a competitor, herbivore, or pathogen at Whitehall prevents plants from fully using moister sites, while a different enemy at Coweeta prevents them from fully using drier sites. Potential competitors seem numerous at Coweeta, where the understory herb layer is dense, but less likely at Whitehall, where the understory is sparse. Fungal pathogens might reduce abundance in moister sites at Whitehall, although we have no evidence for this at present.

Variation in the fundamental niche

The scenario of genetic variation in the species, and in its fundamental niche, is easy to apply to *Ipomopsis*. Based on the initial report of overcompensation in *I. aggregata*, Vail (1992) developed bet-hedging models describing conditions under which different degrees of compensation might be observed in a semelparous plant species. The basic logic is that a sufficiently high probability of herbivore attack can favor an individual that invests less than half of its available resources into an initial reproductive effort. Following

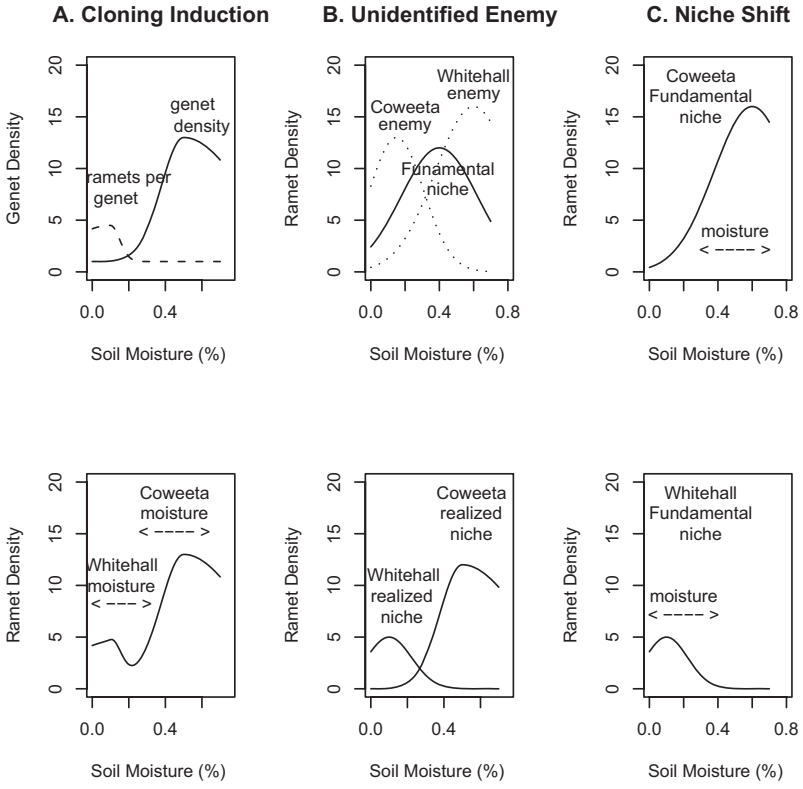

Figure 4.5. Three competing hypotheses to explain differences in the relationship between *Polygonatum* abundance and soil moisture. See text for explanations.

attack, such an individual will be able to surpass the reproductive success of an individual that has not been attacked, under a number of simplifying assumptions. These early models have been refined (see Stowe et al. 2000 and citations therein), but the basic prediction remains. In populations with a history of severe browsing one might observe overcompensation because of an evolved bet-hedging system, whereas in regions where browsing is less frequent one might observe undercompensation. Aarssen (1995) provides additional reasons why removal of the apical meristem and activation of lateral meristems would lead to overcompensation.

The hypothesis of different fundamental niches might likewise explain the observed responses of *Polygonatum* to soil moisture. Imagine an evolutionary change in the fundamental niche (figure 4.5c) such that the optimum condition for growth occurs in drier soils at some sites and moister soils at others. This is a reasonable hypothesis since soil moisture at Whitehall is

lower on average (5–10%) than at Coweeta (15–25%), and natural selection might favor characteristics that allow plants to grow best under the most common moisture conditions. The *Polygonatum* observations are suggestive in another respect: the lower maximum abundance at Whitehall is what one might expect if it were more difficult to adapt morphologically or physiologically to low than to high soil moisture.

How Ecologists Might Best Proceed

We have presented evidence for two species that the magnitude of a niche response and even the sign of that response vary between locations. Furthermore, we have outlined three general hypotheses for such variable niche expression (box 4.2). Two of these hypotheses are consistent with the proposition that the *fundamental* niche is an ecological invariant, remaining sufficiently constant that any location-specific differences result from differences among researchers in methods, or (our second and far more interesting hypothesis) from differences in the niche a species actually realizes in each location. The third hypothesis posits that the fundamental niche evolves differently from site to site. In the remainder of this chapter we do not attempt to choose among these hypotheses for the specific species discussed above, but instead we consider what ecologists can do, in general, to differentiate among the hypotheses.

Standardization of method

How might we determine whether apparent niche variation is an artifact of different methods? The obvious answer is to standardize methods and see whether differences disappear. The Long Term Ecological Research (LTER) initiative of the U.S. National Science Foundation (NSF) provides an example of standardization. Recognizing that many ecological questions are too big to be addressed by individual workers, LTER sought to provide sites for intensive collaborations. As the program grew, so did the desire to compare across these sites, and it was recognized that lack of standardized methods made this difficult (National Science Foundation 2002). The NSF responded by encouraging standardization, especially in data and metadata protocols, and by funding cross-site initiatives that required investigators to use the same methods. At present it is launching an even bigger and more ambitious program, the National Ecological Observatory Network (NEON), to facilitate cross-site comparisons and generalizations.

There are dangers, however, in methods being too rigidly dictated (see, e.g., chapter 5 in Golley 1993). Often progress toward an answer to a puz-

zling scientific question is fastest if the methods used are allowed to evolve as knowledge is gained. More generally, excessive regimentation can stifle the creativity, akin to artistic creativity, that represents the most mysterious and productive aspect of the scientific endeavor.[9] Although "wild ideas" are usually just that, it is equally true that forward leaps in understanding usually are culled from such unorthodoxy, so we would be ill-advised to impose any orthodoxy too strongly.

The ecology of place, natural history intuition, and multiple working hypotheses

Suppose that we show that spatial variation in niche expression is not a result of different methods. Two possibilities remain: that the realized niche varies, or that the fundamental niche does (box 4.2). To go further we need to erect and explore hypotheses for as yet unrecognized influences that might now be molding the realized niche, or that in the past might have caused the evolution of different fundamental niches. To detect such influences we may employ classical experiments, such as reciprocal transplantation among sites,[10] and new technologies such as those that unravel the genetic architecture of quantitative traits involved in niche expression (e.g., Juenger and Bergelson 2000). But none of these approaches replaces "natural history intuition" in getting to a deeper understanding of causes—those differences in ecological context that must ultimately explain differences in realized or fundamental niches.

Natural history intuition is difficult to describe or prescribe (see also Waller and Flader, chapter 3). We propose that it involves an iterative process of observation of nature, attempts at explaining the observations, and modification of one's list of possible explanations based on new observations (see also Price and Billick, introductory remarks to part 3). This process of model building requires time and patience since many natural events are uncommon and, as such, undetectable at first glance. We therefore emphasize the value of the ecology of place, as this term is used throughout this volume: the value of long-term study in a single place, using diverse methods, which allows the development of natural history intuition. Of course, once such detailed understanding is achieved at one place, there is great additional value in testing the generality of that understanding through similar studies at additional places, using common methods (see also Waller and Flader, chapter 3; Rundel, chapter 5; Estes, chapter 8).

We have emphasized above the need to keep an open mind to multiple possible explanations. This is another way of saying that the best way to understand many ecological phenomena (including, but not limited to, the

niche) is to develop multiple working hypotheses, rather than the traditional Fisherian approach which compares a null hypothesis to a single alternative hypothesis. The approach of multiple working hypotheses involves building multiple alternative causal models for the underlying ecological phenomena one has observed. Advocacy of multiple working hypotheses dates at least to the geologist T. C. Chamberlin (1890; see also Railsback 2004), who proposed that hypotheses be erected a priori. We instead imagine them evolving to some extent sequentially, as the ecological detective (sensu Hilborn and Mangel 1997; see also the quotation from Sinclair Lewis at the head of this chapter) accumulates natural history knowledge and recognizes previously ignored factors to be important. In either case, this approach reduces the risk of the investigator becoming attached to a favored hypothesis, and instead increases the likelihood that he or she remains a "skeptical inquirer" prepared to admit that earlier hypotheses were mistaken.

Adopting multiple hypotheses takes us away from the philosophical position that causation can be viewed as an "either/or" dichotomy, and that progress is made by rejecting one possibility in favor of an alternative null hypothesis. Instead, we view causation as potentially more complex (Hilborn and Stearns 1982), although we may still sometimes be able to group hypotheses into classes and make observations that allow us to eliminate entire classes (Platt 1964; for examples in ecology see Waser and Price 1985, Harmon and Franklin 1989). Also, carrying forward a given study across time in one place moves us away in another sense from an either/or perspective on ecological phenomena, by allowing us to say *how often* one finds each of several outcomes. Refining a causal model of ecological phenomena using the approach just described is implicitly a Bayesian process (Hilborn and Mangel 1997, Ellison 2004): through successive observations and experiments we become increasingly confident of a given causal model, using the confidence at each step to erect prior probabilities that affect our interpretation of the next round of observations.

The approach taken so far to understanding how *Ipomopsis* responds to inflorescence browsing, for example, has largely been to test the hypothesis of overcompensation against some null such as no compensation or exact compensation, with a decision being based on some arbitrary (i.e., 5%) chance of accepting a false alternative hypothesis. Faster progress might be made by developing causal hypotheses about how drought conditions, soil nutrient availability, phenology of browsing, phenology of pollinators, and so on interact to determine the expected life histories and final fecundities of browsed and unbrowsed plants. Ultimately one may be able to build a causal model that explains the observed results with enough fidelity, and in enough mechanistic detail, that one has pinpointed likely explana-

tions for variable niche expression. Similarly, in exploring how *Polygonatum* responds to soil moisture we need to answer basic who, what, when, and where questions. Is *Polygonatum* at Whitehall genetically the same as the biological entity at Coweeta? Is the abundance of *P. biflorum* greater where soil moisture is higher? Does *P. biflorum* produce more clones in drier habitats? The analysis presented earlier gives an example of using multiple competing hypotheses and Bayesian analysis to characterize the functional form of the relationship between abundance and soil moisture at different locations. Once such basic patterns are established, the Bayesian approach can be used again to differentiate among multiple competing hypotheses.

Conclusions

We end where we started—with a comparison to the physical sciences—and a simple example from chemistry that not only the rate but also the products of a reaction can vary with the environment. There is no general law that requires the reaction of chemicals X and Y to always yield product Z ($X + Y \rightarrow Z$), but rather a set of conditions (an environment) for which this happens at a predictable rate, and other conditions under which $X + Y \leftarrow Z$ or $X + Y \rightarrow Q$[11]. There is a set of rules to be discovered by observation and experimentation that specify the direction and rate of the reaction. Similarly, in ecology there is no fixed response of a species to an environmental variable, but rather a putative set of rules that predict how the response will change as other environmental variables also change. Accordingly, we should take variation in niche expression, or in any other ecological phenomenon, not as an annoyance but as an opportunity to discover deeper levels of mechanism that explain the observation at a more general level (see also Levin 1981, Tilman 1987).

Said differently, we should not be surprised by location-specific patterns in niche expression—and in other ecological phenomena—but we should persist in searching for their predictability (and here our conclusion seems to differ from that of Feinsinger et al., chapter 18). The key word—and the bugbear—is predictability. Whereas some ecologists interpret nature's variability as pure idiosyncrasy, and despair that conclusions from one location can apply to another, we counter that ecological patterns must be complex realizations of an understandable set of rules governing responses of species across space and time. If one is able to reach this level of understanding by the methods of natural history intuition we have sketched or by some other route, so that one can explain and predict variation in an ecological phenomenon based on a deeper perception of shared mechanisms, then one will have achieved a most crucial form of "ecological invariance."

Acknowledgments

We thank Mary Price for encouragement, Alison Brody and Mary Price for discussing compensation in *Ipomopsis*, and Dave Parkhurst for permission to use his limerick. The *Polygonatum* work has benefited from discussion with students in the Pulliam lab, especially Jeff Diez, Robert Warren, and Itamar Giladi, and was supported by the United States National Science Foundation (DEB-0235371 and DEB-9632854, the Coweeta LTER). Finally, we are indebted to Ian Billick, Emily Jones, Charley Krebs, Michele Lanan, and Mary Price for comments on earlier drafts.

References

Aarssen, L. W. 1995. Hypotheses for the evolution of apical dominance in plants: Implications for the interpretation of overcompensation. *Oikos* 74:149–56.

Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: Environmental niches of five *Eucalyptus* species. *Ecological Monographs* 60:161–77.

Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83:35–47.

Bergelson, J., and M. J. Crawley. 1992a. Herbivory and *Ipomopsis aggregata*: The disadvantages of being eaten. *American Naturalist* 139:870–82.

———. 1992b. The effects of grazers on the performance of individuals and populations of scarlet gilia, *Ipomopsis aggregata*. *Oecologia* 90:435–44.

Bergelson, J., T. Juenger, and M. J. Crawley. 1996. Regrowth following herbivory in *Ipomopsis aggregata*: Compensation but not overcompensation. *American Naturalist* 148:744–55.

Bergey, D. H., J. G. Holt, N. R. Krieg, and P. H. A. Sneath. 1994. *Bergey's Manual of Determinative Bacteriology*. Williams and Wilkens, Baltimore.

Brody, A. K., M. V. Price, and N. M. Waser. 2007. Life-history consequences of vegetative damage in scarlet gilia, a monocarpic plant. *Oikos* 116:975–85.

Brown, J. H., G. B. West, and B. J. Enquist. 2000. Scaling in biology: Process, causes and consequences. Pages 1–24 *in* J. H. Brown and G. B. West, eds., *Scaling in Biology.* Oxford University Press, New York.

Brumfiel, G. 2006. Outrageous fortune. *Nature* 439:10–12.

Calder, W. A. 1987. Southbound through Colorado: Migration of rufous hummingbirds. *National Geographic Research* 3:40–51.

Campbell, D. R., and K. J. Halama. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology* 74:1043–51.

Chamberlin, T. C., 1890. The method of multiple working hypotheses. *Science* (old series) 1592–96 (reprint in *Science* 148:754–59, 1965).

Carlin, B. P., and T. A. Louis. 2000. *Bayes and Empirical Bayes Methods for Data Analysis, 2nd Edition*. Chapman and Hall, Boca Raton, FL.

Charnov, E. L. 1993. *Life History Invariants*. Oxford University Press, Oxford.

Diez, J. M. 2006. Hierarchical patterns of symbiotic orchid germination linked to adult proximity and environmental gradients. *Journal of Ecology* 95:159–70.

Diez, J. M., and H. R. Pulliam. 2007. Hierarchical analysis of species distributions and abundance across environmental gradients. *Ecology* 88:3144–52.

Ellison, A. M. 2004. Bayesian inference in ecology. *Ecology Letters* 7:509–20.

Elton, C. 1927. *Animal Ecology*. Sedgwick and Jackson, London.

Gause, G. F. 1934. *The Struggle for Existence*. Williams and Wilkens, Baltimore.

Giladi, I. 2006. Choosing benefits or partners: A review of the evidence for the evolution of myrmecochory. *Oikos* 112:481–92.

Golley, F. B. 1993. *A History of the Ecosystem Concept in Ecology: More than the Sum of the Parts*. Yale University Press, New Haven, CT.

Grant, V., and D. H. Wilken. 1986. Taxonomy of the *Ipomopsis aggregata* group (Polemoniaceae). *Botanical Gazette* 147:359–71.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. *Auk* 34:427–33.

Gronemeyer, P. A., B. J. Dilger, J. L. Bouzat, and K. N. Paige 1997. The effects of herbivory on paternal fitness in scarlet gilia: Better moms also make better pops. *American Naturalist* 150:592–602.

Harmon, M. E., and J. F. Franklin. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70:48–59.

Hilborn, R., and M. Mangel. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ.

Hilborn, R., and S. C. Stearns. 1982. On inference in ecology and evolutionary biology: The problem of multiple causes. *Acta Biotheoretica* 31:145–64.

Hutchinson, G. E. 1957. Concluding remarks. Population studies: Animal ecology and demography. *Cold Spring Harbor Symposium on Quantitative Biology* 22:415–27.

Juenger, T., and J. Bergelson. 2000 The evolution of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*: Herbivore-imposed natural selection and the quantitative genetics of tolerance. *Evolution* 54:764–77.

Kemp, M. 2005. From science in art to the art of science. Nature 434:308–9.

Langlet, O. 1971. Two hundred years genecology. *Taxon* 20:653–721.

Levin, S. A. 1981. The role of theoretical ecology in the description and understanding of populations in heterogeneous environments. *American Zoologist* 21:865–75.

Lewis, S. 1925. *Arrowsmith.* Harcourt Brace and World, New York.

MacArthur, R. H., and E. O. Wilson 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373–87.

Maguire, B. Jr. 1973. Niche response structure and the analytical potentials of its relationship to habitat. *American Naturalist* 107:213–46.

Marquet, P. A., R. A. Quiñones, S. Abades, F. Labra, M.Tognelli, M. Arim, and M. Rivadeneira. 2005. Scaling and power laws in ecological systems. *Journal of Experimental Biology* 208:1749–69.

Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. *American Naturalist* 134:1–19.

McNaughton, S. I. 1983. Compensatory plant responses to herbivory. *Oikos* 40:329–36.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. *North American Fauna,* no. 3.

National Science Foundation. 2002. Long-term ecological research program: Twenty-year review. Online URL http://intranet.lternet.edu/archives/ documents/reports/20_yr_review/.

Paige, K. N. 1994. Herbivory and *Ipomopsis aggregata*—differences in response, differences in experimental protocol—a reply. *American Naturalist* 143:739–49.

———. 1999. Regrowth following ungulate herbivory in *Ipomopsis aggregata*: Geographic evidence for overcompensation. *Oecologia* 118:316–23.

Paige, K. N., and T. G. Whitham. 1987. Overcompensation in response to mammalian herbivory: The advantage of being eaten. *American Naturalist* 129:407–16.

Paige, K. N., B. Williams, and T. Hickox. 2001. Overcompensation through the paternal component of fitness in *Ipomopsis arizonica*. *Oecologia* 128:72–76.

Platt, J. R. 1964. Strong inference. *Science* 146:347–53.

Press, S. J. 2003. *Subjective and Objective Bayesean Statistics: Principles, Models, and Applications*. John Wiley and Sons, New York.

Price, M. V., N. M. Waser, R. E. Irwin, D. R. Campbell, and A. K. Brody. 2005. Temporal and spatial variation in pollination of a montane herb: A seven-year study. *Ecology* 86:2106–16.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–61.

Railsback, L. B. 2004. T. C. Chamberlin's "Method of Multiple Working Hypotheses": An encapsulation for modern students. Online URL www.gly.uga.edu/railsback/railsback_chamberlin.html.

Schluter, D., and P. R. Grant. 1984. Determinants of morphological patterns in communities of Darwin›s finches. *American Naturalist* 123:175–96.

Sharaf, K. E., and M. V. Price. 2004. Does pollination limit tolerance to browsing in *Ipomopsis aggregata*? *Oecologia* 138:396–404.

Spieglhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesean measures of model complexity and fit. *Journal of the Royal Statistical Society Series B* 64:583–639.

Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics* 31:565–95.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. *American Naturalist* 129:769–74.

Turesson, G. 1922. The genotypical reponse of the plant species to the habitat. *Hereditas* 3:211–350.

Vail, S. G. 1992. Selection for overcompensatory plant responses to herbivory: A mechanism for the evolution of plant-herbivore mutualism. *American Naturalist* 139:1–8.

Waser, N. M. and M. V. Price. 1985. The effect of nectar guides on pollinator preference: Experimental studies with a montane herb. *Oecologia* 67:121–26.

Waser, N. M., M. V. Price, and R. G. Shaw. 2000. Outbreeding depression varies among cohorts of *Ipomopsis aggregata* planted in nature. *Evolution* 54:485–91.

Whitham, T. G., J. Maschinski, K. C. Larson, and K. N. Paige. 1991. Plant responses to herbivory: The continuum from negative to positive and underlying physiological mechanisms. Pages 227–56 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, eds., *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley and Sons, New York.

Wolf, P. G., P. S. Soltis, and D. E. Soltis. 1993. Phylogenetic relationships of the *Ipomopsis aggregata* complex and related species (Polemoniaceae): Evidence from chloroplast DNA restriction site variation. *Systematic Botany* 18:652–62.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Pages 356–66 *in* D. F. Jones, ed. *Proceedings of the Sixth International Congress of Genetics*. Brooklyn Botanical Garden, Brooklyn, NY.

Notes

1. $1/N\, dN/dt$ is a measure of mean fitness. Maguire (1973) represented the Hutchinsonian fundamental niche as a mapping of fitness on environmental variables. The word "map" is appropriate because Maguire drew a three-dimensional topography, with isolines of positive fitness forming hills and mountains on a surface of two environmental dimensions: this is not the same as Wright's (1932) adaptive landscape, which has dimensions of gene frequencies instead of environmental factors, and valleys of negative fitness! Maguire even used his topographic approach to explore a variant of what are now called zero-net-growth isoclines (ZNGIs).

2. For simplicity we have drawn niches along a single axis as unimodal functions. However, fundamental niches might be multimodal because environmental or resource gradients at any location are discontinuous (e.g., discrete classes of seed size and hardness; Schluter and Grant 1984), and realized niches might be multimodal because of the action of other species at the same or different trophic levels. Austin and Smith (1989) and Austin et al. (1990) discuss the actual shapes of niche functions.

3. This brings up interesting thoughts. The mutualism might be critical for our hypothetical plant species to occur, or might simply increase fitness without being essential. In the former case which is the fundamental niche, and which realized? Is realized larger than fundamental? Might mutualists (e.g. mycorrhizae) add extensions to the fundamental niche, these extensions disappearing in their absence, representing a shrinkage to the realized niche (i.e., absence of a beneficial interaction resembles presence of a detrimental one)? These may seem like questions about noise made by trees falling in the forest, but perhaps they illustrate interesting elaborations (limitations?) of the Hutchinsonian niche (see also Pulliam 1988).

4. *Ipomopsis arizonica* is sometimes considered a subspecies of *I. aggregata*, although molecular evidence (Wolf et al. 1993) supports specific status. Undercompensation following browsing, or at best perfect compensation (seed production equal to that of unbrowsed plants), had been reported previously for female reproductive success of this species (Mashinski and Whitham 1989).

5. We personally know of one unpublished case. A. K. Brody, S. Louda, and N. M. Waser (unpublished data), working at the Rocky Mountain Biological Laboratory (RMBL) in western Colorado, found only undercompensation in repeated comparisons of artificially browsed plants to controls.

6. Various authors have objected to this use of "mutualist," because overcompensating plants may have evolved with herbivores to "make the best of a bad deal," and must have lower fecundity than their ancestors that lived without herbivores. For details see Stowe et al. 2000 (pp. 577–78).

7. Not all debates over results are sterile; at best they may resolve apparent differences in results and stimulate wider discussion about appropriate methodology. But at the worst they may generate more heat than light, and inflict substantial harm: this was the case with the "null-model debate" in community ecology, which, despite its merits, and by its acrimony, needlessly depopulated the field for several academic generations at a time when the emerging discipline of conservation biology was identifying burning applied questions at the community level.

8. Molecular phylogenetic methods are making it more possible to confirm the latter, sometimes yielding surprises that "species" are polyphyletic; indeed, this is so for some *Ipomopsis* "species" (Wolf et al. 1993).

9. See Kemp (2005) for one discussion of the links between art and science.

10. Langlet (1971) attempts to put to rest the perception that such studies began with Turesson (1922), tracing their history to silviculture in the 1700s.

11. Indeed, recent advances in string theory suggest the conclusion that values of the physical constants apply only in our own universe, and are effectively chance values among all values realized in an astounding number of parallel universes (Brumfiel 2006). In this regard physical constants and laws might be seen generally to be context-dependent, the complaint often leveled at ecological constants and laws.