

# The portfolio concept in ecology and evolution

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Biological systems have similarities to efficient financial portfolios; the emergent properties of aggregate systems are often less volatile than their components. These portfolio effects derive from statistical averaging across the dynamics of system components, which often correlate weakly or negatively with each other through time and space. The “portfolio” concept when applied to ecological research provides important insights into how ecosystems are organized, how species interact, and how evolutionary strategies develop. It also helps identify appropriate scales for developing robust management and conservation schemes, and offers an approach that does not rely on prescriptive predictions about threats in an uncertain future. Rather, it presents a framework for managing risk from inevitable perturbations, many of which we will not be able to understand or anticipate.

*Front Ecol Environ* 2015; 13(5): 257–263, doi:10.1890/140275

The greatest challenges in ecology and evolution are in understanding how physical and biological processes that play out over extensive spatial, temporal, and taxonomic scales interact to affect the dynamics of genes, phenotypes, populations, and ecosystems. The fact that many biological properties are “scale-dependent” has been recognized for decades; biological systems tend to be extremely variable when observed at some scales but relatively invariant at others (Levin 1992). Scale-dependencies in biological systems are produced by non-linear interactions within systems, and from weak or negative covariances in system components across space and time. While fascinating ecologists for decades in terms of quantifying patterns in nature, scale-dependencies have received limited attention in exhibiting portfolio effects, which have important implications for understanding ecological processes and evolutionary dynamics.

Here, we show how the “portfolio” concept (WebPanel 1) – a construct that developed out of simple probability theory and has been widely adapted in financial investment theory – applies across ecology and evolution, and

provides a framework for understanding how organisms and ecosystems achieve stability in their dynamics despite inherent volatility in their components. The portfolio concept was developed to recognize that diversified financial investment portfolios tended to produce more stable returns than simple portfolios. Thus, the dynamics of financial systems have scale-dependencies analogous to biological systems: dynamics may be extremely volatile at small scales but less variable at more aggregated scales.

Modern portfolio theory was first described through the use of graphical and simple analytical models to show the value of diversification for reducing risks in investment strategies (Markowitz 1952). These models introduced the idea that the selection of an efficient investment portfolio should assess the trade-off between the expected return and the variance of alternative asset collections. The key insight was recognizing that the variability of an aggregate portfolio depends critically on the covariation among the component assets. We contend that the nearly ubiquitous scale-dependencies in biological systems (ie that systems are often less variable when viewed at coarse scales than at fine scales; this is the emergent property of interest, where the whole behaves differently than the individual components; Levin 1992), generated by weak and negative covariation within their components, stabilize the emergent properties of many ecological and evolutionary processes. Examples are evident in phenomena ranging from the behavior of individual organisms, to population and ecosystem dynamics, and even to evolutionary strategies. These portfolio effects produce reliable biological functions in a world characterized by stochasticity and unpredictability, and provide underappreciated options for considering risk in natural resource management and conservation.

## In a nutshell:

- The dynamics of many biological systems are often less variable than the individual components they are composed of, thus showing portfolio effects
- As in financial portfolios, where diversification across assets can stabilize returns (ie reduce risk), a wide assortment of diversifying features in biological systems stabilizes their performance
- Identifying and maintaining key ecological processes that generate complexity in biological systems provides opportunities for conserving ecosystem functions and species viability in the face of a highly uncertain future

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## ■ Species diversity and communities

Ecologists have struggled with understanding the relationship between species diversity and community stability since it was first proposed by MacArthur (1955) and Elton (1958),

who suggested that species-rich communities were less sensitive to perturbations as compared with species-poor communities. Although ecologists have used a wide array of definitions to calculate stability (Ives and Carpenter 2007), McNaughton (1977) proposed that the variability of an aggregate community property was inversely related to community stability. While variance in a biological attribute may have little to do with the dynamic stability often associated with systems that achieve multiple stable states, the inverse of variance in community properties has been the most common indicator of stability used in the enormous literature focused on understanding the diversity–stability relationship in community ecology (Hooper *et al.* 2005).

Whole-ecosystem experiments to assess the ecological effects of environmental stressors, such as acid rain, are among the more convincing examples of how ecosystem functions are maintained by portfolio effects within communities (Schindler 1990; Frost *et al.* 1995). In these studies, experimental acidification of lakes caused extensive changes in the species composition of plankton communities, yet total plankton biomass typically changed little following perturbation. Similarly, species responses to nutrient enrichment in lakes are often erratic and unpredictable, while more aggregate measures of community and ecosystem response (eg total phytoplankton biomass) provide more integrated measures of response to nutrient enrichment (Cottingham and Carpenter 1998). In these cases, portfolio effects expressed at the community or ecosystem level of biological organization are produced through the complementary dynamics of individual species within ecosystems.

Tilman and Downing (1994) were the first to show empirically that the magnitude of damage to a community (in response to drought) was negatively correlated with the number of species present in a system. This diversity effect on variance buffering was not initially attributed to portfolio effects but rather to complementary responses of different species to environmental perturbations. Doak *et al.* (1998) re-analyzed these data to reveal that much of the diversity effect on reliability in this system was produced simply through statistical averaging among species that did not vary synchronously through time, analogous to diversified investment portfolios.

Many studies now demonstrate that higher species diversity tends to be associated with reduced temporal variability (often called increased “reliability”) in community properties. Because this literature has been reviewed in depth (eg Hooper *et al.* 2005), we do not dwell on it here, other than to highlight that portfolio effects have provided an effective conceptual model for organizing our understanding of how species diversity affects ecosystem reliability.

The observed relationship between species diversity and reduced variability in aggregate community properties led to the “insurance hypothesis”, which proposed that diverse ecosystems are more likely to be functionally stable if many species are present (Lachi and Loreau 1999) and that modern portfolio theory could be used to formal-

ize this argument (Koellner and Schmitz 2006). While adoption of the term “insurance” to explain the benefits that species diversity provides to ecosystem reliability is an unfortunate misnomer (insurance does not affect risk, but rather transfers damage once it has occurred; Hummel *et al.* 2009), communities with high species diversity clearly tend to support ecosystem properties that are less variable through time as compared with simple communities. Such portfolio effects are now widely recognized in community ecology (Cardinale *et al.* 2012).

## ■ Habitat and successional pathways

Habitat heterogeneity provides the foundation for a variety of variance-dampening phenomena in ecology. Physical heterogeneity generates portfolio effects by decoupling local habitat conditions from regional drivers of ecological dynamics, such as prevailing climate. For example, the slope, aspect, and elevation of terrain mediate fine-scale responses of habitat characteristics, such as air temperature and water balance, to regional climate conditions (Dobrowski 2011). Species distribution models predict smaller losses of terrestrial habitat due to climate change when accounting for the influence of terrain on local expression of climate in habitat conditions (Dobrowski 2011; Sears *et al.* 2011).

Landscape heterogeneity reduces climate impacts on habitat in aquatic systems as well. For instance, droughts can change the chemistry of lakes because the concentration of solutes depends on the relative rates of inflows, outflows, precipitation, and evaporation (Schindler *et al.* 1990). However, because the components of water balance in ecosystems are controlled by local geomorphic conditions, lakes distributed across a heterogeneous landscape often exhibit opposing chemical responses to the same drought. Groundwater-dominated lakes at low elevations and precipitation-dominated lakes at higher elevations show increases and decreases in the mass of cations, respectively (Webster *et al.* 1996). In both cases, landscape heterogeneity causes component habitats to respond non-systematically to regional stimuli. This reduces the risk of habitat conditions becoming widely unsuitable for organisms, particularly for species that can readily disperse among habitats.

Many ecosystems experience ephemeral disturbances that are followed by prolonged periods of regeneration and succession. This process has the potential to generate large swings in a variety of ecological conditions, such as habitat composition, species abundance, and community structure across landscapes. Portfolio theory provides perspective on how the spatiotemporal patterning of disturbance controls ecological variation at different spatial scales. River floodplains offer a particularly well-studied example: at fine spatial scales, floodplains are highly variable through time as flooding reconfigures habitat by redistributing sediments (Bailey 1995), but the paths of rivers change through time, thereby creating a spatial mosaic of disturbance history across floodplains. Disturbed

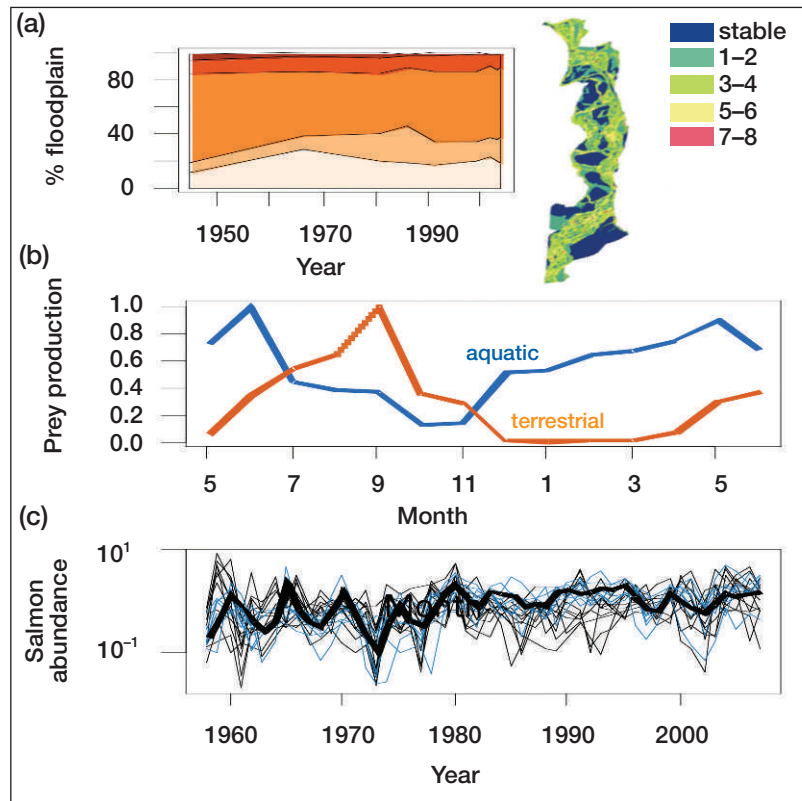
patches are colonized by riparian vegetation and progress toward mature plant communities. The interacting processes of disturbance and succession, therefore, cause the spatial patterning of habitat to change through time (ie a shifting habitat mosaic; Stanford *et al.* 2005).

Whited *et al.* (2007) analyzed changes in habitat of the Nyack floodplain (Flathead River, Montana) and found that 75% of the 10-m<sup>2</sup> patches they examined changed habitat type at least once, and 25% changed habitat type four times, over a 50-year period (Figure 1a). In flood-prone braided river systems (ie where the channel is a network of several interconnected smaller channels), the proportion of floodplain exhibiting habitat turnover can reach 60% in a single year (Arscott *et al.* 2002). Despite this extreme variability at fine spatial scales, floodplain habitat exhibits marked stability at coarser spatial scales; across a 20-km<sup>2</sup> area of the Nyack floodplain, the proportional representation of different habitat types remained essentially constant during the 50-year period of study (Figure 1a; Whited *et al.* 2007). Even in the most dynamic braided systems, attributes such as habitat composition, braiding, and sinuosity were found to remain relatively constant at coarse spatial scales (Arscott *et al.* 2002). The aggregate of floodplain habitat is stable because the component parts are out of sync – habitat units are always changing, but rarely in a coordinated direction.

More generally, spatially asynchronous succession also explains the persistence of species-level diversity in biological communities;

spatial heterogeneity in disturbance (and thus asynchronous succession) is a mechanism involved in the intermediate disturbance hypothesis's explanation of among-patch species coexistence (Roxburgh *et al.* 2004).

The interaction between animal behavior and habitat heterogeneity generates another theme of portfolio effects. An animal can only be in one place at any given time. However, through time, mobile individuals sample a variety of habitats, assembling a collection of habitat “stocks” (ie specific combinations of location and time). Portfolio theory illuminates a theme underlying many behavioral strategies – animals exploit the heterogeneity in their environment by acquiring habitat stocks that exhibit asynchronous trends in quality (eg in food and temperature). Individuals then move among habitat stocks to track favorable conditions. For instance, multiple aquatic species exploit the burrows of alligators and catfish to find refuge during droughts that desiccate most other habitat features (Power *et al.* 1988). A variety of taxa exploit groundwater springs, which



**Figure 1.** Examples of portfolio effects in ecological systems. (a) Proportional contributions of different habitat types to the Nyack floodplain (Montana) through time in response to hydrological disturbance over six decades. The map shows how often individual habitat patches have been disturbed over this time period (Whited *et al.* 2007). (b) Relative seasonal production of terrestrial and aquatic prey for fish and birds in a small forested stream (redrawn from Nakano and Murakami 2001). (c) Standardized annual returns of adult sockeye salmon (*Oncorhynchus nerka*) to the Bristol Bay region of western Alaska (black line), to the nine major rivers that support commercial fisheries in this region (dark blue lines), and to the individual tributaries of an intensely studied river basin (Wood River, light blue lines). All data have been standardized so that a value of 1 equals their long-term average. Data are from Schindler *et al.* (2010).

are decoupled from regional weather and remain cooler during summer heat waves (Torgersen *et al.* 1999) and warmer during winter cold periods. While such phenomena are typically described in terms of refuge-seeking in animals, an alternative view is to consider these habitats as part of a broader habitat portfolio that provides a variety of options for organisms to exploit when faced with substantial changes in overriding environmental conditions.

Food resources are highly variable in time; thus, animals have evolved behavioral strategies to exploit diverse portfolios of trophic resources as a way to stabilize their energy budgets. Food quality for grazers depends on the developmental stage of plants. Plant phenology varies across landscapes, generating weak covariance in foraging quality among locations; in response, grazers move to track the shifting mosaic of nutritious food, and can find plants at phenological stages with high nutritional value for an entire season. This portfolio effect is threatened when landscapes are homogenized, habitat area decreases, or restrictions on



movement prevent animals from tracking variation in vegetation quality (Fryxell *et al.* 2005). Empirical work demonstrated that elk (*Cervus canadensis*) production was lower in years with reduced spatial heterogeneity in vegetation (Wang *et al.* 2006), and simulations suggest that Thomson's gazelle (*Eudorcas thomsonii*) populations are viable only when habitat area and asynchrony in plant phenology are sufficient to deliver adequate portfolio effects. Studies of caribou (*Rangifer tarandus*) in Greenland have shown that recent climate warming has reduced spatial variability in plant phenology, which in turn has increased the average temporal mismatch between caribou and their food supply (Post *et al.* 2008) – providing an illustration where the consumer is poorly buffered from climate variation through heterogeneity in its food resources.

A prominent example of mobile consumers exploiting a portfolio effect produced through **weak spatial covariation** in resources is seen in brown bears (*Ursus arctos*) and rainbow trout (*Oncorhynchus mykiss*) that feed on spawning anadromous salmon and their eggs, respectively. Sockeye salmon (*Oncorhynchus nerka*) populations are locally adapted to individual streams and beach shores, and are vulnerable to consumers primarily when they are spawning. The duration of spawning for a single salmon population typically ranges from 2–4 weeks, so foraging opportunities for bears and trout are ephemeral at fine spatial scales. Yet locally adapted salmon populations spawn at different times depending on water temperature and other habitat attributes (Lisi *et al.* 2014). Across an entire watershed, the asynchrony of salmon spawn timing among populations creates a staggered resource pulse that may last 3 months or longer. Mobile consumers such as brown bears (Schindler *et al.* 2013) and rainbow trout (Ruff *et al.* 2011) can track the shifting wave of resources provided by spawning salmon to vastly extend the duration of time they have access to this high-quality resource.

Although not typically viewed through this lens, the widely observed phenomenon of prey-switching (and hyper-predation) in predators is another illustration of consumers exploiting weak or negative covariation in their environment, in this case among different prey they consume. Stream fish and riparian birds capitalize on the “reciprocal subsidies” of prey produced in aquatic systems versus those produced in riparian systems (Nakano and Murakami 2001). Here the coupled stream–riparian system essentially functions as a diversified portfolio, where the dynamics of system components – which do not vary synchronously – improve the reliability of the aggregate system to predators (Figure 1b).

### ■ Habitat heterogeneity and population diversity

**Population diversity at the landscape scale is often characterized by weakly synchronous or asynchronous population dynamics among individual habitats.** The most extreme example of this involves classic metapopulations where populations at any specific location can go extinct,

only to be re-colonized by neighboring populations that remained viable during the local extinction event (Hanski 1998). A metapopulation is thus typically more stable than its component populations.

**Variable population dynamics are produced by variation in the expression of regional environmental signals at specific locations** (ie where habitat conditions filter broader environmental signals), by stochasticity in population dynamics, by population-specific responses to environmental signals, or by interactions among these factors. However, **biology has tended to emphasize causes of spatial coordination (synchrony) among populations** (Leibold *et al.* 2004), although most populations are only weakly synchronous with each other, even those in close proximity. Subpopulations need not exhibit negative correlations to generate portfolio effects. Even though proximate populations often display positive correlations through time (Leibold *et al.* 2004), weak positive correlations generate variance dampening in the aggregate. Sockeye salmon stocks in Bristol Bay, Alaska, exhibit positive correlations on average (Rogers and Schindler 2008), but their asynchrony is sufficient to provide substantial reductions in economic risk to commercial fisheries that integrate across the stock aggregates (Schindler *et al.* 2010) (Figure 1c).

### ■ Evolutionary strategies

The application of the portfolio concept to evolutionary ecology has been limited or described in different terms. In particular, the concept of bet-hedging has developed in parallel to portfolio theory, but the conceptual connections between these two phenomena are underappreciated.

Genetic variants are exposed, via their phenotypic effects on organisms, to a broader range of environmental conditions than any given individual. Clonal individuals with the same genotype may experience different environmental conditions if they disperse to a variety of habitats or reproduce in different years. In sexual species, relatives will share genes but express them in different contexts. Under such circumstances, the geometric mean fitness of a strategy is a better predictor of long-term evolutionary success as compared with the arithmetic mean fitness of that strategy (Dempster 1955; Lewontin and Cohen 1969). **Geometric mean fitness** is approximated as  $\bar{W} - \sigma^2/(2\bar{W})$ , where  $\bar{W}$  is the arithmetic mean and  $\sigma^2$  is the variance in fitness (Gillespie 1977). If two genotypes have the same expected average fitness (ie the same  $\bar{W}$ ), the one with a lower  $\sigma^2$  may outcompete the other in a variable environment. In population genetics terms, genotypic variance in fitness ( $\sigma^2$ ) can be expressed as the product of two components: individual variance in reproductive success, and correlations in reproductive success among individuals of the same genotype (Frank 2011; Starrfelt and Kokko 2012). Reductions in this second component correspond to evolutionary portfolio effects, which are best illustrated by an example.

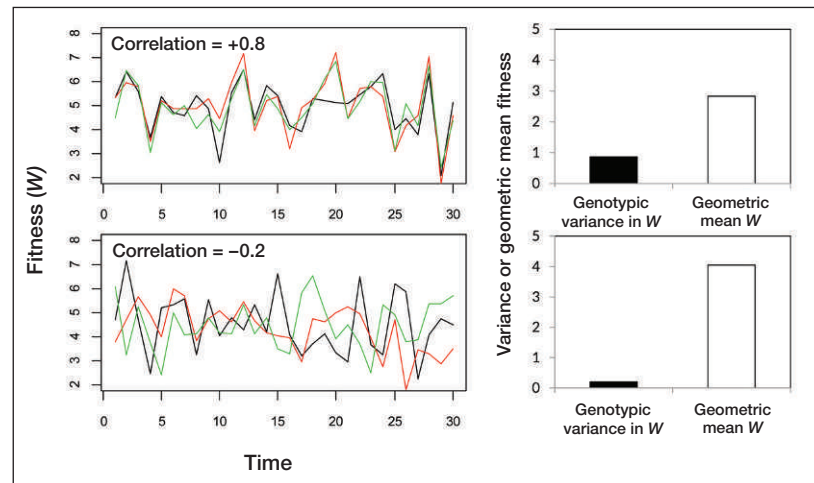
Imagine a plant living in an environment where seedling survival varies unpredictably over time. One strategy would be to produce variation in germination times among seeds, which would reduce the correlation in survival among the offspring of a given lineage. This, in turn, dampens the overall variance in fitness of that lineage, thereby increasing its geometric mean fitness (provided that any associated reductions in arithmetic mean fitness do not outweigh the benefits of reduced variance). If all of the seeds from a single genetic lineage germinated in the same year they would have similar fitness, and the genotypic variance in fitness (measured across years) would then be inflated by temporal synchrony in their performance. In the extreme case, a single “bad” year could wipe out an entire lineage. The portfolio strategy, on the other hand, more traditionally known as “diversified bet-hedging” (Seger and Brockmann 1987), spreads the risk through time by temporally decoupling the fates of individuals of the same genotype or lineage.

At another extreme, habitat conditions may be constant through time but vary across space within the dispersal range of the organism. Here, dispersal itself can adaptively reduce correlations in reproductive success within a genetic lineage by spreading risk across space because individuals sharing genes end up in different habitat patches (Starrfelt and Kokko 2012). In the presence of both temporal and spatial environmental variation (eg Simons 2009), both dispersal and temporal bet-hedging strategies may be selected for simultaneously.

Geometric mean fitness can also be enhanced by conservative bet-hedging, which simply involves minimizing the risks of undesirable events (eg seedling mortality due to a sudden cold snap) from occurring via the production of phenotypes that are suboptimal in the short term but optimal in the long term (eg seed germination later in spring). Starrfelt and Kokko (2012) showed how these contrasting strategies are extremes on a continuum: conservative bet-hedgers achieve reduced genotypic variance by minimizing individual-level variance in performance while diversified bet-hedgers achieve reduced genotypic variance by minimizing the correlation in performance among individuals of the same genotype via the production of a diversity of phenotypes (ie exploiting an evolutionary portfolio effect; see Figure 2).

### ■ Applications of the portfolio effect concept

In addition to providing a generalizable framework for understanding ecological dynamics and evolutionary



**Figure 2.** Example of an evolutionary portfolio effect. The left-hand panels depict correlated time series of fitness ( $W$ ) for three different individuals of the same genotype (for simplicity an asexual species is assumed, but the logic can be extended to sexual species), simulated from a multivariate normal distribution. In the top panels, the expected pairwise correlation among individuals in  $W$  is  $+0.8$ , the individual-level variance in  $W$  is 1, and the expected arithmetic mean  $W$  ( $\bar{W}$ ) is 5. In the bottom panels, the expected pairwise correlation among individuals is  $-0.2$ , the individual-level variance is 1, and  $\bar{W}$  is 4.5. The right-hand panels show the variance at the aggregate genotypic level ( $\sigma^2$ ), calculated by taking the mean  $W$  across the three individuals per time step, and then taking the variance of these means across time steps ( $10^4$  time steps were used here instead of 30 to obtain a more accurate estimate of  $\sigma^2$ ). The geometric mean  $W$  was then approximated using  $\bar{W} - \sigma^2/(2\bar{W})$  (Gillespie 1977). When the correlation among individuals of the same genotype is positive and large,  $\sigma^2$  is higher and hence the geometric mean  $W$  is reduced (top-right panel), relative to the situation where the correlation is weakly negative (bottom-right panel). Such negative correlations could arise, for example, if individuals “hedge their bets” by reproducing at different times or in different places, and a genotype exhibiting this strategy would be expected to outcompete, in the long term, one exhibiting the top strategy (eg where individuals reproduce at similar times or places). Note also that this evolutionary advantage arises despite the fact that the arithmetic mean fitness  $\bar{W}$  of individuals in the top panels is higher than those in the lower panels.

processes, the portfolio concept also offers opportunities for conservation and resource management. While ecology and conservation science tend to assume that a thorough understanding of ecosystems is required for developing effective policy (eg Gilman *et al.* 2010), an alternative and complementary approach is to focus on maintaining options and portfolios for organisms and their ecosystems as a means of spreading risk in the face of future uncertainty.

For instance, fishery yields tend to be more stable through time if multiple species or multiple stocks of the same species are exploited simultaneously (Worm *et al.* 2006; Schindler *et al.* 2010), despite limited understanding of the causes of dynamics of the component parts. Similar dynamics are expressed in agricultural systems, where crop variety and landscape diversity have important positive effects on agricultural resilience to climate change (Lin 2011).

Another case is illustrated by aboriginal North Americans living in coastal ecosystems, whose traditions

increased the reliability of resource flows to communities through the development of cultural mechanisms for exploiting portfolio effects. First, marriages were typically sought outside of an individual's community, as a means to develop community allegiances with access to different ecosystems. Second, resource sharing among communities became a critical component of the social fabric of coastal peoples, providing reliability in access to resources despite potentially extreme fluctuations in local resource abundance (Suttles 1987). These social customs exemplify how human "meta-communities" could produce portfolio effects among distinct villages, thereby dampening the fluctuations in resource abundance that individual communities experienced at local scales.

Modern portfolio theory offers perspectives on developing conservation and management strategies that are a distinct alternative to the belief that comprehensive understanding and accurate forecasting are prerequisites for effective application. In designing natural reserve networks, there has been a tendency to develop conservation strategies around "optimum" spatial distributions of reserves based on current or projected distributions of biodiversity. Yet such static approaches do not necessarily enable the possibility for spatially heterogeneous population dynamics and local extinctions, both of which we have only limited abilities to forecast. If one takes a dynamic view of the problem, assuming that species abundances will vary in response to environmental changes, the "optimal" static design is often distinctly different from a design that attempts to distribute risk to uncertain outcomes (Ando and Mallory 2012), just as evolutionary strategies that work well in the short term are not always those that persist over longer terms. Instead, the better conservation strategy might be to protect networks of habitat and connectivity that, in aggregate, maintain a range of habitat options for organisms, despite the responses of individual parcels showing independent vulnerabilities to swings in climate conditions or other large-scale environmental forcing.

Human activities have tended to homogenize and fragment ecosystems and thereby reduce the complexity that provides the foundation for portfolio effects. Some of this homogenization results from suppression of natural disturbance regimes, such as floods and fires; from land conversion; and from captive breeding programs that reduce genetic diversity (Poff *et al.* 1997; Schoennagel *et al.* 2004; Moore *et al.* 2010; Griffiths *et al.* 2014). Management and conservation plans should develop strategies at scales that include biologically relevant complexity, and also maintain the processes that produce complexity. Biological systems are sufficiently complex that scientists should be honest about the limits of their understanding, their forecasts, and their abilities to manage prescriptively (Schindler and Hilborn 2015). Developing the means to distribute the risks of inevitable uncertainty by maintaining "biological options" and the processes that produce them should be a central feature in applications of the precautionary principle.

## ■ Conclusions

Biologists are challenged to develop effective strategies for promoting conservation of biodiversity and sustainability of the ecosystem services that people rely on. Expanding urbanization, acidifying oceans, changing land use, and intensifying climate change are among the stresses that humans place on the biosphere. We encourage biologists to consider alternative strategies for understanding and managing ecosystems, and suggest that quantifying where and how portfolio effects are expressed in biological systems may help develop paths toward sustainability.

Modern portfolio theory developed in response to the realization that investment analysts had little hope of making reliable forecasts about the specific details of financial systems, despite having access to robust data on the entities they were managing. Instead, by exploiting certain emergent properties of financial systems, diversification across assets could minimize risks to the integrity and productivity of investments over the long term. Similarly, maintaining ecological heterogeneity and the processes that generate it across landscapes should become a more integrated component of management and conservation. Such approaches may provide effective strategies for managing risks to ecosystems in an increasingly uncertain future.

## ■ Acknowledgements

DES thanks the US National Science Foundation—Dynamics of Coupled Natural and Human Systems (CNH) Program, the Gordon and Betty Moore Foundation, and the US Fish and Wildlife Service for support. JBA is currently a Society for Conservation Biology—Smith Post-Doctoral Fellow. TER was supported by the Beaufort Marine Research Award: Fish Population Genetics (Irish Government NDP [2007–2014] administered by the Marine Institute). We also thank S Breslow for information about resource-sharing in aboriginal North Americans.

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