Ecosystem Energy as a Framework for Prioritizing Conservation Vulnerabilities and Management Strategies

Andrew James Hansen

Ecology Department, Montana State University, Bozeman, MT 59717

hansen@montana.edu

Abstract. Ecologists widely agree that context matters. In different places, we recognize that interactions among abiotic variables, ecological processes, species, and humans play out differently. Are there general properties of ecosystems that, if recognized, might help us set conservation goals more reliably? To address this question, I retraced the historical roots from which conservation biology has grown and found one property, ecosystem energy levels, which, while once widely recognized as important, has received little emphasis since. In contrast, the allied fields of ecosystem analyses and biogeography have made ecosystem energy a basis component of their research and its application. In this paper, I first review the current state of knowledge relating ecosystem energy to attributes of populations, communities, and landscapes critical to the interests of conservation biologists. Those hypotheses that are adequately supported are used as the basis to derive generalizations on the traits of ecosystems differing in energy levels and habitat heterogeneity. As a result of the review, I present a scheme that uses ecosystem energy levels as a strategic framework to help identify conservation priorities and those management practices most likely to be effective. Management strategies are then presented for ecosystems of each of three energy levels to achieve conservation objectives. The geographic distribution of each type of ecosystem is illustrated globally and applications are described in case studies of landscapes in the Pacific Northwest, northern Rocky Mountains, and Mid-Atlantic regions of the United States. Finally, I suggest research to reduce uncertainty on the implications of ecosystem energy serving as a framework for conservation planning under changing climate and land-use pressures. It is my hope that the framework will make conservation biology a more predictive science and help managers develop strategies that better meet their objectives.

Key words: biodiversity; conservation; ecosystem energy; management; primary productivity; species richness; vulnerability.

INTRODUCTION

Ecological systems are immensely complex. Developing strategies to conserve native species and ecological processes under increasing human pressure, thus, presents extraordinary challenges. Among these challenges is identifying high priority conservation threats in a given place and applying effective management to resolve them. This challenge has perhaps become more difficult as conservation biology has matured and recognized a growing list of potential vulnerabilities. Consequently, scientists and managers are often unable to crystallize key conservation priorities for their particular place. A typical result can be dissipated and ineffective management. In areas where a single dominant priority is agreed upon, in contrast, such as sustainable forest management in the Pacific Northwest U.S., effective management may result (Lindenmayer and Franklin 2002). Ecologists and managers widely agree, however, that context matters. In different places, the interactions among abiotic variables, ecological processes, species, and humans are known to play out differently. This suggests that there may be general properties of ecosystems that, if recognized, could be used to set conservation goals more effectively. Clues on such general principles may be found in the theoretical roots from which conservation biology has grown.

The development of conservation biology has been guided by theories from ecology and evolutionary biology. Many of these theories arise from classical works reaching back to the early and mid-20th century. In a famous paper of that era by G. Evelyn Hutchinson (1959), the question was posed, “what factors limit the number of species in a place”? Hutchinson identified five variables: habitat heterogeneity, habitat area, trophic structure, evolutionary processes, and available energy. Of these, the first four have been widely applied in conservation biology. For example, the importance of habitat structure was recognized by Hutchinson's student, Robert MacArthur (MacArthur and MacArthur 1961, MacArthur et al. 1966), and has fueled decades of progress in the management of vegetation patterns to achieve biodiversity objectives. Similarly, MacArthur and Wilson's primer on island biogeography (1967) served as a primary construct to predict the effects of habitat fragmentation. Strangely, energy availability (defined here as heat and the organic energy fixed by primary and secondary productivity) has been largely ignored by conservation biologists. In fact, the terms "ecosystem energy" is barely mentioned in conservation biology texts (e.g., Groom et al. 2006, Hunter and Gibbs 2007). Even a recent cutting-edge synthesis of principles for managing landscapes for conservation does not mention the term (Lindenmayer and Hobbs 2007). As a result of this omission, the possibility of using ecosystem energy as a basis for defining conservation strategies remains largely unexplored.

In related fields, however, ecologists and biogeographers have given great attention to ecosystem energy. Wright's (1983) 'Species Energy Theory' purports that available energy limits the size of populations and biodiversity. The theory was initially tested with small plot experiments where primary productivity was manipulated through nutrient additions (Middlebach et al. 2001). Biogeographers enlarged the scale of the theory's application by taking advantage of satellite-remote sensing technology. They discovered that correlations existed between species abundances or richness and spatial variation in various indices of primary production. Among biogeographers, there is now consensus that continental-scale patterns of species richness are driven primarily by kinetic energy (heat), potential energy (foods resulting from primary and secondary productivity), habitat heterogeneity, and the availability of water (Kerr and Packer 1997, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001, Acevedo and Currie 2003, Currie et al. 2004, Pautasso and Gaston 2005, Currie 2006, O'Brien 2006, Waring et al. 2006, Allen et al. 2007, Davies et al. 2007, Hawkins et al. 2007, Kerr et al. 2007, Nightingale et al. 2008, Field et al. 2009).

Some important applications emerge from these studies: measures of energy can be used to identify limits on biodiversity (Brown et al. 2001), define species-area relationships (Wright 1983), and to predict probable rates of extinction (Evans et al. 2005a). Available energy also influences recovery time of populations following disturbance (Huston 1979, 1994) and applies to human populations as well as it does to native flora and fauna (Balmford et al. 2001, Luck 2007a,b, Huston and Wolverton 2011). Based on its widespread acceptance in allied fields, Species Energy Theory should be highly relevant to conservation biologists concerned with the perpetuation of small populations, the assessment of habitat fragmentation, the use of disturbance in management, and, ultimately, in the very design of protected areas.

The limited use of Species Energy Theory in conservation biology may be a result of the history of development of ecology. Brown (1981) suggested that energy was seen by ecologists as one of the major drivers of diversity up into the 1960s as illustrated by Hutchinson (1959) and colleagues. In the 1970s, ecologists diverged, either to study ecosystems or to seek a better understanding of interactions among species. Wright's 1983 paper reopened interest in energy/diversity relationships, but largely among biogeographers and those ecologists concerned with developing models to predict geographic variation in species richness. At the time, conservation biologists remained focused on principles derived from studies in evolution, population, and community dynamics. More recently, ecologists have begun to consider the application of Species Energy Theory to conservation (e.g., Balmford et al. 2001, Huston 2004, Luck 2007b, Phillips et al. 2010, Hansen et al. 2011), but no general synthesis of the topic has emerged.

In this review, my general goal is to introduce ways to identify ecological properties that might provide a framework to set conservation objectives and to derive sounder management strategies. Leading criteria for such a scheme include recognition of spatial variation in productivity, habitat heterogeneity, disturbance patterns, and evolutionary and land-use history. My specific goal is to evaluate the merits of quantifying ecosystem energy as a basis for conservation and management. The paper is partitioned into four sections with the objectives:

To review the current state of knowledge relating ecosystem energy to attributes of populations, communities, and landscapes that are relevant to conservation;

To develop a framework to group ecological systems based on ecosystem energy and other factors that provides a basis for anticipating conservation priorities;

To present management strategies expected to be most effective in these different kinds of ecosystems;

To illustrate the geographic distribution of the ecosystem types described in the framework and to provide case studies from landscapes of low, medium, and high energy levels.

The paper first evaluates the evidence for each of several hypotheses on how ecosystem energy may influence the attributes of populations, communities, landscapes, and human land use that are pertinent to conservation. Those hypotheses that are adequately supported are used as the basis to group ecosystems based on ecosystem energy and key factors including topographic complexity and natural disturbance that interact with energy in influencing organisms. Conservation priorities and biological management strategies are then presented for each group of ecosystems. The global spatial distribution of the ecosystem types is then considered and applications are illustrated in case studies of landscapes in the Pacific Norwest, northern Rocky Mountains, and Mid-Atlantic regions of the United States. Finally, I suggest research to reduce uncertainty on the implications of ecosystem energy serving as a framework for conservation planning.

My intent is not to suggest that ecosystem energy is necessarily the primary factor that should be used to guide conservation. Mainly, I focus on this overlooked aspect of ecological systems to give it equal status to other factors controlling diversity as elucidated by Hutchinson (1959). The resulting conservation framework is designed to identify those conservation concerns likely to be most important in each group of ecosystems and the most appropriate management strategies. In many cases, experienced managers have worked out practical solutions that haven proven successful. The framework offered here may provide theoretical support for their practical insights and help others develop more effective "place-based" conservation programs.

REVIEW OF THE EVIDENCE

As stated above, there is now strong consensus that population sizes and community richness are influenced by ecosystem energy. These are among the suite of traits of populations, communities, and landscapes thought to influence vulnerability to human activities (e.g., Pimm et al 1988). To what extent might ecosystem energy cause variation in each of these traits in ways that are relevant to conservation? Below, I review the literature on this question for several levels of organization. Conclusions on the hypothesized effects of ecosystem energy, key references, implications for conservation, and weight of evidence are summarized in Table 1. Those hypotheses that are considered adequately supported are used as the basis for the conservation framework in the subsequent section. Readers less interested in the details of the hypotheses may choose to skim Table 1 and proceed to the sections on the conservation framework.

Population growth, abundance, extinction risk

Available energy is hypothesized to allow higher survival and/or reproduction of individuals, greater population abundances, and reduced risk of extinction (Preston 1962, MacArthur and Wilson 1967). The enhanced survival and reproduction may result from greater food resources or increased heat, which may allow individuals to divert resources from thermoregulation to activities such as reproduction (Hutchinson 1959, Turner et al. 1988). The positive relationship between available energy and species abundance may flatten at higher energy levels as other factors become limiting. Smaller populations are more prone to extinction due to increasing likelihood of loss of all individuals through genetic, demographic or environmental stochasticity, or catastrophic events (Pimm et al. 1988, Lande, 1993). This hypothesis is central to Wright's (1983) derivation of species–energy theory from the species-area relationship (see below).

A review of the evidence by Evans et al. (2005a) found that many experimental and field studies from invertebrates, birds, and mammals have shown that local population sizes increase with food availability, and many studies have demonstrated positive correlations between energy availability and local population size. They conclude that it is likely that local population sizes are generally limited by energy availability. Moreover, population density has been found to be a significant predictor of extinction for mammal species in 28% of ecoregions studied globally after controlling for geographic range size and body mass (Fritz et al. 2009) and of extinction risk for contemporary carnivores and primates (Purvis et al. 2000). Few studies have tested if extinctions are more prevalent in low-energy environments. However, Evans et al. (2005a) point out that if extinction risk changes with energy availability most dramatically at small population sizes, then the rarest species will show the strongest species–energy relationships. This was found to be the case by Bonn et al. (2004) in southern Africa. However, common species contributed more to species energy relationships for birds in Britain (Evans et al. 2005b,c) and in North America (Evans et al. 2006). Hence, I conclude the evidence is strong for population growth rates and abundance and partially supporting for extinction risk.

In a recent paper focusing primarily on controls on animal body size, Huston and Wolverton (2011) put forth that it is energy fixed during the portion of the year when an animal population is reproducing that most limits population size (and body size), not average annual energy. This distinction is important because the geographic locations highest in primary productivity during the reproductive period (termed ecologically and evolutionary relevant energy, eNPP) are largely in mid-latitudes (50-60 degrees north and south) (Huston and Wolverton 2011). Locations with highest annual primary productivity are largely in the humid tropics (e.g., Luyssaert et al. 2007). Thus, the eNPP hypothesis predicts that energy leads to low animal population sizes and high extinction risk both at high latitudes and in the tropics, while hypotheses based on annual productivity predict these trends primarily for high latitudes. Huston and Wolverton (2011) do not, however, test the effect of eNPP on population abundance directly nor consider alternative hypotheses on controls on body size and population density. Hence, pending further research on this topic, I do not consider the implications of eNPP for population abundance and extinction rates in this paper.

The key implication of the general hypothesis for conservation is that relatively more species will have small populations and be more prone to extinction in low energy environments. Thus, management of small populations to improve viability may be a higher conservation concern in low than in higher energy environments. Within this context, supplementation of energy resources through food provisioning (Gonzalez et al. 2006, Schoech et al. 2007, Lopez-Boa et al. 2009) and manipulation of productivity through irrigation and fertilization (Huston 2004) may be successful strategies for increasing population sizes of species at risk.

Home range size and body size

Home range size is hypothesized to be inversely related to habitat productivity, controlling for body size and trophic level (Harestead and Bunnell 1979). The size of an animal's home range is thought to be dictated by its energetic requirements. Energy requirements are largely determined by body weight and basal metabolic rate. Hence, home range size is known to increase with body weight, is larger for homeotherms than endotherms because of their relatively higher energy requirements, and is larger for carnivores than herbivores because of lower average density of utilizable production at higher trophic levels (McNab 1963, Harestead and Bunnell 1979, Mace and Harvey 1983). Thus, it follows logically that in more productive environments, energy requirements can be met in a smaller area, allowing home ranges to be smaller.

This hypothesis is supported by an analysis of relationships between North American mammal home range size and two indices of productivity, latitude and precipitation. Drawing on

36 previous studies, Harestead and Bunnell (1979) reported that home range size increased with latitude and precipitation, after controlling for body size and trophic level. More recently, Nilsen et al. (2005) found that a remotely sensed index of primary productivity added predictive power to the models of home range size for 8 of 12 carnivore species, and the explanatory power varied between 16% and 71% for the different species. Within species, home range size can vary by orders of magnitude across their ranges. A study of Eurasian lynx (*Lynx lynx*) found an inverse relationship between an index of prey availability and home range size of lynx in a portion of Norway (Herfidal et al. 2005). Across the full range of this species, the authors found an inverse relationship between home range size and indices of primary productivity. Similar results were obtained for male desert mule deer (*Odocoileus hemionus crooki*) in southwest Texas (Relyea et al. 2000) and for elk (*Cervus elaphus*) in Alberta and Wisconsin (Anderson et al. 2005). However, the relationship did not hold for female mule deer in the Texas study. Moreover, for elk in Wyoming, a positive relationship was confirmed. Herfidal et al. 2005, Anderson et al. 2005, and Relyea et al. 2000 all point out that productivity is one of several factors that influence home range size and that these factors may sometimes override the productivity/home range size relationship. With acknowledgement that productivity interacts with other factors to influence home range size, I rate the evidence as strong in support of the hypothesis.

Body size within a species is widely thought to be influenced by thermoregulatory factors such that larger size is favored in colder environments (Bergmann 1847). Huston and Wolverton (2011) put forth an alternative hypothesis that interspecific body size is regulated by available energy. If this hypothesis is correct, it suggests that populations within a species may adjust to local energy availability by either modifying home range or body size or a combination of both. Studies of energy and intraspecific home range size have controlled for body size. It would seem equally important that analyses of energy and body size within a species control for home range size. I conclude that more research is needed on the influence of ecosystem energy on body size before conservation implications can be drawn, especially interactions with home range size.

An understanding of the requirements for use of space is vital in management and conservation to scale the size of management units for a designated species (Herfindal et al. 2004). In the case of protected areas, animals with large home ranges are more likely to roam onto surrounding lands where they are subject to increased human-induced mortality and increased risk of extinction (Woodroffe and Ginsberg, 2000). This effect is predicted to be more pronounced in regions with low productivity. In the case of game harvest units, knowledge of home range size is needed to estimate population abundance and set harvest rates (Relyea et al. 2000). With respect to conservation planning and species recovery programs, it is important to know how much space individuals need when estimating potential carrying capacities for recovery areas (Herfindal et al. 2004).

Migration

Seasonal migration is hypothesized to occur more frequently in ecosystems where favorable thermal conditions and/or food are patchy in space and time. The primary advantages of migration are thought to be exploiting patches of high quality food in areas that cannot be occupied year round and reducing the impacts of predation (Fryxell and Sinclair 1988). For highly vagile groups such as many birds, it is well established that a greater proportion of species are migratory in systems where seasonality causes resources to be temporally variable (Cox 1985, Hurlburt and Haskell 2003). Also, movements of some migratory mammal populations are known to closely follow local spatial and temporal dynamics of forage quality and quantity (Senft et al. 1987, Sinclair 2003, Wang et al. 2006).

I hypothesize that large mammal (mass> 2 kg) migrations are more prevalent in ecosystems where productivity is low to intermediate and patchy in space and time. While this hypothesis has not been directly addressed in the literature, various lines of evidence are relevant. First, among large mammals, the majority of documented migrations involve herbivores. Berger (2004) surveyed the global literature and compiled a list of 94 populations with documented migrations (3-2178 km one way). Among these, 89 were herbivores and five were carnivores. The point is important because Oiff et al. (2002) discovered that large herbivore species richness varies with plant productivity and quality and predicted that herbivore richness is high in particular settings globally. Using data from Africa, they concluded that highest herbivore diversity occurs where plant-available moisture is intermediate and soil nutrients are high. They then modeled herbivore species richness across the tropical to temperate regions of the world based on these variables (Fig. 1). Predicted patterns of richness were low in deserts because of low moisture and in the humid tropics where high rainfall contributes to low soil fertility. Predicted richness was highest in the Great Plains of North America, Argentinian pampa, Gir Forest of India, the Serengeti region of Africa, steppes of Khazakstan and Mongolia, Cordillera of Spain, and the coastal region of Morocco and Algeria, all of which largely comprise grasslands, savanna, and lower density forests. Human land use correlates with plant productivity and soil fertility in a similar fashion (Huston and Wolerton 2011). Consequently, more than half of the area of highest predicted herbivore species richness has been converted to agriculture and lost herbivore diversity. (Oiff et al. 2002). In total, these results suggest that large herbivore richness, and thus the potential for many migratory species, is predicted to be more prevalent in the grassland to low density forest regions that have not been converted to intense human land use.

Colleague Linda Phillips and I (Hansen and Phillips in prep) explored the distribution of the herbivore migrations reported by Berger (2004) across North America relative to plant productivity and patchiness. We used MODIS NDVI data as an index of plant productivity (Zhao et al. 2005) and estimated annual mean, monthly coefficient of variation (CV), and spatial CV in mean annual NDVI within 1° x 1° cells across the continent. The frequency distributions of cells with migrations were compared to a set of cells randomly selected from locations without migrations. We found that migrations occurred more frequently than expected based on aerial extent in locations with intermediate mean annual productivity, intermediate seasonal variation, and/or intermediate spatial variation. No migrations occurred in the productive forests of the southeast and eastern U.S., nor in the fertile central plains of the US, which have largely been converted to agriculture. Migrations were most common in the mountain west, the Great Basin, and the mixed wood zone of central Canada and Alaska. Because more research is needed, I conclude that the evidence is intermediate that large ungulate migrations are most prevalent in ecosystems with intermediate productivity, intermediate patchiness in productivity, and high soil fertility, particularly those without intense land use.

Many conservationists are concerned about habitat connectivity to maintain gene flow among subpopulations, capacity for dispersal under climate change, seasonal migrations, and other reasons. The implication of this hypothesis for conservation is that management for connectivity to facilitate seasonal or spatial migration may be a high priority in the types of ecosystems described above and a low priority in systems where productivity is high and less variable such as in the humid tropics or where intense land use has extirpated large herbivores.

Spatially explicit population dynamics

Spatially-explicit population dynamics such as source sink dynamics are predicted to be more prevalent in ecological systems where limiting resources and/or predation are variable. Source/sink populations are those composed of subpopulations where reproduction exceeds mortality and net population growth is positive (sources) and subpopulations where net population growth is negative (sinks) (Pulliam 1988). The concept is highly relevant to conservation because interactions between source and sink subpopulations influence the stability of the metapopulation (Wiens et al. 2011). Persistence of the sink population requires dispersal from the sources. Ecosystem energy is one of many factors that may influence habitat quality and the prevalence of source sink populations.

Within landscapes that vary spatially in energy, mortality may be relatively high and reproduction relatively low in the patches with lower energy and associated resources, resulting in these patches being sinks that are dependent upon source areas in more productive patches. Accordingly, protected areas that lie in harsher biophysical settings may contain sink populations that are dependent on dispersal from source populations located outside the protected area (Hansen 2011). Land use that impacts these source areas may result in loss of the subpopulation in the protected area. For example, subpopulations of some migratory songbird species within Yellowstone National Park are dependent upon dispersal from source populations in more productive habitats outside of the park. Exurban development in these source habitats has increased nest predation rates and converted them to sinks for some bird species, putting at risk the subpopulations within the park (Hansen and Rotella 2002).

In some cases, low productivity areas may be what are termed “refuge” habitats, where organism survival is relatively high but reproduction is relatively low, so the subpopulation is a weak source (Naves et al., 2003). This typically occurs in “suboptimal refuge areas with scarce nutritional resources but a lower risk of human-induced mortality that may allow for population persistence”, Naves et al. (2003, pg. 1277). Such populations are often either large predators in protected areas or endangered species that have been displaced to the edges of their former ranges. In both cases, these species are highly vulnerable to slight increases in mortality because of human activities. Documented examples include grizzly bears (*Ursus arctos*) in the Cantabrian Mountains of Spain and lynx (*Lynx pardinus*) in the Iberian Peninsula of Spain (see Hansen 2011). Such species are especially at risk if the refuge habitats are surrounded by “attractive sinks”, places where habitat quality is good, allowing potentially high reproduction and high survival, but where either reproduction or survival is reduced by forces that are not detected by the organism (Delibes et al., 2001a). Hence, the organism selects habitat based on perceived quality, but suffers either high mortality or low reproduction there because of hazards that are not detected. More intense land use in the productive lands around refuge habitats may cause these lands to become attractive sinks that can put at risk the subpopulations in the refuge habitats, as is the case for grizzly bears in the Greater Yellowstone Ecosystem, USA (see Hansen 2011).

This hypothesis on spatially explicit population dynamics is well-developed theoretically and confirmed in empirical studies. Thus, I rate it as strongly supported.

Species richness of communities

Brown et al. (2001) hypothesized that species diversity is an emergent property of ecosystems that is often maintained within narrow limits. They termed this property 'carrying capacity for species richness' (S_K) and defined it as a "steady-state level of richness specific to a particular site or local ecosystem, that is set by resource availability and other local conditions and is maintained despite changes in species composition" (pg. 328). They tested the S_K hypothesis with three primary data sets and a review of published studies which tracked species richness over decades to millennia. They concluded that richness has remained remarkably constant over time despite large changes in composition as predicted by the hypothesis. The mechanism they proposed to account for this regulation requires relatively constant levels of productivity and resource availability and an open system with opportunity for compensatory colonizations and extinctions. The many studies concluding that kinetic energy and potential energy are important drivers of species richness (see Introduction) are consistent with and provide support for the S_K hypothesis. The overall conclusion is that ecosystem energy is one of the factors that set the fundamental capacity of an ecosystem to support species richness.

The S_K hypothesis is defined above as occurring under equilibrium conditions, "relatively constant levels of productivity and resource availability". Climate and thus ecosystem energy are known to vary at decadal, centennial, and longer time scales. The extent of equilibrium or disequilibrium in S_K is expected to be a function of the rate of adjustment in species richness to changing resource conditions. It is possible that some of the discrepancies among studies of Species Energy Theory result from some study areas being in equilibrium while others are in disequilibrium due to climate change, natural disturbance, or other factors. Schimel et al. (1997) conclude that vegetation quickly responds to environmental change such that primary productivity strongly reflects the interactive effects of climate, soil fertility, disturbance, and other factors. Thus, primary productivity is typically in equilibrium with ecosystem conditions. Among the various elements of biodiversity, response rates to environmental change are known to vary. Vagile organisms such as birds are expected to respond more quickly than sessile organisms such as vascular plants (White et al. 2010). Among individuals, body mass likely responds most quickly to environmental change followed by reproduction, with survival being slowest to respond. Similarly, within populations, abundance of short lived species may adjust to changing conditions within months to years, but time to extinction may take decades to centuries (Brooks et al. 1999). We do not know enough about response rates of species richness among taxonomic groups and about rates of change in resources in particular ecosystems to determine which systems are in equilibrium or in disequilibrium. We do know, however, that spatial patterns of native species richness across environmental gradients are relatively consistent among continents and across studies, suggesting that species richness does largely reflect the capacity of ecosystems to support species (Studies cited in Introduction). Moreover, in considering the influence of environmental stability on species energy relationships, Evans et al. (2005a) conclude that environmental stability is unlikely in general to confound species-energy relationships. Thus, the concept of S_K remains highly relevant to conservation.

Another area of uncertainty is the shape of the relationship between energy and biodiversity at higher energy levels (e.g., Wright 1983, Rosenzweig and Abramsky 1993, Huston 1994, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001, Whittaker and Heegaard 2003). At continental scales, nearly all studies found a positive linear relationship between species richness and energy at lower levels of energy. At intermediate to high levels of energy, the relationship has been found to be positive linear, positive flattening, or unimodal, where richness peaks at intermediate energy levels and decreases at high-energy levels. Several hypotheses have been proposed to explain both the positive and negative shapes of the relationship, although it is fairly well accepted that different mechanisms apply in different geographic areas based on limiting factors of the particular ecosystem (Rosenzweig 1995). The most widely cited explanation for the positive relationship is the ‘‘More Individuals Hypothesis,’’ which suggests that increasing energy decreases the probability of local extinctions by influencing organism abundances and populations sizes (Wright 1983, Srivastava and Lawton 1998) (see Population Growth, Abundance, Extinction Risk section above). The most widely cited hypothesis explaining the negative slope of the relationship is the ‘‘Dominance Hypothesis,’’ which suggests that at high energy levels, a few plant species are able to dominate and competitively exclude other species, resulting in lower vegetation structure and plant species richness and lower habitat and food diversity for higher trophic levels (Huston 1994). In a metaanalysis of studies on species-energy relationships in plants, Gillman and Wright (2006) found evidence for competitive dominance causing reduced species richness in high energy environments in studies at local spatial scales in some of the studies they reviewed. At continental scales, however, they concluded that nearly all studies of plants show that species richness increases with productivity, which indicates that competitive dominance is not a strong force at these scales. Another hypothesis for the downturn in richness at high energy levels is that high productivity leads to a decrease in the heterogeneity of limiting resources and fewer foraging niches (Huston 1979, Tilman 1982, Tilman and Pacala 1993). However this hypothesis has not been widely tested. Overall, attempts to synthesize the results of species–energy studies among geographic locations, taxonomic groups, or spatial scales have not supported a consistent shape in the species–energy relationship at medium to high energy levels (Waide et al. 1999, Mittelbach et al. 2001, Whittaker and Heegaard 2003, Gillman and Wright 2006).

Colleagues and I examined the shape of the relationship between native landbird richness and several measures of energy across North America (Phillips et al. 2010). We found a strong unimodal relationship between gross primary productivity (GPP) and species richness (Fig. 2a). Net primary productivity (NPP) (new biomass fixed) should theoretically be a better predictor of species richness than GPP because GPP includes energy lost to plant respiration which is not available to consumers. We suspect GPP was a stronger predictor in this study because it is more accurately simulated than NPP in the MODIS data we used. An interesting finding in the study was that samples with similar energy level and slope of relationship were spatially contiguous, with samples in the west and north having positive slope, those in the mid latitude having a flat slope, and those in the SE and Pacific Northwest a negative slope (Fig. 2b). Hence, the fundamental relationship between energy and species richness differed geographically. Similarly, a study of species energy relationships for birds within 1-degree cells across the terrestrial portion of the biosphere similarly found positive and flat to negative slopes within grid cells (Hurlbert and Jetz 2010). The strong relationships and positive slopes were in the high latitudes and in deserts. The weak relationships and slightly positive to slightly negative slopes occurred in areas of higher productivity such as the Amazon Lowlands and the Congo foothills.

I conclude that evidence that ecosystem energy influence species richness is strong. At low to intermediate energy levels there is overwhelming evidence that the relationship is positive. Under what circumstances species richness declines at the highest energy levels is still under considerable debate.

Knowledge of the current spatial distribution of S_K and of human impacts can provide a strong basis for conservation planning, particularly for prioritizing locations for protection and for restoration (Hansen et al. 2011). At the continental scale, locations of high S_K and low human impact should be high priorities for protection because they represent continental hotspots for native species. Locations of high S_K and high human impacts may be high priorities for restoration. By reducing the negative human impacts, native species richness is expected to move on a trajectory towards the higher natural carrying capacity. Within low energy regions, there is often high spatial variation in available energy, with localized hotspots of high energy being especially important to native species (Hansen and Rotella 2002). Prioritizing such locations for conservation can be a cost-effective means of achieving biodiversity objectives in such landscapes. In regions where energy is relatively high and the slope of the species–energy relationship is negative, low-energy places may be localized biodiversity hotspots and benefit from allocation as conservation zones. Because species richness may be depressed by dominance of overstory vegetation, logging, grazing, and prescribed fire may be effective in breaking competitive dominance, releasing early- and mid-seral species, and increasing native species richness (Huston 1979, Odion and Sarr 2007).

Disturbance and succession

The Intermediate Disturbance Hypothesis (Connell 1978) has become solidly rooted in conservation biology and is used to guide application of disturbances such as timber harvests or prescribed fires to maintain native diversity. Some 40 years ago, however, Huston (1979) suggested that the effect of disturbance on diversity is mediated by ecosystem productivity such that diversity peaks at higher rates of disturbance in productive environments (see also Huston 1994). The premise of the Huston's Dynamic Equilibrium Hypothesis (DEH) is that productive environments allow high population growth rates which lead to dominant species competitively excluding other species and reducing species diversity (Fig 3). Disturbance breaks this competitive dominance, frees resources that allow for rapid recovery of post-disturbance communities, and increases species diversity. In low productivity environments, alternatively, recovery following disturbance is predicted to be slow and more variable as resources and conditions limit species growth rates. Disturbance events in these environments typically compounds physiological stress that organisms experience where resources are already limited, resulting in decreased species richness. Hence, depending on the productivity of the ecosystem, disturbance may act to enhance diversity by breaking competitive dominance or reduce diversity through environmental stress.

The Dynamic Equilibrium Hypothesis has been widely tested. Moderate to strong support for the hypothesis was found in aquatic communities (Cardinale et al. 2006), marine communities (Widdicombe et al. 2001, Worm et al. 2002, Svensson et al. 2007, 2010), microbial communities (Scholes et al. 2005, Haddad et al. 2008), plant communities (Proulx and Mazmuder 1998, Osem et al. 2002, Bakker et al. 2006), bird communities (McWethy et al. 2010) and simulated communities (Kondoh 2001). Most of these studies, however, found some level of deviation from the predictions of the hypothesis. It is increasingly understood that this hypothesis is contingent on important underlying assumptions which are not always met, including: potential for competitive exclusion, a large regional species pool, multiple stages in succession, and trade-offs between competition and colonization (see Svensson et al. 2010). It is also widely accepted that the disturbance/productivity interaction effect on diversity varies with disturbance type (Svensson et al. 2007, 2010) and the life history attributes of the species in the community (Scholes et al. 2005, Haddad et al. 2008).

Nonetheless, the effect of productivity on community response to disturbance was dramatic enough in a study of 85 streams in the Mid-Atlantic United States to lead Cardinale et al. (2006) to argue that univariate explanations of diversity (e.g. disturbance or productivity alone) are antiquated, limited to too narrow a range of variables to represent generalities, or are altogether incorrect. Similarly, the strong results of a meta-analysis of 30 studies of diverse grazing systems led Proulx and Mazumder (1998) to conclude that plant species richness decreases with high grazing in nutrient-poor ecosystems, while it increases with high grazing in nutrient-rich ecosystems. In forested systems, McWethy et al. (2010) found that bird species richness in stands increased with higher levels of disturbance in the surrounding landscape within a highly productive environment, but richness decreased with increasing disturbance in the surrounding landscape within a less productive setting. Within the assumptions stated above, I consider the evidence in favor of the hypothesis to be strong.

One of the most fundamental decisions natural resource managers face is how much disturbance is required to achieve biodiversity and other objectives. Where the Dynamic Equilibrium Hypothesis applies, the answer depends upon the productivity of the system (Proulx and Mazumder 1998, Odian and Sarr 2007, Verschuyl et al. 2008, McWethy et al. 2010). Timber harvest, grazing, prescribed fire and other induced disturbances should be applied at higher rates (frequency and/or intensity) in highly productive systems where species have been lost because of competitive exclusion to allow the maintenance of both late and early seral species. In low productivity systems, prescribed disturbance should be applied at lower rates to reduce loss of species because of disturbance and post-disturbance stress. Application of disturbance in productive settings in the humid tropics should be approached with caution. Warm, moist environments often have high levels of leeching of nutrients from soil (Huston and Wolvertion 2011). Where parent materials are not refreshed by geologic and other processes, such as in the Amazon Basin, soil fertility can be low with most nutrients bound in vegetation.

Disturbances that remove vegetation can result in depleted nutrients, slow recovery, and a long-term loss of species richness. On the richer, volcanically derived soils in parts of SE Asia, disturbance may have a positive effect on species richness as predicted by the Dynamic Equilibrium Hypothesis.

Another important implication for conservation is that human impact on disturbance and productivity should not be assessed or managed in isolation (Worm et al. 2002, Cardinale et al. 2006). Human alterations of the nutrient cycles (e.g., nitrogen, phosphorus) have increased productivity in many terrestrial, freshwater and coastal ecosystems. Dams, alteration of riparian zones, fire exclusion, and manipulation of herbivore and predator populations have changed both disturbance regimes and consumer pressure. Rapid change in species composition and loss of diversity is expected when, for example, disturbance is reduced while the availability of nutrients or water availability are increased, as often occurs with intensification of land use.

Within-patch vegetation structure

The effect of within-patch vegetation structure on species richness is hypothesized to be reduced in lower energy environments where available energy limits population sizes and niche specialization (MacArther et al. 1966, Hansen and Rotella 1999, Verschuyl et al. 2008). In a classic paper, MacArthur and MacArthur (1961) quantified the striking relationship between bird diversity and diversity of canopy layers in forests (termed foliage height diversity). They speculated that increased vegetation structural complexity provided a greater range of resources and conditions, allowing more species to obtain adequate niche space. MacArthur (1964) expanded the concept to include horizontal structural complexity. Since then, numerous studies have provided support for the hypothesis that species diversity is positively related to vertical and horizontal structural complexity in canopy layers, live plant size and density, and dead plant abundance and decay class (Verner et al. 1986, McCoy et al. 1991). These elements of vegetation structure are now known to also influence microclimate, nutrient cycling, disturbance, habitat for hiding, foraging, and reproduction, and availability of foods including leaves, seeds, fruits, and their consumers such as invertebrates (Hunter and Gibbs 2006). The hypothesis is now fully integrated into conservation biology, and managing for structural complexity is a key strategy of sustainable practices in forestry and agriculture (Lindenmayer and Franklin 2002, Magdoff 2007).

Although largely overlooked in modern ecology and conservation biology, both Hutchinson (1959) and MacArthur (1961, 1969) speculated on interactions between available energy and vegetation structural complexity in limiting species richness. Hutchinson (1959) noted that species richness may be low in low-energy environments because vegetation productivity is too low to support forested habitats with multiple canopy strata, among other reasons. MacArthur et al. (1966) found that forests in Panama had much higher bird species richness than those in the temperate US, but similar foliage height diversity. They proposed that more species can inhabit each canopy layer in the more productive tropical forest because of the enhanced food resources available. Building on this logic, Hansen and Rotella (1999) suggested that vegetation structural complexity accounts for less variation in low energy environments because energy is too limiting to support viable population sizes of some species. This hypothesis was tested along a transect in the Pacific and Inland Northwest US extending from the productive maritime forests west of the crest of the Cascades Mountains to the cold temperate forests on the east side of the Rocky Mountains (Fig 4a). Verschuyl et al. (2008) found that structural complexity explained more than 40% of the variation in bird species richness beyond that explained by primary productivity in productive maritime forests. In the less productive cold temperate forests, structural complexity explained only 15% additional variance beyond primary productivity (Fig 4b). Because this hypothesis was tested by only one study, support for it is considered intermediate.

If these findings are borne out by additional studies, the key implication for conservation is that management for forest structural complexity to benefit biodiversity should yield good results in productive environments, but the benefits will likely be reduced in low-energy environments.

Habitat edge effects

Available energy may also influence species responses to vegetation structure at the landscape level. The Biomass Accumulation Hypothesis (Hansen and Rotella 2000) asserts that landscape edge effects are more pronounced in productive forests with lower rates of disturbance that build high levels of aboveground biomass. In such forests, dense vegetation significantly modifies microclimate, resulting in large differences between disturbance patch edges and forest interior in vegetation structure, microclimate, and nutrient cycling. This allows finer habitat partitioning by organisms of the edge to interior gradient than is the case in lower biomass ecosystems. An initial test of this hypothesis reported that the abundances of significantly more bird species varied with edge density in a productive PNW landscape where vegetation structure differed considerably between open and closed-canopy patches than in lower productivity landscape where vegetation structure differed less between open and closed-canopy patches (McWethy et al. 2009). A stronger test of the hypothesis involved a meta-analysis of 31 published studies from the major forest biomes of the world. Hansen et al. (in review) found that magnitude of edge influence of microclimate was significantly related to forest biomass for light intensity and relative humidity. The percent of vertebrate species that specialized on forest interiors was significantly related to biomass for mammals and birds, and nearly significant for beetles (Fig 5). No forest interior species were found in four studies in boreal forests (aboveground biomass < 75 t/ha). In temperate and moist tropical forests (aboveground biomass > 400 t/ha), five studies found 17-32% of species were significantly more abundant in forest interiors than near forest edges and one study found 50% of beetles were forest interior specialists. While these two initial studies provide support, the evidence for the hypothesis is considered intermediate pending further testing.

The results suggest that forest fragmentation is most likely to influence forest species negatively in high biomass ecosystems such as tropical and temperate rainforests, but may have little influence in low-biomass ecosystems such as boreal or subalpine forests. Thus, forest managers in high biomass forests should not be confused by the ambiguous results of edge studies globally and continue to take seriously the management of habitat configuration within their forests. In ecosystems with low biomass accumulation such as boreal, dry, or cold forests, conservation strategies to manage edge effects may be a lower priority.

Trophic structure

A major thrust in conservation biology is the maintenance or restoration of top predators. This is often motivated by the goal of reducing overabundant herbivore populations and countering negative effects of over grazing. Such "top down" control of trophic structure where top predators cause cascading effects at lower trophic levels has been documented in some ecosystems (see Estes et al. 2011). In many systems, however, trophic structure is controlled not by top predators but by “bottom-up” factors – abiotic conditions and primary producers (Sinclair and Krebs 2002). Factors causing top-down vs. bottom-up control of ecosystems are not well understood (Sinclair 2003). A recent study suggested that top-down control is more common in lower productivity environments.

Melis et al. (2009) examined the influence of predation on the population dynamics of roe deer (*Capreolus capreolus*) across the wide gradient in climate and productivity found across the European continent. They concluded that deer densities varied with indices of forage productivity and winter severity across the continent. The effect of predation by wolf (*Canus lupus*) and lynx on population dynamics was stronger with declining environmental productivity and increasing harshness of winter. In the most productive regions, deer populations with predators present attained 60-80% of the predator-free population density. In the least productive regions, populations with predation had densities less that 10% of those without predators. The authors speculated that the mechanisms underlying this effect are: (1) an inverse density dependence of the impact of predation (percentage of population killed by predators being higher at low than at high densities of prey); and (2) the additive character of predator-caused and winter-caused mortality of roe deer in harsher regions.

While the results of this study are intriguing, clearly more theory and empirical study is needed to understand the influence of ecosystem productivity on trophic cascades. Schmidt (2010) points out those top-down effects are expected when herbivore effects on plants are not density dependent. In this case, plant growth rates in highly productive environments should more fully compensate for loss of plant biomass to herbivory than in unproductive environments, reducing the indirect effect of predators on forage production. The factors that influence density dependence of herbivores on forage and how these vary with ecological productivity, however, are not well known (see also Hegel et al. 2010). Thus I rate the hypothesis that top-down effects are more likely in low productivity environments as inadequately tested.

Better understanding of the factors controlling trophic cascades is needed for improved management of predators. Such programs are often controversial because of the high risk that top predators can present to humans, livestock, pets, and hunted ungulate populations. Knowledge of the conditions under which top predators are likely to have the desired effect on community structure would help managers execute such reintroductions where they are likely to be most effective. This knowledge could also be used to guide predator reduction efforts to the conditions under which they will best improve prey populations.

Invasive species

Places with high native plant diversity also tend to have high numbers of invasive species (Stohlgren et al. 1998, 2001, Brown and Peet 2003). This "rich get richer" situation is attributed to: 1) exotic species as a group have the same suite of life history traits as native communities; and 2) they are more prevalent in warm, moist environments with high soil nutrients (Huston 1994, Sax 2002, Shea and Chesson 2002). Disturbance rates are thought to interact with site quality to influence invasibility by exotics. Huston (2004) extended the Dynamic Equilibrium Hypothesis to invasive plants and predicted that invasives (like native species) have the highest richness in productive sites with high disturbance rates. Disturbance opens the site, allowing invasion, and high growth rates allow the invaders to gain dominance. In sites with low productivity and low disturbance, in contrast, probability of establishment is high due to low competitive dominance, but the probability of dominance is low due to slow growth rates. Under these conditions, exotic species are predicted to have relatively little negative impact, and to assimilate into the native community. Studies with results that are consistent with these predictions include Burke and Grime 1996, Brown and Peet 2003, Stohlgren et al. 2005, Davies et al. 2007. However, there have been no direct tests of the hypothesis. Hence, I rate the hypothesis as inadequately untested.

The implications of the Dynamic Equilibrium Hypotheses for management of invasive species are examined in detail in Huston (2004) and include:

- Environments that are both productive and disturbed, such as agricultural or riparian areas, often have serious exotic problems caused by dominance of the invading species.
- Two primary options for controlling or eliminating exotic species are manipulation of the disturbance regime and manipulation of productivity.
- Invasives are best controlled in productive environments by reducing disturbance, (which will often allow native species to out-compete exotics) and in unproductive environments by increasing disturbance to the levels that native species are best adapted.
- Increases in nutrients or water in productive areas may reduce exotics through competition from native species.
- These strategies will sometimes similarly inhibit native species as they do invasives, and so need be used with caution.

Land use

Human population density varies greatly over the globe and is presumably driven by a complex array of social, economic, political, historical, and ecological factors (Huston 2005). Nonetheless, measures of ecosystem energy explain some 28-65% of the variation in human population density within studies done at national to continental scales (Balmford et al. 2001, Evans and Gaston 2005, Vazquez and Gaston 2005, Hansen et al. in prep.) (Fig 6a). The relationship is positive or positive flattening within the range of energy values found at national scales (Chown et al. 2003, Evans and Gaston 2005, Vazquez and Gaston 2005, Luck 2007b, Hugo and van Rensburg 2008) and unimodal across larger spatial extents such as sub-Saharan Africa and North America, which have wider energy gradients and include areas with very high energy levels and decreasing human density (Balmford et al. 2001, Hansen et al. in prep).

The positive portion of the unimodal human density/energy relationship may be partially explained by preferential human settlement in places with productive natural resources (Huston 2005, Luck et al. 2010). People have also settled near transportation corridors such as coastlines and river valleys, which coincidentally may be more productive than other random locations. In recent decades, digital advances in technology has increasingly allowed people to live where they choose. Many have chosen locations with high natural amenities, which has led to high rates of exurban development (Brown 2005), particularly around national parks, wildernesses, and other areas with high quality scenery, wildlife, and recreation (McGranahan 1999). In the US, exurban development has taken place both in regions of high productivity (e.g., upper Midwest and southeast) and in areas of low productivity (e.g., Rocky Mountains and the southwest). The factors accounting for the negative portion of the human density/energy relationship (e.g., why human settlement is less dense in the most productive places such as northwest coastal forests in the U.S. and the Congo in sub-Saharan Africa) are not well understood. Huston and Wolverton (2011) make the case that the relatively poor soils portions of the humid tropics and the resulting low agricultural productivity explain the lower human population density in such areas.

At regional scales, the spatial distribution of human land use often differs between low and intermediate productivity environments. Across North America, regions low in mean productivity have relatively high variation in productivity (Hansen et al. 2010). Within such regions, human land use is often concentrated on localized areas of better climate and soils, and higher productivity (Hansen et al. 2002). In contrast, regions high in mean productivity have low variation in productivity. Land use intensity in such regions is more evenly distributed spatially.

Human population density also is positively associated with species richness of many taxonomic groups at coarser spatial scales ($>=1^{o}$ latitude and longitude) (see Luck et al. 2010 for a review) (Fig 6b). At these scales, this relationship is thought to be correlational and to result because humans and native species favor similar biophysical settings, namely places of intermediate productivity and high habitat heterogeneity (Balmford et al. 2001). This positive association between people and biodiversity at broader spatial scales raises concern about conservation of biodiversity in the areas of high richness (Balmford et al. 2001, Luck et al. 2010). This is because human activities can have causal effects on biodiversity at local spatial scales. While species and guilds vary individualistically in response to humans, human land use at moderate intensities may increase native species richness by increasing primary productivity, supplementing food resources, and increasing habitat heterogeneity (Hugo and van Rensburg 2008, McKinney 2002a). As land use intensifies, however, many native guilds of species decline while exotic species and synanthropic species (those that do well under higher human densities) increase (McKinney 2002b, Radeloff et al. 2010) because of habitat destruction, very high or low primary productivity, increased mesopredators and non-native species, and human disturbance or persecution of native species (Hansen et al. 2005). Thus, the evidence that human population density is correlated with primary productivity and with species richness is strong. The mechanisms underlying the relationship, however, are poorly understood.

These relationships between ecosystem energy, humans, and species richness have several implications for conservation. Continental and global hotspots for biodiversity are disproportionately high in human density and subjected to intense negative human effects that reduce native species richness. Protected areas are under-represented in productive settings (Scott et al. 2001, Hansen et al. 2011). Thus protecting remaining natural areas in such hotspots is important to reduce additional loss of biodiversity in these areas. Evidence of the effectiveness of this approach comes from Luck et al. 2010 who found in Australia that the proportion of land in conservation status was more strongly related to native species diversity in productive regions than in low energy environments. Similarly, areas in such hotspots that have been degraded by intense human activities should be high priorities for restoration. The high biophysical potential to support native species in such locations should lead to strong positive results from restoration. In regions with relatively low ecosystem energy, human density is relatively low and the extent of protected areas is relatively high, suggesting that conservation challenges are less severe. Within such regions, however, people and native species are often concentrated in the same small proportion of the landscape that offers favorable biophysical conditions. The increased exurban development fueled by advances in technology is particularly rapid in such local hotspots (Gude et al. 2007). Hence, prudent conservation strategies are also a high priority in these locales.

GENERALIZATIONS ON TRAITS OF ECOSYSTEMS

This review of hypotheses reveals that ecologists have long considered the influence of ecosystem energy on populations, communities, and landscapes. The resulting theory and empirical evidence suggests that ecosystem energy is sometimes a strong causal factor in ecological systems and that the effects of energy can be nonlinear, causing positive relationships at low energy levels and negative relationships at high energy levels. A reoccurring theme in the review is that ecosystem energy interacts with both disturbance and habitat structure in influencing biodiversity. Moreover, biological response to primary productivity is sometimes mediated by soil fertility, which can influence plant quality for consumers, recovery time following disturbance, and patterns of human land use.

This body of work can be synthesized into generalizations on the traits of ecological systems based on ecosystem energy and habitat heterogeneity (Fig. 7). I consider primary production of ecosystems as a key property because it integrates the effects of temperature, moisture, soils, and other biophysical factors (Schimel et al. 1997) and thus is frequently found to be the strongest univariate predictor of species richness (e.g., Phillips et al. 2008). The three levels recognized in this review are meant to qualitatively approximately the positive, flat, and declining portions of the unimodal species energy relationship and the human population density richness relationship.

Disturbance and habitat structure are integrated for the y axis in Fig. 7. Habitat heterogeneity refers to both the seral stage diversity resulting from “natural” disturbance and habitat complexity resulting from topographic, edaphic, and other geomorphic factors. The nonhuman disturbance regime in an ecosystem may be driven by regional to global exogenous factors such as, for example, climatic systems that generate hurricanes. They may also be driven by internal dynamics such as the effect of vegetation growth on fuel loads and fire regimes, or by the interaction of these exogenous and endogenous factors (Shugart 1984). The consequence is that many ecosystems have characteristic disturbance regimes that are highly relevant to biodiversity and conservation. For example, hurricane-prone terrestrial ecosystems occur where ocean temperatures are warm enough to generate these storms and where prevailing winds blow them on shore. These conditions are met in the Caribbean and southeastern US, southeast Africa, India and southeast Asia, and northern Australia. Natural disturbance and seral stage diversity are expected to be relatively high in such ecosystems compared to ecosystems at similar latitudes where the prevailing winds are offshore (e.g., the Congo). Similarly, geomorphic habitat complexity differs among ecosystems and is known to be a strong predictor of species richness (Davies et al. 2007). Whereas seral stage diversity as driven by disturbance and regrowth and geomorphic habitat complexity do not have identical effects on biodiversity, we group them here into one axis to represent ecosystems with relatively high or low total habitat complexity.

According to the presented scheme, low productivity ecosystems tend to include species with low population growth rates, small populations, large home ranges, migratory habits and spatially explicit population dynamics. Communities tend to be low in S_K overall but increase in richness with energy in the interval, suffer high stress following disturbance, and possibly show strong top-down predator effects. Human land use is often low in overall intensity, but concentrated in biodiversity hotspots. Invisibility by non-native species is possibly low in these systems, but especially low in those with little disturbance. Low energy systems with higher habitat heterogeneity tend to have slightly higher S_K and stronger spatially explicit population dynamics than where habitat is more homogenous. Ecosystems with high energy levels tend to have populations with fast growth rates, high abundances, and small home ranges. Communities experience strong competitive exclusion and recover rapidly following disturbance, except where soils are poor. Many species specialize on the diverse microhabitats within stands or across landscapes and thus are strongly influenced by stand and landscape pattern and human habitat fragmentation. The intensity of land use is variable depending on soil fertility. S_K may decline at the highest levels of productivity where competitive dominance is prevalent or where soils are poor, but can be very high on more fertile soils and in locations with high habitat heterogeneity. Invasiveness is especially high where these systems have high natural disturbance. Ecosystems with intermediate energy levels often have high S_K because competitive exclusion is not an overly strong force in reducing diversity as in high-energy systems. This is especially true where habitat heterogeneity is high. Human density and land use tend to be high across much of the landscape. Consequently species richness may be substantially changed from S_K by the direct and indirect effects of human activities on biodiversity, including loss of top predators and expanded mesocarnivores. Invasive species richness may be high due to the intense land use.

FRAMEWORK FOR CONSERVATION BASED ON ECOSYSTEM ENERGY

The varying traits of ecosystems across gradients in ecosystem energy and habitat heterogeneity provide a basis for grouping ecosystems to inform conservation and management. Table 2 provides a framework for prioritizing biological management strategies for achieving conservation objectives among locations based on the ecosystem energy levels described above. The framework suggests high priority management strategies for major categories of conservation concern for low, medium, and high energy ecosystems.

Low- energy ecosystems

Many native species may be sensitive to land use change in low energy systems because of the effects of energy limitation on population dynamics. Species with low abundances, large home ranges, seasonal migration, and/or source sink or other spatially explicit dynamics may be at risk in these systems (Purvis et al. 2000, Fritz et al. 2009, Woodroffe and Ginsberg 2000, Berger 2004, Wiens et al. 2011). Large carnivores are most likely to have some or all of these traits. Some large carnivores are confined to the lowest productivity portion of their remaining habitats by human land use in other parts of the landscape (Naves et al. 2003). Such species occupy refuge source areas where survival is high due to low human-induced mortality and reproduction is low due to resource limitation. Slight increases in human-induced mortality can convert these refuge sources into sink habitats. Such mortality is difficult to avoid because these carnivores are often dangerous to humans or livestock and may be killed as a consequence (Woodroffe and Ginsberg 2000). Such populations, along with many other types of species, are also vulnerable to loss of individuals to attractive sinks in the more productive portion of the landscape (Delibes et al. 2001a). Because of potentially strong top-down controls in such systems, loss of top predators can lead to trophic cascades which have negative consequences for lower trophic levels (Schmidt 2010). Mammalian herbivores and other species may migrate seasonally to cope with variable resources and depend on maintenance of migration corridors. Their winter or wet season habitats often have higher intensity of human land use than summer or dry season habitats (Berger 2004). Consequently, exchange of diseases among livestock and native herbivores, competition for forage, and property damage may all be management challenges on these seasonal habitats (e.g., Cleaveland et al. 2001, Cross et al. 2007).

Disturbance such as timber harvest, livestock grazing, or prescribed fire can cause high mortality in many species and lead to slow rates of recovery in low productivity systems (Huston 1994). In addition to jeopardizing individual species, the low vegetation productivity and biomass following disturbance may depress community richness for relatively long periods of time. Low productivity systems, nonetheless, typically include some early and late seral specialists (Hansen et al. 1999). Thus, some level of disturbance is required in these systems. However, disturbance frequency and intensity should be carefully tailored to the steep biophysical gradients in these systems to meet biodiversity objectives. Disturbance in the localized hotspots of high productivity and high species diversity and possible population source areas should be applied especially judiciously (Phillips et al. 2010). In systems low in habitat heterogeneity, careful use of prescribed disturbance may increase species richness.

Strategies to increasing productivity and resource availability in low energy systems can have conservation benefits but are generally not feasible at landscape and larger spatial scales (Huston 2004). Supplemental feeding programs have proven successful in recovering populations of top level consumers such as the Spanish imperial eagle (*Aquila adalberti*) (Gonsalez et al. 2006). Fertilization of individual stands or fields has occasionally been used to increase rates of recovery after disturbance and to enhance community diversity (Huston 2004). The history of over-fertilization and unintended negative consequences, however, suggests such strategies should be used very carefully.

Low productivity systems are often relatively variable in productivity and in habitat type due to relatively steep gradients in temperature, moisture, soil fertility, and other biophysical conditions. Consequently, species population dynamics, natural disturbance regimes, community diversity, and other ecological factors often vary across low energy landscapes as driven by biophysical factors (Hansen and Rotella 1999). Management of landscape composition should emphasize the maintenance of the mosaic of biophysically-determined habitats in such low energy systems. As mentioned above, these biophysical habitats may act as population source or sink areas for some species (Hansen 2011). Demographic studies are needed for identifying species with strong spatially explicit population dynamics. Management strategies can then be targeted to maintain population source areas and to reduce population loss in sink areas. Seral stage diversity is important in low-energy systems that have long experienced fire, herbivory and other natural disturbances (Hutto 1995). The distribution of seral stage mosaics across the landscape should be tailored to the local biophysical gradients. While maintenance of within-stand vegetation structural complexity may not benefit biodiversity as much as in higher energy systems (Verschuyl et al. 2008), this is still important for reducing stress on species recovering from disturbance.

The management of landscape configuration should emphasize connectivity over concern about patch size and edge design. The population viability of some species in low energy systems is dependent upon adequate habitat for movements within home ranges, seasonal migrations, and/or dispersal movements to new territories or among source and sink habitats (Berger 2004). The landscape conditions that confer high connectivity are not well understood and likely vary among species and conditions. More research and adaptive management is needed to improve our capacity to manage for connectivity. Because relatively few species specialize on particular locations along the patch edge-to-interior gradient, management of patch size and edge density is a lower priority in low energy systems (Hansen et al. in review).

Predation may be a key type of biotic interaction in low-energy systems. Initial studies (Melis et al. 2009) suggest predators have stronger top-down effects in such systems and loss of top carnivores can lead to herbivore expansion, reduced plant biomass and species diversity and reduced diversity of vegetation-dependent communities such as invertebrates and birds (Estes et al. 2011). Maintenance or restoration of top predators should be a high priority in such systems. If predators are lost, ungulate control measures through hunting or culling may be necessary. Fencing and other deterrents to over-consumption of forage and browse may be used in limited situations to maintain key plant communities and the species that depend upon them. Competitive exclusion is less pronounced in mid to late seral stages in low energy systems, and there is less need for frequent disturbance to maintain species richness (Huston 1994).

Protected areas in low energy systems often need to be relatively large and designed to include key habitats (Herfindal et al. 2004). These key habitats may include the mosaic of biophysical habitat types, localized hotspots, population source areas, movement habitats, and large expanses of habitat required by species with low densities and large home ranges such as top carnivores (Hansen and DeFries 2007).

Because many protected areas in low-energy systems are not large enough to meet the goals described above, management of the surrounding matrix of multiple use public lands and private lands is often essential to achieve biodiversity goals (Defries et al. 2007). Collaborative management among private land owners, public multiple use land managers, and protected area managers is often difficult but essential for effective conservation across the large spatial scales of these low energy systems. Conservation easements and other incentive-based approaches can be used to secure localized areas of high ecological value such as hot spots for productivity and species richness (Theobald et al. 2005). Because much of the landscape may not yet be developed, land use planning can emphasize placing new development on portions of the landscape with lower ecological value. Placing new development near existing development can be used to reduce the total footprint of intense human influence on remaining wildlands (Gude et al. 2007).

Restoration efforts may not be required in such landscapes because adequate wildland habitats remain. However, localized places of high ecological value that have been degraded may be candidate locations for restoration.

In low-energy systems that contain extensive wildlands, a relatively high proportion of citizens may interact with wildland species and ecological processes where they live or recreate (Green 2001). Public education should emphasize how to reduce negative impacts on wildland species. This could include for exurban residents living at the edge of public wildlands, for example, methods to control pets, avoiding attracting dangerous wildlife, and inhibiting spread of invasive species (Hansen et al. 2005). Backcountry recreationists and hunters can be taught how to minimize negative interactions with dangerous wildlife species.

In sum, the overarching conservation priorities in low-energy systems is to maintain large, well connected natural landscapes that include the full gradient of biophysical conditions and provide for wildland species with large area requirements.

Medium-energy ecosystems

Ecosystems that are intermediate in energy are often unique in having high S_K and highest human densities (Phillips et al. 2010, Hansen et al. 2011). The natural portions of these systems may be continental hotspots for native species richness due to their location at the asymptote of the species energy relationship. However, intense land use is typically widespread over these systems (Huston and Wolverton 2011). Consequently, sensitive species within them are likely to be those that are intolerant of human impacts, are heavily harvested, or are persecuted by humans. Thus, many wildland species are under-represented in these systems (McKinney 2002a, Prugh 2009). Synanthropic native species are often abundant and can strongly impact other native species. Among these species that thrive around humans are several species of mesocarnivores that may reach high population densities because of the extirpation of top carnivores (Prugh et al. 2009). Invasive species may be widespread due to frequent introductions and high human disturbance. Thus, actual species richness may differ substantially from S_K due to these human effects (Radeloff et al. 2010).

Many aspects of ecological processes and landscape composition and configuration should be managed intermediately between low- and high-energy systems. However, emphasis should be placed on maintaining remaining natural and semi-natural areas because of their likely high native species richness (Hansen et al. 2011). Care need be taken in smaller patches of natural and semi-natural habitats because they may now be attractive sinks for native species due to the expanded mesocarnivore and invasive communities favored by intense land use (Delibes et al. 2001b). Landscape configuration should be managed to minimize these effects. Connectivity for home range and dispersal movements of native species may also be reduced by intense land use. This loss of connectivity may be mitigated through use of highway overpasses, semi-natural corridors, and other means (Forman 2003). However, these strategies may also favor harmful synanthropic and exotic species, so need be applied with caution.

The high land use intensities typical in these systems may also lead to strong human edge effects penetrating into protected areas (Hansen and DeFries 2007). Management to buffer protected areas from these human effects is important. Management of the matrix surrounding protected areas may be challenging because much of it may be privately owned. Emphasis should be placed on the protection of remaining natural habitats through conservation easements and other incentives-based methods (Theobald et al. 2005). Restoration of degraded lands can yield good results because of the high S_K of these systems. Education programs should emphasize ways to incorporate consideration of biodiversity into the design and management of farms, neighborhoods, and cities. “Backyard conservation” programs are increasingly widespread in urban areas and are thought to yield good results for conservation in densely populated areas (Rosenzweig 2003). These programs deal both with habitat management and with ways of favoring non-synanthropic native species while dissuading harmful native synanthropic and invasive species. In sum, the key conservation priority in these medium energy systems is to mitigate the heavy human influence, which has the potential to degrade these continental to global hotspots for biodiversity.

High-energy ecosystems

The potentially high growth rates, population densities, moderate human population densities, and potential to build high levels of biomass in high energy systems lead to the prediction that species at risk will be those that are heavily influenced by interactions with other species (e.g., Schemske et al. 2009) and those that specialize on particular vegetation configurations. In the absence of frequent disturbance, species that are poor competitors are likely to be sensitive (Huston 1994). This is most obvious for plants that are unable to compete for resources with more dominant species (Waring et al. 2006). Also at risk in such systems may be species at higher trophic levels that are dependent on the plant species lost through competition or microhabitat diversity. The modification of microclimate and plant growth rates under dense vegetation may lead to wide gradients in ecological conditions between recently disturbed patches and late seral patches (Hansen and Rotella 2000). Niche partitioning of these gradients can led to many species specializing in particular seral stages, elements of within stand vegetation structure, patch edges, or patch interiors. Consequently, within stand vegetation structure and landscape configuration are important determinants of species performance and community diversity (Odion and Sarr 2007, Verschuyl et al. 2008, Hansen et al. in review). Invasive species are expected to be well represented in these systems due to high resource levels and moderate to high human land use, except those that are outcompeted by native species (Huston 2004).

In these high energy systems on fertile soils, frequent disturbance may be required to break competitive dominance (Huston 1994). Moreover, the rapid recovery of many species following disturbance leads to a flush of resources that favors high species richness (McWethy et al. 2010, Betts et al. 2010). Nonetheless, many species also specialize in late seral stands that have finer-scale gap phase disturbance dynamics (Hansen et al. 1991). Consequently, disturbance should be used differentially across the landscape (Odion and Sarr 2007). Stand replacement disturbances should be applied relatively frequently in some locations to break competitive dominance and favor early seral species and high species richness. In other places only relatively infrequent gap-scale disturbance should be allowed or provided to maintain late seral stands and the species that depend upon them. High levels of structural complexity should be maintained in all seral stages because of the relatively high number of species that specialize on particular structural conditions (Verschuyl et al. 2008). Where soil is poor, frequent and intense disturbance in warm, wet systems may lead to high rates of erosion and leaching of nutrients and reduce long-term productivity (Huston and Wolverton 2011). Management strategies to reduce erosion and leaching are required.

Management of landscape composition should especially focus on the spatial and temporal distribution of seral stages. Because most portions of the landscape are relatively high in productivity, disturbance can be distributed across the landscape (assuming soil degradation is not an issue). Maintaining a dynamic steady-state equilibrium of seral stages over time (Bormann and Likens 1979) may best accomplish conservation objectives. Under this model, disturbance size and frequency is shifted over the landscape such that while any one place is undergoing disturbance and succession, the total area of each seral stage remains constant over time. Maintenance of within stand vegetation structural complexity in all seral stages is especially important because of the relatively high number of species specializing on particular structural conditions. Although biophysical gradients are typically less pronounced in many high energy systems, maintaining the range of biophysical habitat types that are present is important. Source and sink habitats due to biophysical conditions are less likely in these systems. Those due to humans creating attractive sinks are especially likely due to moderate to high land use intensity.

Design of landscape configuration should focus on patch size, juxtapositioning, and edge type and density. Because many species specialize in distance from edge into both early seral and late seral stands, maintenance of a variety of patch sizes and edge densities is required to maintain many native species (McWethy et al. 2009, Hansen et al. in review). Some seral stage specialists may be unable to disperse across even narrow expanses of unsuitable habitat, thus, fine scale juxtapositioning of habitats and seral stages may be important (Hadley and Betts 2009). Human-created edges may become attractive sinks and reduce the viability of the metapopulation population (Delibes et al. 2001b). Hence, attention to edge type is required to minimize these negative effects. Seasonal migration and long-distance dispersal among mammals is less likely in these systems due to the greater equitability of resources in space and time, hence connectivity for long-distance movements may be less important.

Protected areas can often meet the needs of native species within smaller areas in high energy systems. They should include any low-energy patches and high-energy locations with high biophysical habitat heterogeneity. In the surrounding matrix, conservation easements should be focused on remaining natural areas with lower productivity and on those with high habitat heterogeneity. Human land use may be moderate to high in these systems and the strategies recommended for medium-energy systems may be beneficial. Education for citizens should focus on the important role of soil fertility, disturbance and vegetation pattern in these systems.

To summarize, the overarching conservation priority is to manage soils, disturbance and vegetation pattern to maintain the large number of microhabitat specialists and high potential species richness in these systems.

GEOGRAPHICAL ILLUSTRATION

How might the ecosystem types depicted in Figure 7 and described in Table 2 be distributed globally? The terrestrial ecosystems of the world could perhaps best be classified through quantitative classification and ordination based on: species energy relationships across taxonomic groups; human land use and energy relationships; and distributions of natural disturbance and geomorphic heterogeneity. For illustrative purposes here, we can use three intervals of terrestrial annual GPP globally to suggest potential locations of low, medium, and high energy ecosystems (Fig 8). Low energy regions are associated with the dry regions centered on 30 degrees N and S latitude, cold and dry high latitude areas, and high mountains. Medium energy regions occur primary in moist subtropical areas and in the temperate zones centered on 60 degrees N latitude. The high energy regions are mostly located in the humid tropical and subtropical areas and in temperate rainforest such as the NW U.S. In lieu of maps integrating geomorphic and disturbance induced habitat heterogeneity, topographic complexity can be used to illustrate potential habitat heterogeneity (hatched areas in Fig 8). Notice that topographic complexity is relatively widely distributed across the low and medium energy zones. The high energy zone includes primarily areas of low topographical complexity. Exceptions to this are the foothills of the Andes Mountains in Amazonia, localized areas in East Africa, and across southeast Asia. These are also areas where soils are more fertile than in the Amazon and Congo lowlands (Huston and Wolverton 2011). Probably as a consequence of high primary productivity, fertile soils, and topographical complexity, these locations are global hotspots for biodiversity (Myers et al. 2000, Davies et al. 2007). Until more sophisticated analyses are done, land managers and conservationists may want to locate their ecosystems of interest within the six zones depicted in Fig. 8 and evaluate the management recommendations for their zones in Table 2. Below, I illustrate such an approach for three case study regions in the U.S. (Fig. 9). The data and analyses underlying these case studies are drawn primarily from Hansen et al. (2011) and Phillips et al. (2010).

Greater Yellowstone – low energy

The Greater Yellowstone Ecosystem in the Northern Rockies of the US is centered on the volcanically uplifted Yellowstone Plateau and surrounding mountains. The relatively harsh continental climate and nutrient-poor volcanic soils heavily pattern vegetation and productivity.

Montane coniferous forests cover most of the system, with grass and shrublands in drier settings, and deciduous woodlands along major rivers. Annual GPP is low and variable (mean=301 g C/m^2/yr, CV=0.53), and is relatively high only on toe slopes and more fertile valley bottoms. S_K for birds is positively related to productivity, and S_K hotspots (>=80% of maximum) cover just 22% of the ecosystem. Dominant carnivores in the ecosystem include grizzly bear, wolf (*Canus lupus*), cougar (*Felis concolor*), and wolverine (*Gulo gulo*). The wolf is known to drive strong top-down trophic cascades in portions of the ecosystem (e.g. Estes et al. 2011). The grizzly and wolverine especially have low densities, large home ranges, and roam over the full biophysical gradient (e.g., Schwartz et al. 2007). Ungulates include elk, pronghorn antelope (*Antilocapra americana*), bison (*Bison bison*), and mule deer (*Odocoileus hemionus*), which exhibit long distance migrations between summer and winter ranges (Berger 2004). Private lands cover 39% of the region, and only 7% of ecosystem has been converted to agriculture, suburban, and urban land uses. Exurban development has been growing, however, and is concentrated near the biodiversity hotspots (Hansen et al. 2002). Human land use has converted many of these hotspots to attractive sinks for grizzly bears and some migratory songbirds (Hansen 2011). Among the key conservation issues that have received attention in this system are: protecting undeveloped private lands of high ecological value (hotspots, migration habitats, population source areas), restoring the wolf to promote top-down trophic cascades, and maintaining viable populations of top carnivores and migratory ungulates while minimizing risk to humans (human mortality, loss of livestock, spread of disease) (Hansen 2009). An example of misplaced conservation priorities involved proposed logging in a national forest within the GYE in the 1990s. Conservationists were concerned that the logging would fragment late seral conifer forests and reduce connectivity for large carnivores. Subsequent research showed that these conifer forests: had formed largely in the past century because of fire exclusion by humans and livestock grazing; encroached on important grassland and aspen habitats; few wildlife species specialize on the interiors of these forests; and that connectivity for large carnivores is resilient to forest cover (Gallant et al. 2002).

Locations similar to GYE that are relatively low in energy, have higher habitat heterogeneity, have a mix of forest and grassland habitats, and support wildland species might include: most of the Rocky Mountains of North America, some of the savanna systems in east and southern Africa, and the montane portions of Argentina and Chile.

Coastal Pacific Northwest – high energy and fertile soils

Temperate rainforests dominate the west slope of the Cascade Range and the Coast Range in western Oregon and Washington (Norse 1990). The Mediterranean maritime climate and fertile soils allow these to be among the most productive forests in the world, and spatial variation in productivity is relatively low (mean=1151 g C/m^2/yr, CV=0.27). Bird diversity is relatively evenly distributed over the landscape but lower in the most productive forests. Hotspots of S_K for native birds cover 73% of the area. Dominant carnivores were extirpated from the area over the past century. Ungulates largely do not exhibit long distance migrations. Many species of plants and animals specialize on components of vegetation structure, seral stages, and locations along the edge to interior gradient (Norse 1990). Old growth forest specialists include spotted owl (*Strix occidentalis*), marbled murrelet (*Brachyramphus marmoratus*), red tree vole (*Arborimus longicaudus)*, and various salamanders. Several species of birds and plants specialize on early seral forests (Betts et al. 2010). Denser human populations and agriculture are concentrated primarily in the lower-productivity Willamette

Valley where finer alluvial soils favor savanna vegetation and agriculture, suburban, and urban land uses cover 13% of the area. Across the forested portion of the regions, a primary management challenge is how to manage logging and fire disturbance to maintain the various vegetation structure, seral stage, and edge and interior specialists while producing forest products for humans. Decades of debate lead in the 1990s to the Northwest Forest Plan, which protected large areas of old growth forest on public lands (Thomas et al. 2006). An important aspect that has been largely overlooked on public lands is the importance of tailoring disturbance to biophysical gradients to balance breaking competitive dominance and providing habitat for the several early seral species in the system, many of which are considered sensitive species (Betts et al. 2010), with minimizing disturbance-induced stress in drier forests and at higher elevations. Efforts are now being made to better tailor forest management to biophysical gradients (Johnson and Franklin 2009).

Ecosystems similar to this one in having high productivity and high habitat heterogeneity may include the other temperate rainforest systems of the world and sub-tropical to tropical rainforests with topographic complexity, high natural disturbance rates, and fertile soils such as the foothills of the Andes Mountains in Peru and the Himalaya in India. In comparison, the Amazon Basin and Congo Basin have high productivity but lower habitat heterogeneity and poorer soils. Thus, they require extreme caution in applying disturbance.

Mid Atlantic U.S. – medium energy

The mid Atlantic US from the Appalachian Mountains to the Atlantic coast is heavily human-dominated with 81% of the area being privately owned and agricultural, suburban, and urban areas covering 32% of the region. The temperate continental climate and relatively fertile soils support largely temperate deciduous forest in areas not converted to human land uses. Portions of the region were largely deforested for agriculture in previous centuries. Forest cover has been increasing since the mid 1800's. Ecosystem productivity is intermediate (GPP mean=1063 g C/m^2/yr, CV=0.17) across the region. S_K for birds is among the highest in North America and relatively evenly distributed over the landscape (hotspots cover 75% of the area that has not been converted to intensive land uses). Actual native species richness has been substantially reduced in many parts of the area through deforestation and other human activities (Radeloff 2010). Top carnivores and large ungulates were extirpated centuries ago (Prugh et al. 2010). Mesocarnivores, synanthropic species, over-abundant deer populations, and invasives are widespread across the landscape. Consequently, much of the area is an attractive sink for many native species (Terborgh 1989) and over browsing by deer strongly influences forest composition. Conservation here is largely focused on mitigating the heavy human impact on water quality, habitat fragmentation, species invasions, and overabundant herbivores and mesocarnivores (Jantz et al. 2005, Goetz and Fiske 2008). One topic that has been largely overlooked here is the area's role as a continental hotspot for species richness (at least for birds) and the potential to contribute to national conservation by protecting remaining natural areas and restoring degraded lands.

Other locations of intermediate energy and high human influence include much of Europe and portions of Korea and Japan.

CLIMATE CHANGE

Rates of global climate are expected to be accelerated in coming decades due to human activities (IPCC). The hypotheses in Table 1 suggest some of the fundamental changes in populations, communities, and landscapes that may be expected under changing climate. Increases or decreases in ecosystem energy under climate change may push elements of ecological systems across thresholds in response, such as from a positive relationship with energy to a flattening relationship or a negative relationship. Thus, given ecosystems may shift among the three energy levels outlined in Table 2 and key priorities for conservation may change accordingly. Some places that have historically been water limited and have low primary productivity are predicted to experience increased precipitation, shift to higher levels of primary productivity, and increase in species richness (e.g., Currie 2002, Lemoine et al., 2007). Many places, in contrast, are expected to decrease in primary productivity because of the increases in evapotranspiration associated with increased temperatures and decrease in species richness. Such changes are expected to vary at relatively fine spatial scales as driven by the nature of climate change in a particular place relative to the tolerances of the organisms in that place (Running et al. 2004). Such patchy responses in primary productivity across landscapes and regions have already been observed for the climate change that has occurred in the recent past (Nemani et al. 2003). The nature of such shifts should be predictable based on the direction and magnitude of change in climate in a place, the tolerances of primary producers in the place, and the responses of organisms at higher trophic levels. Some species may be able to adjust to changing climate and energy to track suitable habitats and conditions. Other species and especially community characteristics such as S_K may trail changes in climate, resulting in disequilibrium conditions, such that, for example, S_K deviates from predictions based on energy. Currie (2002) predicts, for example, that in the coming decades to centuries species richness will decrease, even in areas where richness is predicted to increase in the long term. This is because species that are intolerant of changing local conditions may disappear relatively quickly, while migration of new species into the area may be quite slow. This framework for prioritizing conservation based on ecosystem energy should help in anticipating such changes and hopefully will contribute to the new ecological theory and proactive conservation that will likely be needed to maintain native biodiversity under future climate change.

FUTURE RESEARCH

My hope is that this review stimulates thinking, research, and tests of applications on ways that knowledge of ecosystem energy can advance conservation and management. Towards that end, I offer suggestions on the kinds of research that might be most rewarding. Key questions are highlighted in Table 3.

Spatial and temporal patterns of potential drivers of biodiversity are not fully resolved. Primary productivity has now been mapped globally for nearly 30 years (Running et al. 2004). Nonetheless, questions remain about the accuracy of these maps and levels of productivity in humid tropics relative to the humid temperate zone (Huston and Wolverton 2011). Efforts to compare primary productivity among biomes using field, flux tower, and simulation methods emphasize that measurement is difficult and show that levels of variability within some biomes is high relative to differences among biomes (e.g., Zhao et al. 2005, Luyssaert et al. 2007). Quantification of soil fertility effects in simulation modeling approaches has proven especially challenging. Continued efforts to improve and validate the widely available global data sets on primary productivity are underway (e.g., Zhao and Running 2011). Mapping disturbance regimes globally has proven even more challenging than primary productivity, although progress is now being made using multitemporal methods (e.g., Huange et al. 2010). Products such as these in conjunction with consideration of major storm tracks, climatic conditions favoring fire regimes (Westerling et al. 2003), and other factors could be used to identify ecosystems globally that are more disturbance prone. Finally, while global patterns of land use are increasingly understood, the interactions of human density and land use with biophysical factors including ecosystem energy are not well known (e.g. Huston and Wolverton 2011). Better quantification of primary productivity, disturbance, and land use is needed to predict which ecosystems are most vulnerable to changes in these factors.

Many questions remain on the responses of populations and communities to primary productivity, land use, and other major driving factors. For example, species energy theory is largely based on the premise that high energy favors population density, reduced rate of extinction, and high species richness (Wright 1983 and many others). This is thought to be a major factor explaining high species richness in the tropics. However, Huston and Wolverton (2011) provide data suggesting that population density for many species is lower in the humid tropics because populations are driven by productivity during their seasonal reproductive periods. They argue that this eNPP is highest in mid to high latitudes where growing seasons are short but intense. The role of soil fertility in influencing both rates of primary productivity and plant quality to consumers is also poorly understood (e.g., Oiff et al. 2002). It is important to test hypotheses on these topics because of their obvious implications for protected area size and other geographically-based conservation strategies. Each of the hypotheses on biological response to ecosystem energy in Table 1 has some level of uncertainty. Additional research is especially needed on those hypotheses that were rated to be inadequately or partially tested.

These include those related to invasiveness, trophic cascades, migration, and the shape of the species energy relationship at high productivity levels. Finally, rates of biological response to changing climate and ecosystem energy are needed to better understand questions of equilibrium and disequilibrium.

With regards to classifying ecosystems, a premise of this paper is that ecosystems can be grouped in ways that predict their vulnerability to various human impacts and that provide a basis for prioritizing conservation strategies to mitigate these impacts. This premise could be tested through comparative analysis of ecological response to past human activities across ecosystems that differ in fundamental properties. For example, one could ask if the life histories of species that have gone extinct differ predictably as a function of various ecosystem properties. A remaining challenge is to identify the most effective criteria for grouping ecosystems. As suggested earlier, candidates include habitat heterogeneity, disturbance, evolutionary history, land use history, and ecosystem energy. While vigorous debates are often fueled by posing single opposing answers to complex questions, ecological systems are often controlled by multiple interacting factors and the challenge is to understand those interactions. An example from this review is how the effect of disturbance rates on species richness can be directly opposite depending on level of primary productivity. While the framework for grouping ecosystems presented here involves primarily ecosystem energy, including interactions with habitat heterogeneity, ultimately multiple interacting factors need fully be evaluated and used as a basis for classification of ecosystems.

Finally, much is to be learned about how answers to the questions above can be used to better tailor conservation management strategies to local ecosystems. Surveys are needed on the extent to which current conservation priorities and management vary among ecosystem types.

More detailed thinking and development is needed on the implementation of suites of management prescriptions that are most likely to be effective in particular places.

If the rates of climate change increase as projected, conserving biodiversity will be an increasing challenge. To meet this challenge, the science of conservation biology must contribute by providing more general and validated approaches. I believe that the conceptual framework for classification, as presented in Table 2, merits evaluation and rigorous testing. If proved acceptable, it should make conservation biology a more predictive science and help managers develop strategies that better meet their objectives.

Acknowledgements

Support from NASA's Biodiversity and Ecological Forecasting, Land Cover Land Use Change, Terrestrial Ecosystems, and Applied Science Programs over several years helped the author develop many of ideas and findings presented here. Montana State University provided sabbatical support, which provided me the opportunity to review and complete this paper. Jerry Franklin and members of his laboratory hosted the sabbatical and provided critical comments on the conservation framework. Linda Phillips performed the spatial analyses and prepared all the graphics. Discussions with Ralph Dubayah, Jerry Franklin, Scott Goetz, Michael Huston, Steve Running, Thomas Stohlgren, David Schimel, and Richard Waring helped clarify key issues. Drafts of the manuscript were reviewed by Kent Redford, David Schimel, Katharine Suding, and Richard Waring. I especially thank Richard Waring for stimulating my original interest in these topics and for editing the manuscript.

LITERATURE CITED

Acevedo, D. H. and D. J. Currie. 2003. Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. Global Ecology and Biogeography 12:461-473.

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2007. Recasting the species–energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. Pages 283–299 in D. Storch, P. A. Marquet, and J. H. Brown, editors. Scaling biodiversity. Cambridge University Press, New York, New York, USA.

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao and M. S. Boyce. 2005. Factors influencing female home range sizes in elk (Cervus elaphus) in North American landscapes. Landscape Ecology 20:257–271.

Bakker E. S., M. E. Ritche, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9:780–788.

Balmford, A., J. L. Moore, T. Brooks, N. Burgess, L. A. Hansen, P. Williams, and C. Rahbek. 2001. Conservation conflicts across Africa. Science 291:2616–2619.

Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320-331.

Bergmann, C. 1847. Uber die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. Gottinger Studien 3:595–708.

Betts, M. G., J. C. Hagar, J. W. Rivers, J. D. Alexander, K. McGarigal, and B. C. McComb. 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. Ecological Applications 20:2116–2130.

Bonn, A., D. Storch, K. J. Gaston. 2004. Structure of the species-energy relationship. Proceedings of the Royal Society of London B. 271:1685–1691.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.

Brooks TM, Pimm SL, Oyugi JO. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conservation Biology 13:1140–1150.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land use trends in the conterminous U.S., 1950–2000. Ecological Applications 15:1851–1863.

Brown, J. H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. American Zoologist 21:877–888.

Brown, J. H., S. K. M Ernest, J. M. Parody and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126:321–332.

Brown, R. L. and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. Ecology 84:32–39.

Burke, M. J. W. and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:796–790.

Cardinale, B. J., H. Hillebrand, and D. F. Charles. 2006. Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. Journal of Ecology 94:609–618.

Chown, S. L., B. J. Van Rensburg, K .J. Gaston, A. S. L. Rodrigues, and A. S. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. Ecological Applications 13:1223–1241.

Cleaveland, S., M. K. Laurenson and L. H. Taylor. 2001. Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. Phil. Trans. R. Soc. Lond. B. 356:991-999.

Connell, J. H., 1978. Diversity in tropical forests and coral reefs. Science 199:1302–1309.

Cox, G. W. 1985. The Evolution of Avian Migration Systems between Temperate and Tropical Regions of the New World. The American Naturalist 126:451-474.

Cross, P. C., W. H. Edwards, B. M. Scurlock, E. J. Maichak, and J. D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. Ecological Applications 17:957–964

Currie, D. J. 2002. Projected effects of climate change on patterns of vertebrate and tree species richness in the conterminous United States. Ecosystems 2:216–225.

Currie, D. J. 2006. Regional- to global patterns of biodiversity, and what they have to say about mechanisms. In Scaling Biodiversity, ed. D. Storch and P A. Marquet, New York: Cambridge University Press.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brian, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121-1134.

Davies K. F, S. Harrison, H. D. Safford, and J. H. Viers. 2007. Productivity alters the scale dependence of the diversity–invisibility relationship. Ecology 88:1940–1947.

Davies, R. G., C. D. L. Orme, D. Storch, V. A. Olson, G. H. Thomas, S. G. Ross, T. Ding, P. C. Rasmussen, P. M. Bennett, I. P. F. Owens, T. M. Blackburn, and K. J. Gaston. 2007. Topography, energy and the global distribution of bird species richness. Proceedings of the Royal Society B 274:1189-1197.

DeFries, R., A. J. Hansen, B. L. Turner, R. S. Reid and J. Liu. 2007. Towards scientific principles for regional management of landscapes surrounding protected areas. Ecological Applications 17:1031-1038.

Delibes, M., P. Gaona, and P. Ferreras. 2001a. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist 3:277–285.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, et al. 2011. Trophic downgrading of planet earth. Science 333:301-306.

Evans, K. L., and K. J. Gaston. 2005. People, energy and avian species richness. Global Ecology and Biogeography 14:187–196.

Evans, K. L., P. H. Warren, and K. J. Gaston. 2005a. Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80:1-25

Evans, K. L., J. J. D. Greenwood, K. J. Gaston. 2005b. Relative contributions of abundant and rare species to species-energy relationships. Biology Letters. 1:87-90.

Evans, K. L., J. J. D. Greenwood, and K. J. Gaston. 2005c. The roles of extinction and colonization in generating species-energy relationships. Journal of Animal Ecology 74:498-507.

Evans, K. L., N. A. James, and K .J. Gaston. 2006. Abundance, species richness and energy availability in the North American avifauna. Global Ecology and Biogeogrraphy 15: 372-385.

Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, and A. F. Diniz-Filho. 2009. Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36:132-147.

Forman, R. T. T. 2003. Road Ecology: Science and Solutions. Island Press, New York.

Fritz ,S. A., O. R. P. Bininda-Emonds, and A. Purvis. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecology Letters 12: 538–549.

Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237-241.

Gallant, A. L. A. J. Hansen, J. S. Councilman, D. K. Monte, and D. W. Betz. 2003. Vegetation Dynamics under fire exclusion and logging in a Rocky Mountain watershed: 1856-1996. Ecological Applications 13:385-403.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

Gillman, L. N., and S. D. Wright. 2006. The influence of productivity on the species richness of plants: A critical assessment. Ecology 87:1234-1243.

Goetz, S. J., and G. Fiske. 2008. Linking the diversity and abundance of stream biota to landscapes in the mid-Atlantic USA. Remote Sensing of Environment 112:4075-4085.

González, L. M., A. Margalidab, R. Sánchezc, and J. Oriad. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (Aquila adalberti) Biological Conservation 129:477-486.

Green, G. P. 2001. Amenities and community economic development: Strategies for sustainability. Journal of Regional Analysis and Policy 31:61–75.

Groom, M. J., G. K. Meffe, and C. R. Carroll. 2006. Principles of Conservation Biology, Third Edition. Sinauer, New York.

Gude, P. H., A.J . Hansen, and D. A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. Ecological Applications, 17:1004-1018.

Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. Ecology Letters 11:348–356.

Hadley, A. S., and M.G. Betts. 2009. Tropical deforestation alters hummingbird movement patterns. Biology Letters 5:207-210.

Hansen, A. J. 2009. Species and habitats most at risk in Greater Yellowstone. Yellowstone Science 17(3):27-36.

Hansen, A. J. 2011. Contribution of source-sink theory to protected area science. Pgs 339-360 in J. Liu, V., Hull, A. Morzillo, and J. Wiens, eds. Sources, Sinks, and Sustainability across Landscapes. Cambridge University Press.

Hansen, A. J. and J. J. Rotella. 1999. Abiotic factors. Pages 161-209. In: M. L Hunter, Jr. (ed.). Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, U.K.

Hansen, A. J., and J. J. Rotella. 2000. Bird responses to forest fragmentation. In: R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, W. L. Baker (Eds.), Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press, Boulder, CO, pp. 202–221.

Hansen, A. J., and J. J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology 16:1-12.

Hansen, A.J. and R. DeFries. 2007. Land use change around nature reserves: Implications for sustaining biodiversity. Ecological Applications, 17(4) 972-973.

Hansen, A.J., T. Spies, F. Swanson and J. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience 41(3):382-392.

Hansen, A. J., R. Rasker, B. Maxwell, J. J. Rotella, A. Wright, U. Langner, W. Cohen, R. Lawrence, and J. Johnson. 2002. Ecology and socioeconomics in the New West: A case study from Greater Yellowstone. BioScience 52:151–168.

Hansen, A. J., R. Knight, J. Marzluff, S. Powell, K. Brown, P. Hernandez, and K. Jones. 2005. Effects of exurban development on biodiversity: Patterns, mechanisms, research needs. Ecological Applications 15:1893–1905.

Hansen, A. J., L. B. Phillips, C. H., Flather and J. R. Cox. 2011. Carrying capacity for species richness as a context for conservation: A case study of North American breeding birds. Global Ecology and Biogeography. In Press.

Hansen, A. J., L. Baril, J. Watts, F. Kasmer, T Ipolyi, R. Winton. In Review. Towards generality in fragmentation theory: Does ecosystem biomass predict edge effects? Forest Ecology and Management.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight-A reevaluation. Ecology 60:389-402.

Hawkins, B. A., J. A. Felizola Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2007a. Climate, niche conservatism, and the global bird diversity gradient. The American Naturalist 170:s2, S16-S27.

Hegel, T., A. Mysterud, F. Huettmann and N. C. Stenseth, 2010. Interacting effect of wolves and climate on recruitment in a northern mountain caribou population. Oikos 119:1453–1461.

Herfindal, I., J. D. C. Linnell, J. Odden, E. B. Nilsen, and R. Andersen. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). Journal of Zoology 265: 63–71.

Huang, C., S. N. Goward, J. G. Masek, N. Thomas, Z. Zhu, and J. E. Vogelmann. 2010. An automated approach for reconstructing recent forest disturbance history using dense Landsat time series stacks. Remote Sensing of Environment 114:183−198.

Hugo, S., and B. J. van Rensburg. 2008. The maintenance of a positive spatial correlation between South African bird species richness and human population density. Global Ecology and Biogeography 17:611–621.

Hunter, M. L. Jr., and J. P. Gibbs. 2006. Fundamentals of Conservation Biology, 3rd Edition Wiley-Blackwell.

Hurlbert, A. H., and J. P. Haskell. 2003. The effects of energy and seasonality on avian richness and community composition. American Naturalist 161:83–97.

Hurlbert, A. H. and W. Jetz. 2010. More than "more individuals": the non-equivalence of area and energy in the scaling of species richness. The American Naturalist. 176:E50-E65.

Huston, M. A. 1979. A general hypothesis of species diversity. Am Naturalist 113:81–101.

Huston, M. A. 1994. Biological diversity–the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, Great Britain.

Huston, M. A. 2004. Management strategies for plant invasions: manipulations productivity, disturbance, and competition. Divers Distrib 10:167–178.

Huston, M. A. 2005. The three phases of land-use change: implications for biodiversity. Ecological Applications 15:1864–1878.

Huston, M. A., and S. Wolverton. 2011. Regulation of animal body size by eNPP, Bergmann's rule, and related phenomena. Ecological Monographs 81:349-405.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why there are so many kinds of animals. American Naturalist 93:145–149.

Hutto, R. L. 1995. Composition of Bird Communities Following Stand-Replacement Fires in Northern Rocky Mountain (U.S.A.) Conifer Forests. Conservation Biology 9:1041-1058.

Jantz, P., S. J. Goetz, and C. A. Jantz. 2005. Urbanization and loss of resource lands in the Chesapeake Bay watershed. Environmental Management 36:808-825.

Johnson, K. N., and J. F. Franklin. 2009. Restoration of federal forests in the Pacific Northwest: Strategies and Management Implications. 120 p. Unpublished report.

Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252–254.

Kerr, J. T., H. M. Kharouba, D. J. Currie. 2007. The macroecological contribution to global change solutions. Science 316:1581-1584.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proc. R. Soc. Lond. Ser. B-Biol. Sci. 268:269–271.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142: 911–927.

Lemoine, N., H. C. Schaefer, and K. Böhning-Gaese. 2007. Species richness of migratory birds is influenced by global climate change. Global Ecology and Biogeography 16:55-64.

Lindenmayer, D. B. and J. F. Franklin. 2002. Conserving Forest Biodiversity. A Comprehensive Multiscaled Approach, Island Press.

Lindenmayer, D., R. Hobbs, Eds. 2007. Managing and Designing Landscapes for Conservation: Moving from Perspectives to Principles. Wiley-Blackwell.

López-Bao, J. V., F. Palomares, A. Rodríguez, and M. Delibes. 2010. Effects of food supplementation on home-range size, reproductive success, productivity and recruitment in a small population of Iberian lynx. Animal Conservation 13:35–42.

Luck, G. W. 2007a. A review of the relationships between human population density and biodiversity. Biological Reviews 82:607–645.

Luck, G. W. 2007b. The relationships between net primary productivity, human population density and species conservation. Journal of Biogeography 34:201–212.

Luck, G. W., L. Smallbone, S. McDonald, and D. Duffy. 2010. What drives the positive correlation between human population density and bird species richness in Australia? Global Ecology and Biogeography 19:673–683.

Luyssaert, S., I. Inglima, M. Jung, A. D. Richardson, M. Reichstein, et al. 2007. CO2 balance of boreal, temperate, and tropical forests derived from a global database. Global Change Biology 13:2509–2537.

Lyndermayer D. B. and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Covello.

MacArthur, R. H. 1964. Environmental factors affecting species diversity. American Naturalist 98:387-398.

MacArthur, R. H. 1969. Patterns of communities in the Tropics. Biol J. Linn. Soc. 1:19-30.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42: 594-598.

Macarthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.

MacArthur, R. H., H. Recher, and M. L. Cody. 1966. On the relation between habitat selection and species diversity. American Naturalist 100: 319-327.

Mace, G. M., P. H. Harvey. 1983. Constraints on home-range size. The American Naturalist. 121:120-132.

Magdoff, F. 2007. Ecological agriculture: Principles, practices, and constraints. Renewable Agriculture and Food Systems 22:109-117.

McCoy, E. D., S. S. Bell, H. R. Mushinsky. 1991. Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London.

McGranahan, D. A. 1999. Natural amenities drive rural population change. In Food and Rural Economics Division, Economic Research Service, U.S. Department of Agriculture. Agricultural Economic Report No. 781.

McKinney, M. L. 2002a. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

McKinney, M. L. 2002b. Do human activities raise species richness? Contrasting patterns in United States plants and fishes. Global Ecology and Biogeography 11:343–348.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97:133-144.

McWethy, D. B., A. J. Hansen, and J. P. Verschuyl. 2009. Edge effects for songbirds vary with forest productivity. Forest Ecology and Management 257:665-678.

McWethy, D. B., A. J. Hansen, and J. P. Verschuyl. 2010. Bird response to disturbance varies with forest productivity in the northwestern United States, Landscape Ecology 25:533-549.

Melis, C., B. Jedrzejewska, M.Apollonio, K. A. Barton, W. Jedrzejewski, J. D. C. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K.Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka, and S. Zhyla. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 18:724–734.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381-2396.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. Conservation Biology 17:1276-1289.

Nemani, R. R., C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myeni, and S. W. Running. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563.

Nightingale, J. M., W. Fan, N. C. Coops, and R. H. Waring. 2008. Predicting tree diversity across the U.S.A. as a function of modeled gross primary production. Ecological Applications 18:93-103

Nilsen, E. B., I. Herfindal, J. D. C. Linnell. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? Ecoscience 12:68-75.

Norse, E. 1990. Ancient Forests of the Pacific Northwest. Island Press. New York.

O'Brien, E. M. 2006. Biological relativity to water–energy dynamics. Journal of Biogeography, 33:1868–1888.

Odion D. C., and D. A. Sarr. 2007. Managing disturbance regimes to maintain biological diversity in forested ecosystems of the Pacific Northwest. Forest Ecology and Management 246:57–65.

Oiff, H., M. E. Richie, and H. H. T. Prins. 2002. Global environmental controls of diversity in large herbivores. Nature 415:901-904.

Osem Y., A. Perevolotsky, and J. Kigel. 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. Journal of Ecology 90:936–946.

Pautasso, M., and K. J. Gaston. 2005. Resources and global avian assemblage structure in forests. Ecology Letters 8:282-289.

Phillips, L. B., A. J. Hansen, and C. H. Flather. 2008. Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production, Remote Sensing of Environment, 112:4381-4392.

Phillips, L. B., A. J. Hansen, C. H. Flather, and J. R. Cox. 2010. Applying species-energy theory to conservation: a case study for North American birds. Ecological Applications 20(7) 2207-2023.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757–785.

Preston, F. W. 1962. The canonical distribution of commonness and rarity I and II. Ecology 43: 185–215 and 410–432.

Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79:2581–2592.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, J. S. Brashares. 2009. The rise of the mesopredator. Bioscience 59:779-791.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proc Biol Sci. 267:1947–1952.

Radeloff V. C., S. I. Stewart, T .J. Hawbaker U. Gimmi, A. M. Pidgeon, C. H. Flather, R. B. Hammer, and D. P. Helmers. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences 107:940–945.

Relyea, R. A., R. K. Lawrence, and S. Demarais. 2000. Home Range of Desert Mule Deer: Testing the Body-Size and Habitat-Productivity Hypotheses. The Journal of Wildlife Management 64:146-153.

Rosenzweig, M. L. 1995. Species diversity through space and time. Cambridge University Press, Cambridge, UK.

Rosenzweig, M. L. 2003. Win-Win Ecology: How the Earth's Species can Survive in the Midst of Human Enterprise. Oxford University Press, New York.

Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 in R. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Running, S. W., R. R. Nemani, F. A. Heinsch, Z. Zhao, M. Reeves, and H. Hashimoto. 2004. A continuous satellite derived measure of global terrestrial primary production. BioScience 54:547–560.

Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Diversity and Distributions 8:193–210.

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic Interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–69

Schimel, D. S., B. H. Braswell, W. J. Parton. 1997. Equilibration of terrestrial water, nitrogen, and carbon cycles. Proceedings of the National Academy of Sciences USA 94:8280-8283.

Schmitz, O. 2010. Resolving Ecosystem Complexity. Princeton University Press, Princeton, New Jersey.

Schoech, S. J., E. S. Bridge, R. K. Boughton, S. J. Reynolds,, J. A. Atwell, and R. Bowman. 2008. Food supplementation: a tool to increase reproductive output? A case study in the threatened Florida scrub-jay. Biological Conservation 141:162–173.

Scholes, L., P. H. Warren, and A. P. Beckerman. 2005. The combined effects of energy and disturbance on species richness in protist microcosms. Ecology Letters 8:730–738.

Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2007. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161, 1-68.

Scott M., F. W. Davis, R. G. McGhie, R. G. Wright, and J. Estes. 2001. Nature reserves: Do they capture the full range of America's biological diversity. Ecological Applications 11:999-1007.

Senft R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala and D. M. Swift. 1987. Large Herbivore Foraging and Ecological Hierarchies. BioScience 37:89-795 and 798-799.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176.

Shugart, H. H. 1984. A theory of forest dynamics: The ecological implications of forest succession models. Springer, New York.

Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Phil. Trans. R. Soc. Lond. B 358:1729-1740.

Sinclair, A. R. E., and C. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1221–1231.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. American Naturalist 152:510–529.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species. Plant Ecology 138:113–125.

Stohlgren, T. J., Y. Otsuki, C. Villa, M. Lee, and J. Belnap. 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. Biological Invasions 3:37–50.

Stohlgren, T. J., D. Barnett, C. Flather, J. Kartesz, and B. Peterjohn. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology 86:2298 – 2309.

Svensson, J. R., M. Lindegarth, M. Siccha, M. Lenz, M. Molis, M. Wahl, and H. Pavia. 2007. Maximum species richness at intermediate frequencies of disturbance: Consistency among levels of productivity. Ecology 88:830–838.

Svensson, J. R., M. Lindegarth, and H. Pavia. 2010. Physical and biological disturbances interact differently with productivity: effects on floral and faunal richness. Ecology 91:3069–3080.

Terborgh, J. 1989. Where Have All the Birds Gone? Princeton University Press, Princeton, N.J.

Theobald, D. M., T. Spies, J. Kline, B. Maxwell, N. T. Hobbs, and V. H. Dale. 2005. Ecological support for rural land use planning. Ecological Applications 15:1906–1914.

Thomas, J. W., J. F. Franklin, J. Gordon, K. N. Johnson. 2006. The Northwest Forest Plan: Origins, components, implementation experience, and suggestions for Change. Conservation Biology 20:277-287.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Turner, J. R. G., J. J. Lennon, and J. A. Lawrenson. 1988. British bird species distributions and the energy theory. Nature 335:539–541.

Vázquez, L. B., and K. J. Gaston. 2006. People and mammals in Mexico: conservation conflicts at a national scale. Biodiversity and Conservation 15: 2397–2414.

Verner, J., M. L. Morrison, and C. J. Ralph, eds. 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison.

Verschuyl, J. P., A. J. Hansen, D. B. McWethy, R. Sallabanks, and R. L. Hutto. 2008. Is the effect of forest structure on bird diversity modified by forest productivity? Ecological Applications 18:1155-1170

Waide, R. B., M. R. Willig, C. F. Steiner, G.Mittelbach, L.Gough, S. I.Dodson, G. P. Juday, and R. Parmeter. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30:257–300.

Waring R. H., N. C. Coops, W. Fan, J. M. Nightingale. 2006. MODIS enhanced vegetation index predicts tree species richness across forested ecoregions in the contiguous U.S.A. Remote Sensing of Environment 103:218–226.

Wang, G., N. T. Hobbs, R. B. Boone, A. W. Illisu, I. J Gordon, J. E. Gross, K. L. Hamalin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95–102.

Westerling A. L., T. J. Brown, A. Gershunov, D. R. Cayan, M. D. Dettinger. 2003. Climate and wildfire in the western United States. Bulletin of the American Meteorological Society 84:595–604.

White, E. P, S. K. M. Ernest, P. B. Adler, A. H. Hurlbert, and S. K. Lyons. 2010. Integrating spatial and temporal approaches to understanding species richness. Philosophical Transactions of the Royal Society B, 365: 3633-3643.

Whittaker, R. J., and E. Heegaard. 2003. What is the observed relationship between species richness and productivity? Comment. Ecology 84:3384–3390.

Widdicombe, S. 2001. The interaction between physical disturbance and organic enrichment: an important element in structuring benthic communities. Limnol Oceanogr 46:1720–1730

Wiens, J. A., and B. Van Horne. 2011. Sources and sinks: what is the reality? Pgs 507-519 in J. Liu, V., Hull, A. Morzillo, and J. Wiens, eds. Sources, Sinks, and Sustainability across Landscapes. Cambridge University Press.

Woodroffe, R., and J. R. Ginsberg. 2000. Ranging behaviour and vulnerability to extinction in carnivores. In Behaviour and conservation: 125–140. Gosling, L. M., and W. J. Sutherland (Eds). Cambridge: Cambridge University Press.

Worm, B., H. K. Lotze, H. Heillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–851.

Wright, D. H. 1983. Species–energy theory, an extension of species-area theory. Oikos 41: 496–506.

Zhao, M., and S. W. Running. Response to comments on "Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 Through 2009". Science 333:1093-e.

Zhao, M., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. Remote Sensing of Environment 95:164–176.

Tables

Table 1. Hypotheses on the effects of ecosystem energy on biodiversity at several levels of organization. Positive relationships are denoted by "+" and negative relationships by "-". Weight of evidence is evaluated as: Inadequately tested – either untested or not strongly tested; partial – some studies offer support, others do not; intermediate – supported by one or two studies; strong – well supported by >2 studies.

Topic	Predicted Relationship with Energy	References	Weight of Evidence	Implication for Conservation and Management
Population growth rate, abundance, extinction risk	+ or flattening,	Macarthur and Wilson 1967 Wright 1983 Evans et al. 2005a	Strong Strong Partial	Small population issues including extinction risk are more pronounced in low energy systems.
Home range size	-	Haresrad and Bunnell 1979 Herfidal et al. 2005 Nilsen et al. 2005	Strong	Larger home ranges in low energy systems increase frequency of wildlife roaming outside of protected area boundaries and incurring human-induced mortality.
Large	+ with	Fryxell and	Intermediate	Maintenance of migration

ungulate migrations	patchiness, especially in ecosystems with intermediate productivity and fertile soils	Sinclair 1988 Oiff et al. 2002 Berger 2004		habitats is a higher priority in environments with intermediate productivity and patchiness in productivity, and high soil fertility.
Body size	+	Huston and Wolverton 2011	Inadequately tested	Smaller individuals within a species may have lower reproductive rates.
Spatially explicit population dynamics	+ with patchiness	Pulliam 1988 Delibes et al. 2001 Naves et al. 2003	Strong	Human activities that alter source or sink population dynamics may cause the extinction of the metapopulation.
Carrying capacity for species richness	+, flattening, or unimodal	Wright 1983 Brown et al. 2001 Hansen et al. 2011	Strong	Knowledge of S_K can be used to prioritize locations for protection and restoration and to guide application of disturbance.
Disturbance	diversity	Huston 1979,	Strong	The rate of prescribed

and Succession	peaks at higher rates disturbance in productive environments	1994 Proulx and Mazumder 1998 McWethy et al. 2010 Svensson et al. 2010		disturbance applied by managers should vary with ecosystem productivity. Human impacts on disturbance and productivity should not be assessed or managed in isolation.
Within-patch vegetation structure	The effect of vegetation structure on richness declines in low-energy environments	MacArthur et al. 1966 Hansen and Rotella 1999 Verschuyl et al. 2008	Intermediate	Management for forest structural complexity to benefit biodiversity should yield good results in productive environments, but the benefits will likely be increasingly reduced in low-energy environments.
Habitat edge effects	+ with biomass accumulation	Hansen and Rotella 2000 McWethy et al. 2009 Hansen et al. in review	Intermediate	Creation of edges through forest fragmentation is most likely to negatively influence forest species in high biomass ecosystems such as tropical and temperate rainforests, but may have little influence on forest

				species in low-biomass ecosystems such as boreal or subalpine forests.
Trophic cascades	"Top-down" effects are more likely in low productivity environments	Melis et al. 2009	Inadequately tested	Predator restoration efforts aimed at reducing overgrazing and expanding lower trophic levels will be most effective in low productivity systems.
Invasive species	+	Huston 2004 Stohlgren et al. 2005	Inadequately tested	Invasive species are most prevalent in productive and disturbed systems. Manipulation of disturbance and productivity can be used to control invasives.
Land use intensity	+, flattening, or unimodal	Balmford et al. 2001 Luck et al. 2010	Strong	Land use is most intense in ecosystems with higher species richness due to both being associated with intermediate energy levels.

Table 2. Framework for managing biodiversity based on ecosystem energy. Listed are conservation strategies that are predicted to be high priorities in low, medium, and high energy ecosystems. Strategies in italics should be considered with caution because they are based on hypotheses that were considered inadequately supported by previous study. They are included here to stimulate further thinking and research.

Conservation Category	**Ecosystem Energy Level**		
	Low	**Medium**	**High**
Individual species			
Sensitive species	Focus on species at risk due to slow growth rates, low abundances, large home ranges, migratory habits, and/or source sink dynamics.	Species at risk are most likely those that cannot tolerate humans; are overharvested or are persecuted by humans.	Species at risk are likely to be poor competitors; and specialists on particular seral stages, vegetation structures, and patch size and edge configurations.
Invasive species	*Invasive species richness expected to be lower in less productive systems, but species that establish and expand may need management attention.*	*Invasives are possibly reasonably high due to frequent introductions and intense human disturbance.*	*Invasives are especially likely in productive systems with high disturbance rates.*
Ecological processes			
Disturbance	Vary prescribed disturbance regimes along biophysical gradients to balance the stress disturbance placed on some species with the need for seral stage diversity; Use prescribed disturbance	Manage intermediately.	Use disturbance differentially across the landscape: relatively high rates in some locations to break competitive dominance and favor early seral species and high species richness; and relatively

	judiciously in localized hotspots;		low rates in some locations to maintain late seral species. Maintain high levels of structural complexity in all seral stages. Reduce erosion and leaching associated with disturbance.
Productivity	Supplemental feeding may be effective in recovering species at risk due to food limitations; *Fertilization or irrigation may be effective in limited situations for favoring native plants over exotics and for increasing community diversity.*		*Reduce productivity to favor native species.*
Landscape composition			
Biophysical gradients	Maintain the wide mosaic of biophysically-determined habitat types.	Manage to maintain all natural areas.	Maintain the narrower range of biophysical habitat types that are likely present. Localized low-energy patches are especially important because of their higher richness.
Source and sink habitats	Use demographic study to identify source and sink habitats and manage them differentially to maintain population viability for species at risk.	Attractive sinks are widespread in these systems due to intense human land use.	Similar to medium-energy ecosystems.
Seral stages	Tailor seral stage mosaics to the	Manage intermediately.	Maintain a dynamic steady- state

	biophysical gradient.		equilibrium of seral stages across the landscape.
Within-stand vegetation structure	Maintain vegetation structural complexity to enhance recovery in post disturbance stands.	Manage intermediately.	Vegetation structural complexity in all seral stages is especially important because of the relatively high number of species specializing on particular structural conditions.
Landscape configuration			
Connectivity	Manage for high levels of connectivity to allow within home range, migratory, and dispersal movements.	Intense land use may reduce connectivity for many species. Mitigation through highway overpasses, semi natural corridors, and other means may be required.	Seasonal mammal migration and long-distance dispersal is less likely in these systems due to the greater equitability of resources in space and time.
Patch size/edge	Lower priority for management attention.	Manage to reduce creation of attractive sinks due to intense human land use.	Management of patch size, juxtapositioning, and edge type and density are high priorities.
Biotic interactions			
Trophic cascades	*Maintain or restore top carnivores because of their possible strong top-down positive effects on lower trophic levels;* *Consider controlling released herbivore populations through*	If top carnivores were extripated due to human activities, attempt to reduce release of mesocarnivores through management of foods associated with trash, pets, and	*Stronger bottom-up control is possibly expected, hence management of vegetation strongly influences biodiversity.*

	hunting and/or culling if predators are lost; *Locally apply fencing or other deterrents to over grazing if needed to protect key plant communities.*	livestock.	
Competitive exclusion	Not as high a priority for management as in higher-energy systems.	Manage intermediately.	Manage disturbance to break competitive dominance to allow persistence of species that are poorer competitors.
Land use			
Protected areas	Design protected areas to include the mosaic of biophysical habitat types, localized hotspots, migration and other movement habitats, large areas of habitat for species at risk.	Manage to buffer protected areas from surrounding human influence.	Protected areas can be smaller. They should include any low-energy patches and high-energy locations with high biophysical habitat complexity and/or high disturbance rates.
Matrix	Encourage collaborative management among the many land owners and stakeholders across the large landscapes required for achieving conservation goals in these low-energy systems; Focus conservation easements on localized areas of very high ecological value (hot spots, source areas, movement habitats); Focus development on locations of	Focus conservation easements on remaining natural areas; Emphasize consideration of biodiversity in agricultural and residential settings.	Focus conservation easements on remaining natural areas with lower productivity and on those with high habitat heterogeneity

	lower ecological value; Concentrate development near existing development to reduce total footprint of intense human influence on remaining wildlands.		
Restoration	Focus restoration efforts on hotspot and movement habitats that have been degraded.	Emphasize restoration of degraded places and "backyard" conservation.	On poor soils, focus restoration on places where human disturbance has elevated soil erosion and leeching. On fertile soils, restore disturbance regimes where they have been constrained by human activities.
Public education	Educate exurban residents on minimizing negative impacts on wildland species and reducing introduction of invasive species and diseases into wildlands.	Educate citizens on methods to integrate consideration of biodiversity into agricultural, residential, and urban settings; And means of favoring nonsynanthropic native species and dissuading harmful native synanthropic and invasive species.	Educate citizens on important role of soil fertility, disturbance and vegetation pattern in these systems.
Overarching conservation priority	**Maintain large, well connected natural landscapes that include the full gradient of biophysical conditions and provide for wildland species with large area**	**Mitigate the heavy human influence in these systems which have the potential to be global hotspots for biodiversity.**	**Manage soils, disturbance and vegetation pattern to maintain the large number of microhabitat specialists and high potential species richness**

	requirements.		**in these systems.**

Table 3. Questions for future research.

Topic	Question
Biophysical drivers	What is the global distribution and variance of annual net primary productivity (NPP) and of ecologically and evolutionary relevant NPP (eNPP)?
	In relatively warm, moist environments, how does soil fertility interact with primary productivity to influence the quantity and quality of plant biomass available to consumers?
	Can major natural disturbance regimes be mapped across terrestrial biomes based on hurricane tracks and other climatic and geomorphic factors?
	To what extent do measures of ecosystem energy influence mean and variance in spatial patterns of human density, land use? What are the shapes of these relationships? What are the mechanisms underlying potential effects?
Biological responses to ecosystem energy	For which trophic levels and taxonomic groups does eNPP best account for variation in home range size, body size, population density, and extinction rates as compared to annual NPP?
	Does the response of a population to the temporal formulation of NPP vary with the length of its reproductive period?
	How do the population dynamics of consumers in productive systems vary with soil fertility and plant quality?
	Controlling for human and land use effects to what extent is gene flow, migration, and dispersal of organisms influenced by mean and variation in primary productivity?
	For tropic levels and taxonomic groups of interest, what is the strength and shape

	of the relationship between primary productivity and species richness?
	What factors cause infliction points in these relationships (e.g. from increasing to flat; from flat to decreasing?). How prevalent is the are cases where species richness declines at high productivity levels and what are the relative effects of competitive dominance, plant quality, human impacts, and other factors in driving this response?
	What are the geographic locations where these relationships are increasing, flat, or decreasing?
	Under what conditions are populations and communities in equilibrium vs disequilibrium with the biophysical state of an ecosystem? Is some of the confusion in our understanding of species energy relationships a product of disequilibrium conditions?
	How does prevalence of invasive species vary with ecosystem energy and disturbance?
	Are top-down trophic cascades more prevalent in low-energy systems?
	How does human modification of primary productivity, disturbance, and habitat diversity influence species and communities? What are thresholds in these relationships where native species benefit or are degraded?
Grouping ecosystems	Under which criteria can ecosystems best be grouped to anticipate their vulnerabilities to human impacts and climate change and that provide a basis for prioritizing conservation strategies to mitigate potential impacts?
	How much variation in ecosystem vulnerability can be accounted for through such a classification?

Effective management	To what extent are current conservation priorities and management strategies consistent with the vulnerabilities of local ecosystems?
	Can conservation effectiveness be improved through improved predictive theory on ecosystem vulnerabilities?
	How feasibly can the sort of general management guidelines presented in Table 2 be developed into management prescriptions that specify strategies to effectively reduce vulnerabilities in local ecosystems?

Figure Legends

Figure 1. a) Map of species richness of large herbivores, as a percentage of continental species pool, predicted based on indices for plant-available moisture and soil nutrients. No data for potential evapotranspiration were available for the boreal zones, hence no diversity predictions were made for that region. From Oiff et al. (2002).

Figure 2. (a) Observed points and predicted generalized least squares (GLS) regression lines for log-transformed species richness in three intervals across the productivity gradient (gross primary production, GPP), with a positive slope in blue, a flat slope in green, and a negative slope in red. (b) The spatial pattern of Breeding Bird Survey (BBS) routes in the three gross primary production (GPP) intervals indicates that energy levels within bird conservation regions (BCRs) are not randomly distributed but rather have frequencies that are higher than expected in most regions. The conservation region colors indicate that energy classes were found significantly more frequently than expected if randomly distributed. The point colors coincide with the colors of regression lines in (a). Numbers within regions correspond to BCRs. From Phillips et al. (2010).

Figure 3. Diversity patterns predicted by the Dynamic Equilibrium Hypothesis (Huston 1979, 1994) along combined energy and disturbance gradients. Lighter shading indicates higher diversity. In the upper left half of the grid, extinctions are because of an inability to recover from disturbances. In the lower right half of the grid, extinctions are because of competitive exclusions. From Scholes et al. (2006).

Figure 4. (a) Locations of study landscapes arrayed across the biophysical gradients of the Pacific and Inland Northwest. (b) Model coefficient odf determination (R^2) and percentage of total model R^2 resulting from the addition of five predictors of forest structure to a five predictor energy model for the study landscapes. Mean gross primary productivity (g C/ m^{-2}/day^{-1}*10^{3}) is indicated below the study site names. From Verschuyl et al. (2008).

Figure 5. Relationships between percentages of species sampled that were significantly associated with forest interiors and aboveground biomass for birds, beetles, and mammals across the major forest biomes of the world. From Hansen et al. (in review).

Figure 6. Relationships between (a) human population density and net primary productivity and (b) vertebrate species richness and NPP across sub-Saharan Africa. From Balmford et al. (2001).

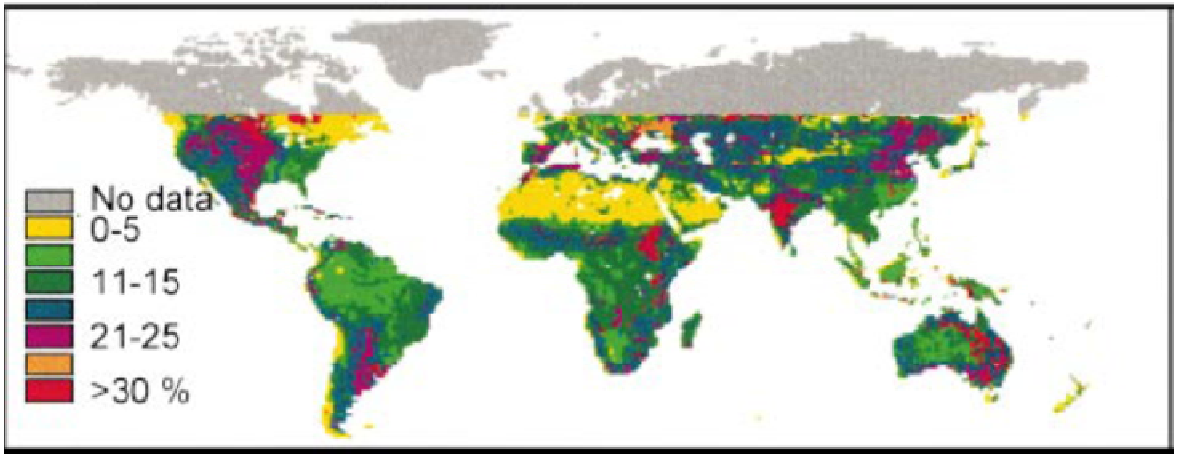
Figure 7. Summary of traits of ecological systems relevant to conservation arrayed along axes in ecosystem energy and habitat heterogeneity as revealed by the review of current knowledge in this paper. Traits in italics should be considered with caution because they are based on hypotheses that were considered inadequately supported by previous study. They are included here to stimulate further thinking and research.

Figure 8. Distribution of annual gross primary productivity (GPP) and areas of high topographical complexity across the Earth's land area. GPP is depicted in three intervals that equate to the low (blue), medium (green), and high (red) energy systems as described in the conservation framework. GPP intervals are 0-9, 9-18, >=18 g C/ m-^{2}/day-1. Topographic

complexity was quantified as elevation range within 5x5 km zonal areas. Areas with >= 150 m elevation range are indicated by the black hatching.

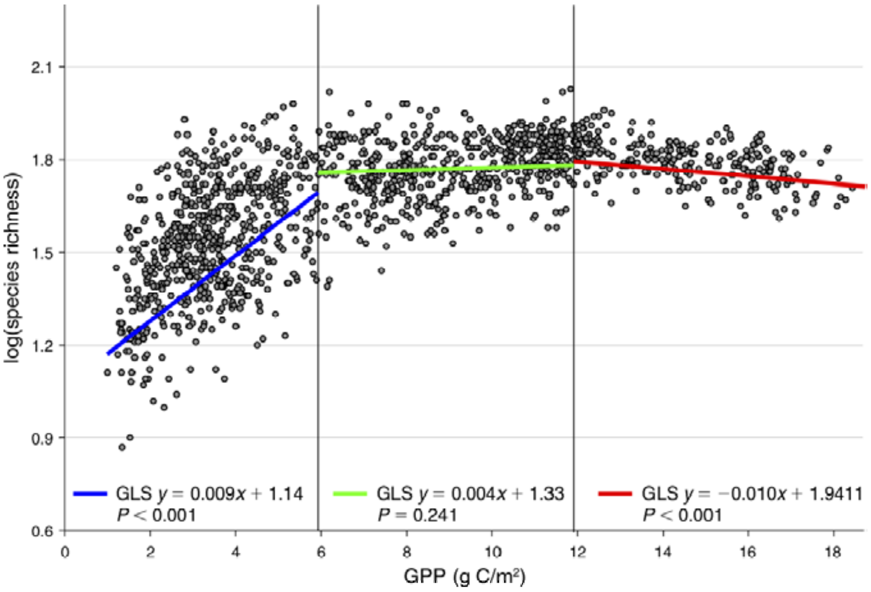
Figure 9. Landscapes illustrating low, intermediate, and high energy levels arranged from west to east across the U.S. Shown within each landscape are the distributions of local hotspots for modeled S_K for birds (>20% of maximum S_K) and of more intense land uses. Based on Hansen et al. (2011).

Figures



Predicted large herbivore biodiversity (% of continental species pool)

Fig 1.



2.1
1.8
1.5
1.2
0.9
0.6
log(species richness)
0
2
4
6
8
10
12
14
16
18
GPP (g C/m²)
GLS y = 0.009x + 1.14
P < 0.001
GLS y = 0.004x + 1.33
P = 0.241
GLS y = −0.010x + 1.9411
P < 0.001

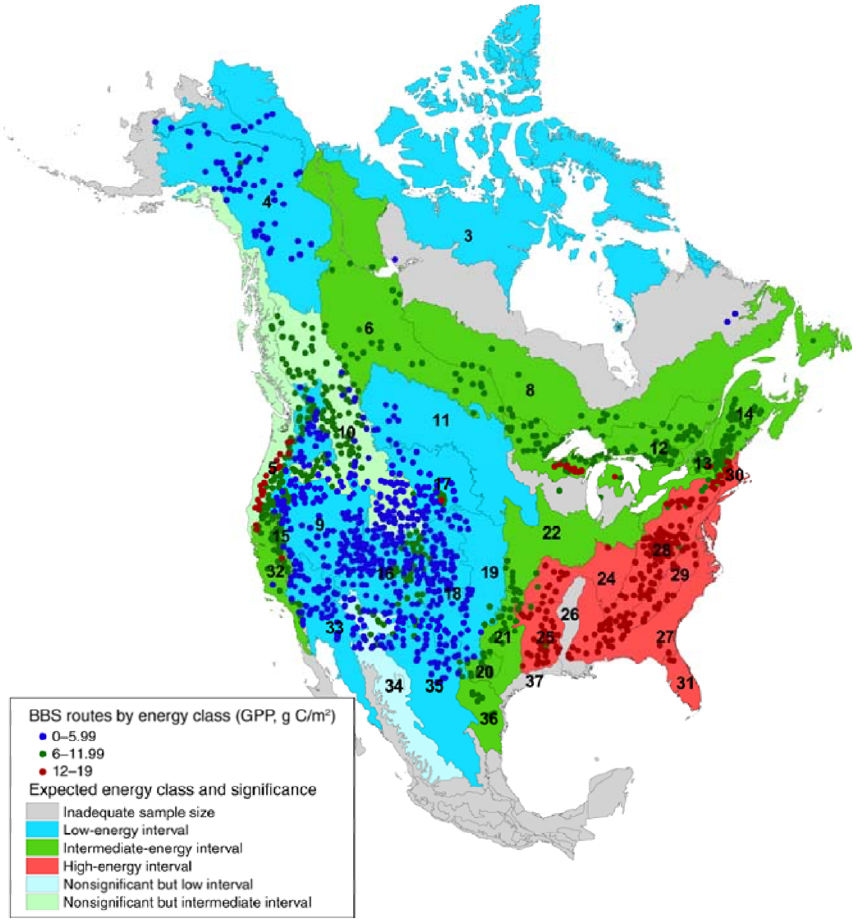

3
4
6
8
11
10
14
12
13
5
17
30
9
22
15
28
32
16
19
24
29
18
26
33
21
25
27
20
34
35
37
31
36
BBS routes by energy class (GPP, g C/m²)
● 0–5.99
● 6–11.99
● 12–19
Expected energy class and significance
Inadequate sample size
Low-energy interval
Intermediate-energy interval
High-energy interval
Nonsignificant but low interval
Nonsignificant but intermediate interval

Fig. 2 a and b

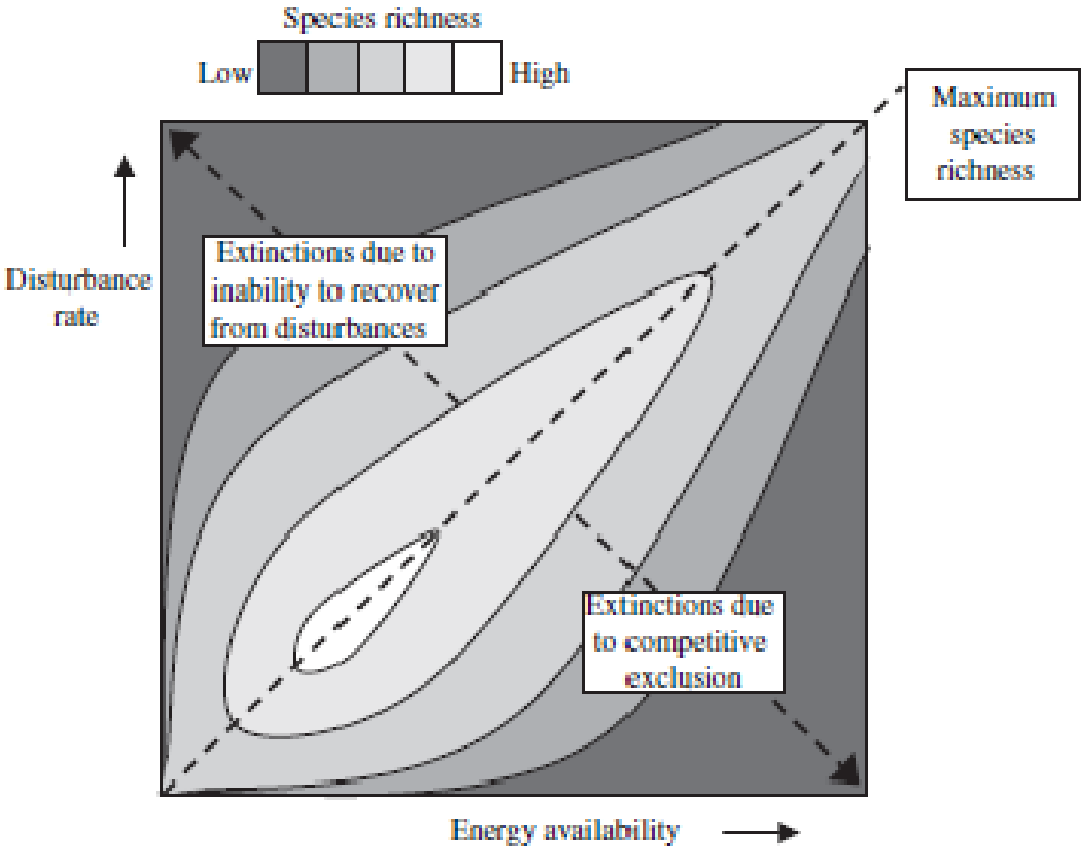

Species richness
Low
High
Maximum species richness
Disturbance rate
Extinctions due to inability to recover from disturbances
Extinctions due to competitive exclusion
Energy availability

Fig 3.

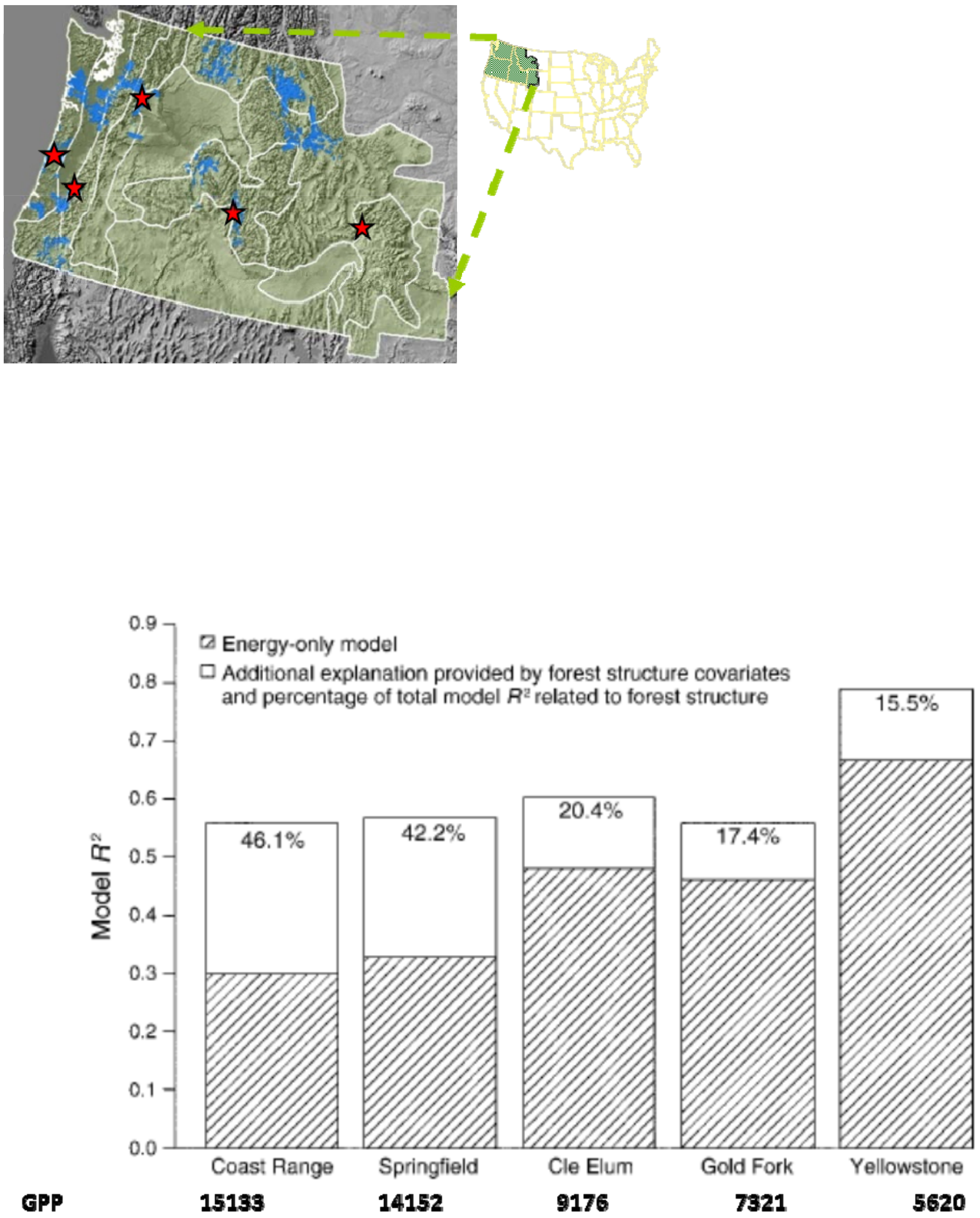

▨ Energy-only model
☐ Additional explanation provided by forest structure covariates and percentage of total model R^2 related to forest structure
Model R^2
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
46.1%
42.2%
20.4%
17.4%
15.5%
Coast Range
Springfield
Cle Elum
Gold Fork
Yellowstone
GPP
15133
14152
9176
7321
5620

Fig 4 a and b

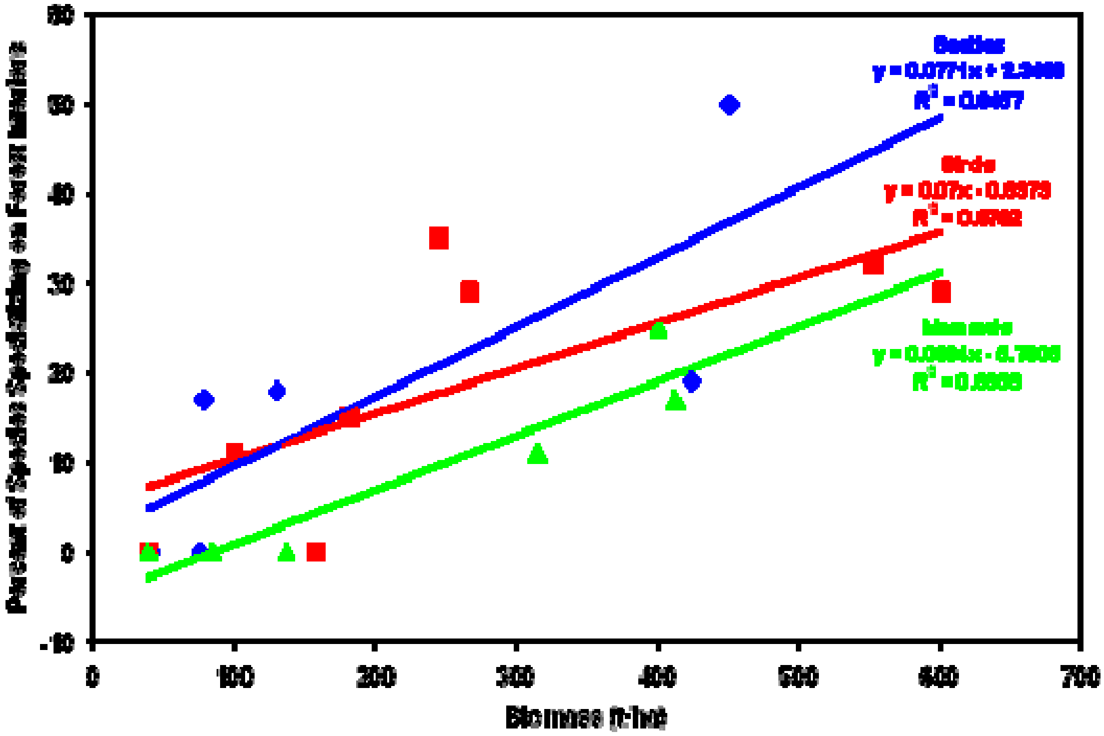

Beetles
y = 0.0771x + 2.3488
R² = 0.6457
Birds
y = 0.07x - 0.8373
R² = 0.6762
Mammals
y = 0.0594x - 4.7806
R² = 0.6608
60
50
40
30
20
10
0
-10
0
100
200
300
400
500
600
700
Percent of Species Specializing on Forest Interiors
Biomass (t/ha)

Fig. 5

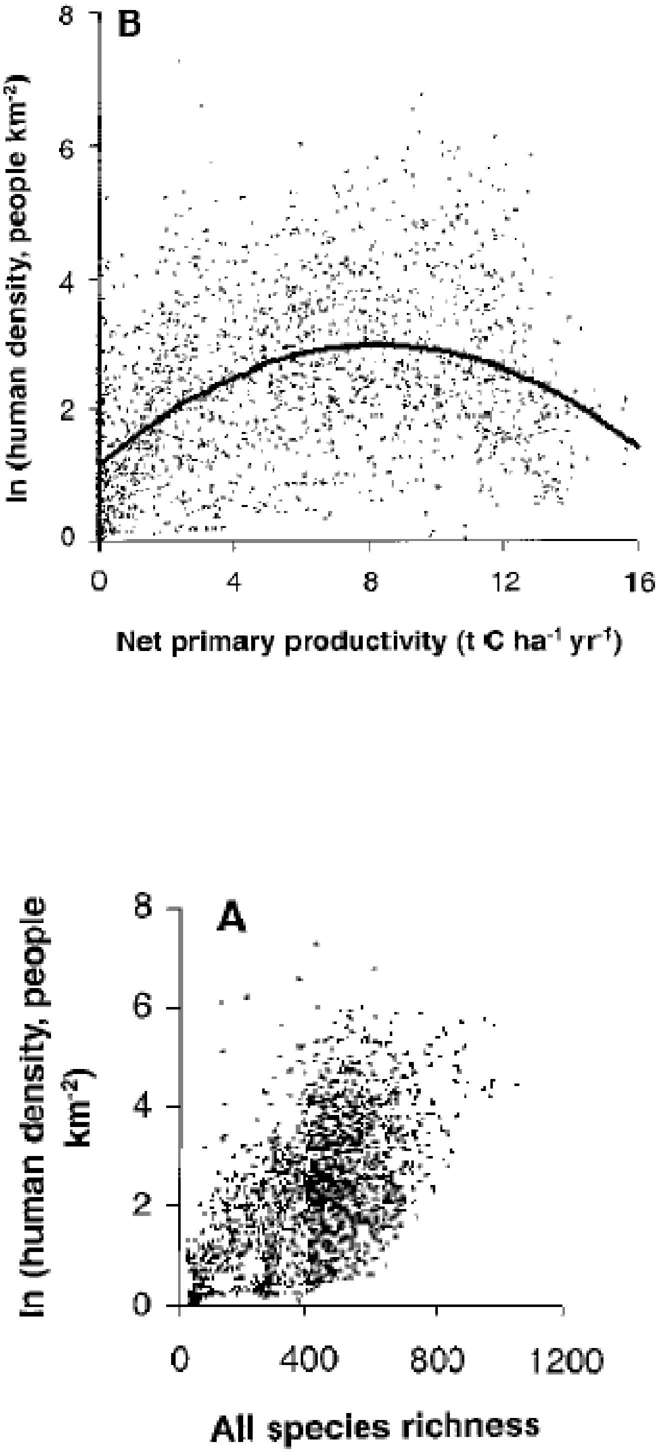
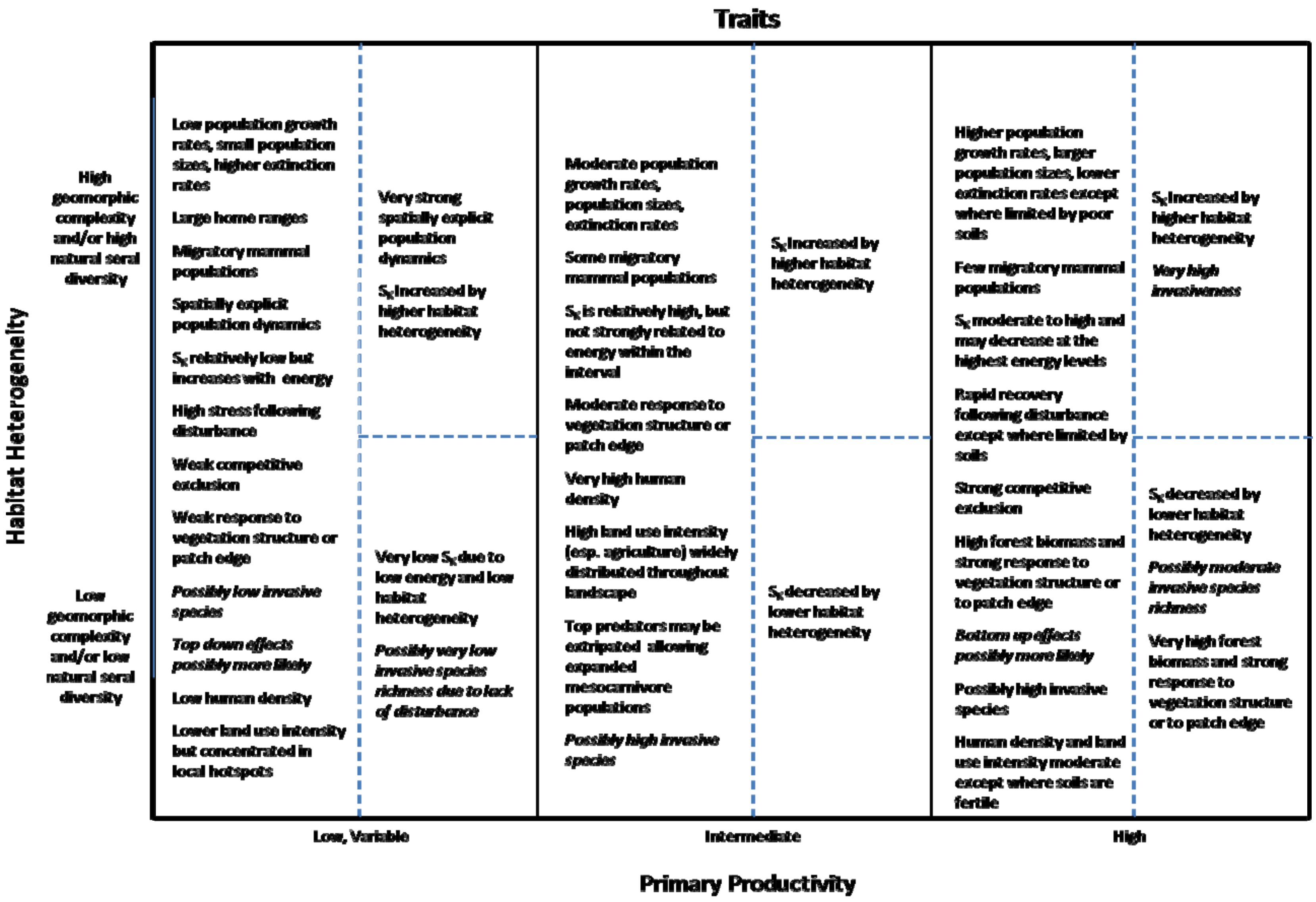

B
ln (human density, people km-2)
8
6
4
2
0
0
4
8
12
16
Net primary productivity (t C ha-1 yr-1)
A
ln (human density, people km-2)
8
6
4
2
0
0
400
800
1200
All species richness

Fig 6 a and b

Fig 7



Low population growth rates, small population sizes, higher extinction rates

Large home ranges

Migratory mammal populations

Spatially explicit population dynamics

S_K relatively low but increases with energy

High stress following disturbance

Weak competitive exclusion

Weak response to vegetation structure or patch edge

Possibly low invasive species

Top down effects possibly more likely

Low human density

Lower land use intensity but concentrated in local hotspots

Very strong spatially explicit population dynamics

S_K increased by higher habitat heterogeneity

Very low S_K due to low energy and low habitat heterogeneity

Possibly very low invasive species richness due to lack of disturbance

Moderate population growth rates, population sizes, extinction rates

Some migratory mammal populations

S_K is relatively high, but not strongly related to energy within the interval

Moderate response to vegetation structure or patch edge

Very high human density

High land use intensity (esp. agriculture) widely distributed throughout landscape

Top predators may be extirpated allowing expanded mesocarnivore populations

Possibly high invasive species

S_K increased by higher habitat heterogeneity

S_K decreased by lower habitat heterogeneity

Higher population growth rates, larger population sizes, lower extinction rates except where limited by poor soils

Few migratory mammal populations

S_K moderate to high and may decrease at the highest energy levels

Rapid recovery following disturbance except where limited by soils

Strong competitive exclusion

High forest biomass and strong response to vegetation structure or to patch edge

Bottom up effects possibly more likely

Possibly high invasive species

Human density and land use intensity moderate except where soils are fertile

S_K increased by higher habitat heterogeneity

Very high invasiveness

S_K decreased by lower habitat heterogeneity

Possibly moderate invasive species richness

Very high forest biomass and strong response to vegetation structure or to patch edge

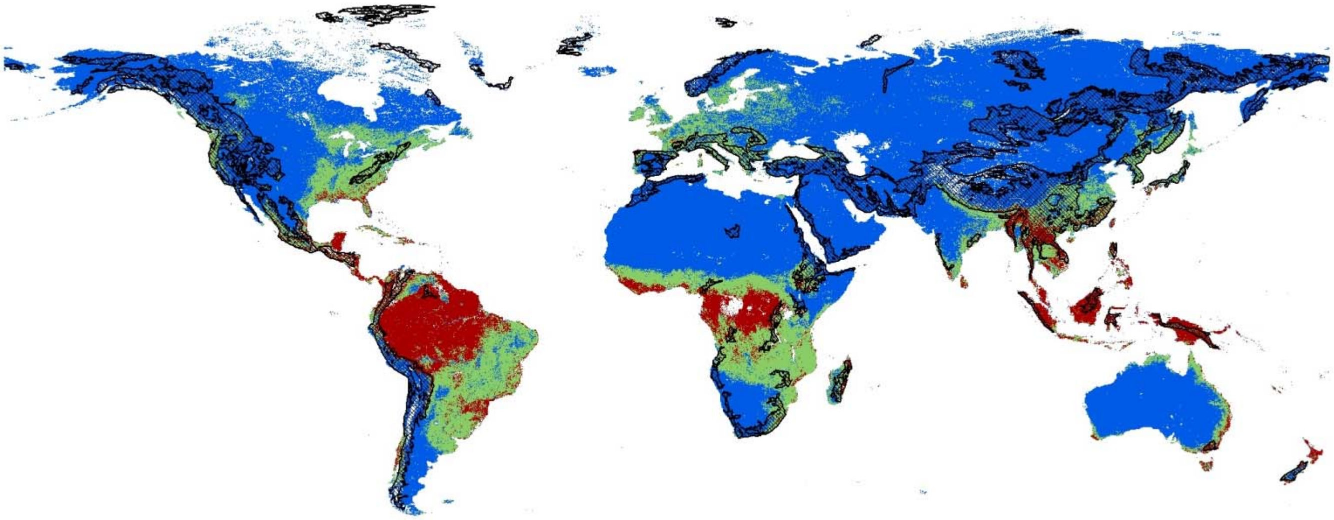


Fig 8.

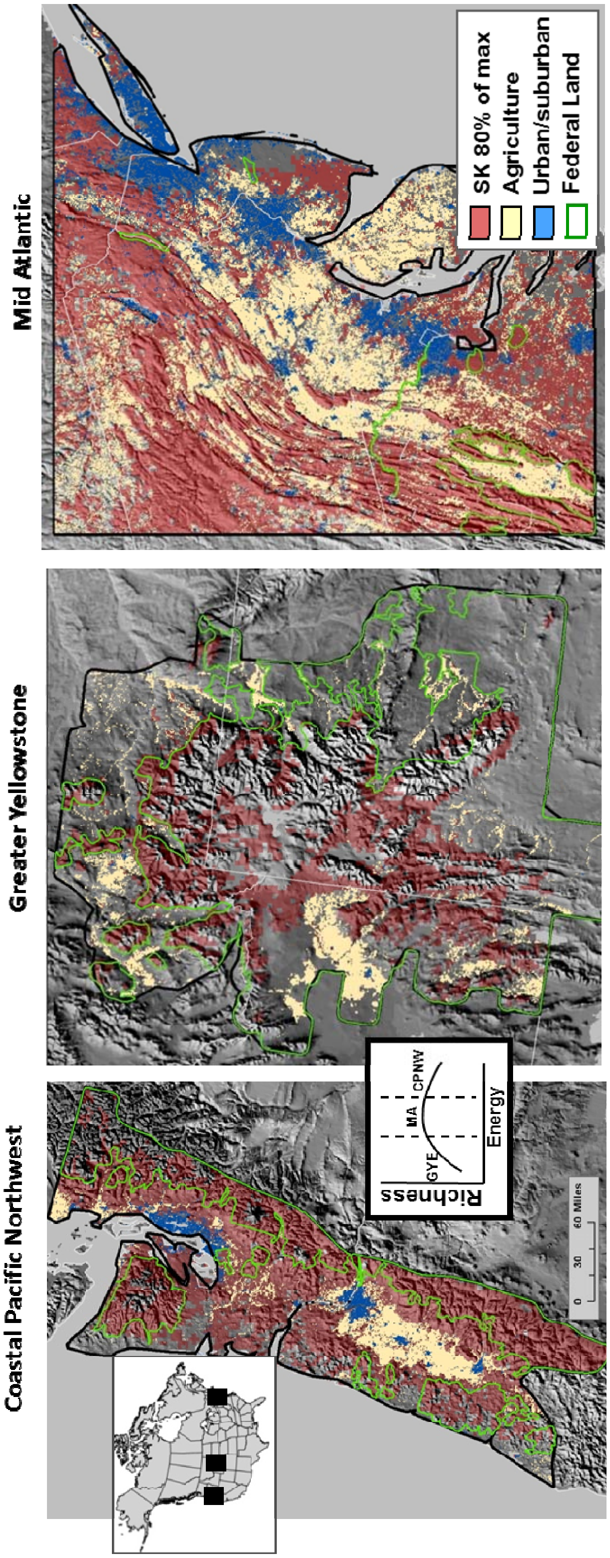

Mid Atlantic
SK 80% of max
Agriculture
Urban/suburban
Federal Land
Greater Yellowstone
Coastal Pacific Northwest
Richness
Energy
GYE
MA
CPNW
0
30
60 Miles

Fig 9.