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Biodiversity and the lexicon zoo

Bruce G. Marcot *

USDA Forest Service, Pacific Northwest Research Station, 620 SW Main Street, Suite 400, Portland, OR 97205, USA

Abstract

Ecologists and natural resource managers struggle to define and relate biodiversity, biocomplexity, ecological integrity, ecosystem services, and related concepts; to describe effects of disturbance dynamics on biodiversity; and to understand how biodiversity relates to resilience, resistance, and stability of ecosystems and sustainability of resource conditions. Further diversifying this ''lexicon zoo'' are the ecological roles of rare species and refugia, and measures of surrogates and indicators of biodiversity parameters. To impart order on this lexicon zoo, a ''concept map'' framework is suggested for clearly defining biodiversity parameters and related terms, relating biodiversity to ecosystem services and sustainability, describing how disturbance affects biodiversity, and identifying biodiversity parameters for management and monitoring. Many relations among these concepts are poorly understood in managed forest environments and are presented here as testable tenets.
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Keywords: Biodiversity; Ecosystem management; Ecosystem integrity; Sustainability; Ecosystem services; Ecosystem stability; Disturbance

1. Introduction: biodiversity in the context of forest ecology and management

Since at least the early 1960s, the concept of biological diversity or ''biodiversity'' has been an important focus for ecological research (Allen, 1963). In the 1980s, the need to incorporate biodiversity in management of public forests in the U.S. was promoted by Herbst (1980), Norse et al. (1986), Shen (1987), and many others. At present, literature on concepts, management, and research on forest biodiversity is confusing, incredibly extensive, and covers a vast arena of related ecological topics.

In the ecological literature (Pielou, 1966), ''diversity'' has traditionally referred to the number of species (species richness) in a community or area and their relative abundance (species evenness) or some variations of these measures. A number of authors and organizations have suggested conceptual frameworks and specific definitions of biodiversity that decompose the term into various levels of biological organization and spatial scales (e.g., Christensen et al., 1996; DeLong, 1996; Noss, 1990, 1999; Niemi and McDonald, 2004). Some authors have related biodiversity to other concepts such as ecosystem integrity (e.g., DeLeo and Levin, 1997). But the natural resource manager is still left with making sense of a growing lexicon of biodiversity-related topics and how to address them in forest planning and management actions. The purpose of this paper is to suggest an order to this morass that may be useful for researchers and especially for forest ecosystem managers interested in biodiversity conservation and restoration.

1.1. Definitions of biodiversity

Baydack and Campa (1998) recounted some 19 definitions of biodiversity. An often-cited and general definition of biodiversity is ''the variety of life and its processes'' (Noss and Cooperrider, 1994). Other definitions describe or evaluate biodiversity more strictly in terms of species richness (Scott et al., 1987). In 1987, Office of Technology Assessment defined biodiversity as the ''variety and variability among living organisms and the ecological complexes in which those organisms occur, encompassing many levels of biological organization and spatial extent'' (OTA, 1987). Similar variations also can be found for definitions of related terms such as ecosystem integrity, disturbance, and ecosystem services. It is no wonder that the term has been interpreted in so many different ways by managers and, in part because of its complexity, has been downplayed in the latest revisions of USDA Forest Service's Planning Rule (USDA Forest Service, 2005).

1.2. Definition, framework, and measures

I suggest that we should debate no further on the concept of biodiversity, and instead, to help focus research and manage-

* Tel.: +1 503 808 2010; fax: +1 503 808 2020.
E-mail address: bmarcot@fs.fed.us.

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Table 1
Examples of forest biodiversity variables within the conceptual framework of Noss (1990)

Composition	Structure	Function
Gene/genome		
Allelic diversity	Effective pop size	Inbreeding depression
Rare alleles	Heterozygosity	Gene flow
Population/species		
Abundance	Dispersion, range	Vital rates
Biomass	Population structure	Metapopulation trends Phenology
Community/ecosystem		
Functional groups	Vegetation structure	Key ecological functions
Number of species	Physical features	Nutrient cycling

ment, we should use (1) a broad definition, (2) a conceptual framework, and (3) specific measures. The broad definition – the variety of life and its processes – has great heuristic value and is well established in the literature. The conceptual framework suggested here is that of Noss (1990): to view biodiversity in dimensions of composition, structure, and function, at various levels of biological organization (Table 1). Then, within this conceptual framework, specific measurable variables can be listed and prioritized for research, management, and monitoring (Noss, 1999).

Unfortunately, the complexity represented in Noss' conceptual framework is lost on many authors who commonly reduce biodiversity to just species richness. This reduction is understandable given the overwhelming breadth of parameters that his framework encompasses, and that species richness is an important and somewhat easily measured component. But species richness is only one part of the framework, that is, just one aspect of the compositional element of the ecological community level of biological organization (Table 1). To focus only on species richness may be tractable, but this approach has severe limitations (Fleishman et al., 2006 and many others) that rob understanding and unduly constrain conservation and management objectives.

Instead, the forest manager could begin by filling in the framework with potential parameters and measures (e.g., Table 1), relating each cell in the framework to their management mandates and goals, and prioritizing or trimming the cells and parameters to those necessary to meet their specific mandates and goals. Financial and social considerations will also factor into defining mandates and goals. For example, if a private forest owner is participating in a habitat conservation plan (HCP) under Section 10 of the U.S. Endangered Species Act, they may identify species- or ecological community-specific goals for the HCP. In turn, this may suggest which cells of the biodiversity framework, and which specific parameters and measures, are of priority for conservation or restoration in the HCP area, such as structural and compositional dimensions of species or community levels of biological organization. Other mandates and goals might variously draw focus more on ecosystem functional parameters, such as ensuring soil productivity, restoring or mimicking natural variation in fire or floodplain regimes, or restoration of forest ecosystem integrity. But this just sets the stage for considering how parameters and dimensions of biodiversity relate to other concepts.

2. Biodiversity-related concepts and ecological relations

2.1. A concept map of biodiversity relations

The interactions among biodiversity concepts can be displayed in what I call a concept map of biodiversity relations (Fig. 1). A concept map is a graphical representation of a knowledge structure. This particular concept map displays logical and causal relations among many concepts pertaining to biodiversity and that may be of main interest to forest ecosystem managers. I developed this concept map through a very broad but selected review and analysis of the literature (>2000 references) in which I linked references according to common terms that appeared in key words, titles, or abstracts, such as ‘‘biodiversity and ecosystem services’’ (Uren et al., 2006).

I organized the concept map into four sections (Fig. 1, A–D) according to how biodiversity (A) is affected by disturbances, (B) relates to ecosystem services and sustainability of natural resources, (C) can be described as elements of biocomplexity, and (D) can be managed and monitored through surrogates or indicators. Doubtless, this concept map can be organized in many different ways, so I offer it as one possible way to structure the relations among an array of confusing concepts and terms.

In this section, I focus on the arrows of that diagram, that is, the relations between the concepts, which I present as a series of

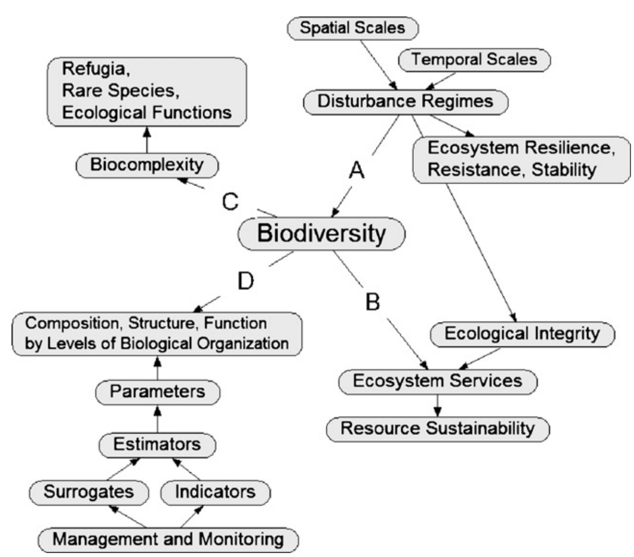

Fig. 1. A framework for ordering the biodiversity lexicon zoo. This is a concept map showing logical and ecological influences related to biodiversity. A = relations to disturbance and ecosystem responses; B = relations to ecosystem services and resource sustainability; C = relations to biocomplexity, species rarity and endemism, and ecological functions; D = parameters, estimators, and indicators for monitoring and management.

ecological tenets. I present each tenet with examples and briefly discuss pertinence and implications for forest ecosystem management.

2.2. Ecological relations and management hypotheses

The following tenets and implications for forest management can be described from the biodiversity concept map. To illustrate each tenet, I include examples from forest and some non-forest ecosystems.

2.2.1. Disturbance and ecosystem responses (A)

The influence of disturbance events on forest biodiversity and how forest diversity in turn influences the occurrence of disturbance events have become major themes in the management of forests in western North America, which have been subject to decades of fire suppression, fuels buildup, and perhaps regional climate change (Knapp et al., 2005; Dymond et al., 2006). In recent years, major stand-replacing fires and outbreaks of insect pests have changed the structure, age-class distribution of trees, and the entire composition of tree species in many forests. These and other relations between biodiversity and disturbance (Fig. 1, A) can be described as the following tenets.

Tenet. *Disturbance frequency varies as a function of spatial scale.*

Disturbances such as wildfire vary in frequency of occurrence depending on the spatial extent of the area of interest (Reilly et al., 2006). For example, Arno and Peterson (1983) calculated that mean fire return intervals in montane forests on Bitterroot National Forest in southwest Montana and Idaho were longest (25 years) at the scale of a single tree and shortest (10 years) at the scale of a large stand (80–320 ha). In this example, such predictable area–fire relationships may result from the assumption that fire ignition is a spatially random process. Implications of this tenet are that forest managers may need to specify the spatial scale when conveying disturbance frequency data (e.g., Barbour et al., 2005).

Tenet. *Disturbance frequency varies as a function of temporal scale.*

Disturbance events can occur with overlapping temporal frequencies, as well. Examples include hydrographs of river discharge rates which typically show nested frequencies of various flood stage levels occurring in daily, storm-event, seasonal, and annual time intervals (Swanston, 1991). In forest ecosystems, the frequency of disturbances such as wildfire, insect outbreaks, and windthrow varies by the length of the time period considered. Benedetti-Cecchi (2003) suggested that expressing the temporal pattern of disturbance events simply as a frequency confounds the variance in effect size of the disturbance. Forest managers can use this finding by characterizing and predicting the temporal nature of disturbance regimes by considering temporal frequency of occurrence and effect size independently. Moreover, for effective restoration projects, managers may need to characterize and accept the degree of temporal variability of specific disturbance events, such as variability of flood disturbances in restoring European floodplain forests (Hughes et al., 2005). Large infrequent disturbances, such as catastrophic wildfires, occur as a result of multiple perturbation events and are of major social importance in forest management. They also provide long-term forest legacy elements such as remnant old trees and large down wood (Paine et al., 1998; Foster et al., 1998).

Tenet. *An optimal disturbance regime results in the most diverse system.*

Although the initial idea for this relation came from the marine intertidal zone (Paine, 1974), it has been applied to many terrestrial systems including forests. For example, Rejmánek et al. (2004) suggested an intermediate disturbance hypothesis where species richness and diversity reach maximum levels at some intermediate disturbance frequency, intensity, extent, and duration. They presented data that showed that plant species diversity on calcareous scree reached a maximum value at intermediate levels of percent vegetation cover which served as a proxy to ground disturbance events. The implication of this tenet for forest management is to mimic some intermediate level of natural disturbances (Bengtsson et al., 2000). However, anthropogenic disturbances such as clear-cutting and fuels removal may not mimic effects of natural disturbances (Franklin et al., 2000), and resilience of the biota to such management activities need to be determined through empirical testing including experimentation (Niemelä, 1999).

Moreover, a major review of the literature by Mackey and Currie (2001) revealed that most studies have shown no relation between disturbance intensity and species richness, diversity, or evenness. Also, optimal (''peaked'') relations found in <20% of all cases may result from study artifacts of small sample area and few disturbance levels, and occur more often with natural rather than anthropogenic disturbances. These findings suggest that the manager might need to empirically measure the actual effects on biodiversity from a proposed optimal disturbance management regime.

More recently, the concept of a ''dynamic regime'' or ''multiple steady states'' has been discussed in the literature (Schroder et al., 2005). This concept, initially popular in the 1970s (e.g., Marks and Bormann, 1972), posits that a system might have multiple community states that can be stable over time and that may result from different disturbance regimes. Identifying such potential stable states can help forest managers formulate alternative restoration objectives (Mayer and Rietkerk, 2004; Fukami and Lee, 2006).

Research suggests that some disturbances can alter the functional composition of an ecological community but not the taxonomic diversity. For example, Pavao-Zuckerman and Coleman (2007) reported that urban land use of soils had little affect on genera of nematodes but greater affect on the trophic groups of nematode species, with urbanization resulting in lower abundances of predatory and omnivorous nematodes. My own experience (unpublished data), however, with soil and terrestrial invertebrates in young plantations and old stands of conifer forests of the Cascade Mountains of Washington state suggests the opposite, that clearcutting generally retained all trophic functional groups but altered their species composition. Thus, it appears that further studies are needed of disturbances effects on taxonomic diversity, species composition, and ecological functions before generalizations can be made.

Tenet. *A more biodiverse system is more resilient to disturbances.*

Much has been hypothesized about relations between diversity and resilience of ecosystems (e.g., Elmqvist et al., 2003; Peterson et al., 1998), although evidence from experimental ecosystems is scant. One study by Steiner et al. (2006) suggests that species diversity can enhance system resilience at the community level, particularly with low-productivity systems, but there was no relation between diversity and population resilience of individual species. Moffat (1996) also suggested that diversity stabilizes an ecosystem as a whole but does not confer such stability onto individual species which may undergo drastic fluctuations from complex interactions within a system. However, another study by Pfisterer and Schmid (2002) contradicts these findings, but it might simply suggest the apparent resilience of early-successional conditions which typically consist of disturbance-tolerant species. Extended to forest ecosystems, early-successional forest stages consisting of many pioneer plant species may seem to be more resilient than later, less species-rich stages.

Lemma 1. *Stability imparts diversity.*

This lemma to the above tenet is the modern converse of an old ecological tenet that more diverse systems are more stable. Instead, ecologists now tend to hold the view that more stable (equable) environments provide conditions for development of greater levels of biodiversity than do unstable environments. However, at the scale of broad geographic areas and long time frames, even this has been challenged by research showing that variation in climate and other abiotic conditions can serve as a basis for longer-term development of biological diversity. An example is the inconstancy of wet tropical rainforests of Africa and South America, where long-term periodic climatic cycles of aridity and high precipitation have led to high levels of allopatric speciation in guenons and antbirds, respectively (Kingdon, 1989; Kricher, 1997). For forest managers, this lemma likely does not pertain to stand-level and short-term conditions, but may pertain to identifying conditions for long-term evolutionary potential of species as one facet of landscape ecosystem management.

Lemma 2. *Low-diversity systems may be more susceptible to dramatic disturbance events.*

It is well established that disturbance events can affect various parameters of biodiversity. The converse is also known, where the structural or compositional diversity of an ecosystem can influence the type, frequency, and severity of disturbances (Allison, 2004). Monocultures of crops and forests may be more susceptible to radical change or loss from disturbances such as insect pest, pathogen, and disease outbreaks, and may hold low levels of biodiversity although this relation may vary by tree species (Kanowski et al., 2005). The forest manager may wish to gauge the degree of such susceptibility when reducing the structural and compositional diversity of stands and forest landscapes.

Tenet. *Fragmentation of forests leads to lower biodiversity.*

The literature on this relation is rather vast. Adverse effects on biodiversity from fragmenting forests has been hypothesized at least since the late 1970s and early 1980s (e.g., Whitcomb et al., 1981) and includes much work on edge effects (e.g., Parker et al., 2005; Asquith and Mejía-Chang, 2005). More recent research has focused on determining the causal mechanisms of fragmentation-biodiversity relations, such as from ‘‘extinction debt’’ (Tilman et al., 1994) which occurs when the disappearance of species from a habitat remnant lags behind the creation of the remnant (Vellend et al., 2006), and from the influence of life-history traits of plants on susceptibility to local extirpation from habitat fragmentation (Kolb and Diekmann, 2005). Many mapping tools and models are available to forest managers to evaluate fragmentation patterns and to predict changes in species richness, abundance, and composition (e.g., McGarigal and Marks, 1995; Jha et al., 2005).

Tenet. *Anthropogenic disturbances can compound to affect overall system biodiversity and resilience.*

There are not many studies to quantify this relation, and most examples pertain to effects of compound sources of pollution on human health (Serveiss, 2002) or to multiple stressors on animal species abundance (Paine et al., 1998). As an example of the latter, Rohr et al. (2004) studied the adverse influence on salamanders from herbicides, food limitations, and hydroperiod, but only the first of these was anthropogenic. Zurlini et al. (2006) described a methodology to evaluate the effect of spatial scale on identifying geographic locations where multiple human disturbances overlap, resulting in socio-ecosystems with low biodiversity, high fragility, and low resilience. Forest managers could use such a methodology to predict effects of multiple human disturbances and delineate areas needing special conservation or restoration activity.

2.2.2. Ecosystem services and resource sustainability (B)

Ecological integrity – also called biological integrity and ecosystem integrity in the literature – has many definitions but generally refers to the degree to which an existing ecological community or ecosystem has retained its native or historic components of species and functions (DeLeo and Levin, 1997). Ecosystem services refer to the array of ecological processes, including key ecological functions of organisms, that provide conditions and products of interest to people (Kremen and Ostfeld, 2005). Resource sustainability refers to the degree to which renewable natural resources can be extracted and used by people at a nondeclining rate (Amaranthus, 1997). The following tenets arise from this portion of the biodiversity concept map.

Tenet. *More diverse systems are more productive.*

Although this tenet has appeared in the literature for some time, most examples come from models and theory (e.g., Tilman et al., 1997) or from non-forest systems. The general models of Yachi and Loreau (1999) suggested that diversity provides a buffer against temporal variance of productivity and can enhance overall system productivity, and thus, provides an ‘‘insurance’’ policy against disturbances. Naeem et al. (1999) summarized six hypothetical functional relations between biodiversity and ecosystem processes. These relationships included linear, redundant, keystone, and discontinuous functions, and all generally suggested positive effects of diversity on ecosystem processes.

In empirical work, Bell et al. (2005) reported that soil bacterial respiration varied directly as a function of species richness. In an experimental study in a marine intertidal system, O’Connor and Crowe (2005) found no relation between ecosystem functioning and diversity, but that different, strongly interacting invertebrate species had idiosyncratic effects. This suggested that this tenet might not hold for systems with functionally dominant or keystone species. How this might pertain to forest systems needs clarification such as in forests naturally dominated by one or few tree species. In experimental semi-arid grasslands, Kahmen et al. (2005) found that simple measures of biodiversity poorly predicted productivity but that plant community composition was a better predictor than were environmental variables of soil and site characteristics or management regimes.

Diversity–productivity relationships also vary according to effects from disturbances (Cardinale et al., 2005) and depend on community history (Fukami and Morin, 2003). Thus, the biodiversity concept map (Fig. 1) includes an explicit link from the disturbance segment to the ecosystem services segment. Hooper et al. (2005) reviewed the literature and found broad scientific consensus that biodiversity–productivity relations are influenced by species-specific ecological roles and can be idiosyncratic, according to specific ecosystem conditions. They also concluded that ecological roles of some species are complementary and, most importantly here, a diversity of species with different environmental responses can stabilize rates of ecosystem processes and maintain management options.

An important exception to this tenet may be in intensively managed monocultures of tree farms that can far out-produce timber production over more species-rich conditions. Such an inverse relationship was also suggested by Rosenzweig (1992) who argued that experiments and empirical evidence show that diversity declines as productivity increases. Thus, this tenet begs a strict definition of ‘‘productive’’ and its veracity depends on the type of productivity of interest. Whether such monocultures, some of which may consist of exotic or off-site species, can be maintained in perpetuity in the face of disturbance events is a further question, best answered within a framework of risk analysis and risk management (Blennow and Sallnas, 2006). However, if the forest management objective is to promote biodiversity, then at least in some circumstances, activities promoting productivity also may provide for protection of endangered systems as well as for economic output (Ferraro and Simpson, 2005).

Tenet. *More diverse systems provide a greater range of ecosystem services.*

This relation is implied in a number of publications that posit the greater economic and social values of more biodiverse systems (e.g., Pearce and Moran, 1994) or that hypothesize or demonstrate the degradation of ecosystem services from reductions in biodiversity (Ostfeld and LoGiudice, 2003; Dobson et al., 2006). The forest manager can use this tenet to promote biodiversity conservation as a means to providing a wider array of forest ecosystem services although tangible economic incentives still need to be developed (Wallinger et al., 2006).

Tenet. *Ecosystems with greater integrity provide services more reliably.*

This relation posits that ecosystems that have retained a fuller complement of their historic or potential species and functions may provide their services with less temporal variability than would more altered or debased ecosystems. This tenet arises from the diversity–stability tenet. In a grassland field experiment, Pfisterer and Schmid (2002) found that biodiversity increased biomass production but did not necessarily impart system stability. The veracity of this tenet in forest ecosystems may depend on the type of ecosystem services of interest and how reliability is measured.

2.2.3. Biocomplexity, species rarity and endemism, and ecological functions (C)

How do the components of biodiversity provide for arrays of biological entities and conditions for their persistence? Michener et al. (2001) defined biocomplexity as ‘‘properties emerging from the interplay of behavioral, biological, chemical, physical, and social interactions that affect, sustain, or are modified by living organisms, including humans.’’ Pickett et al. (2005) also described biocomplexity as resulting from coupled human-natural systems, and Cadenasso et al. (2006) emphasized how biocomplexity is affected by heterogeneity, connectivity, and history. Some elements of biocomplexity include the persistence of refugia, rare species, and ecological functional groups. The term ecological complexity often is used more or less synonymously with biocomplexity (Maurer, 1999).

Tenet. *More biodiverse systems provide for greater arrays of ecological functions.*

This tenet follows from the biodiversity-productivity tenet but specifically relates to categories and rates of ecological functions. Examples of this relationship can be found from studies of relations between plant diversity and productivity (Kahmen et al., 2006; Gillman and Wright, 2006). Other examples can be found from plant community studies of the relations between functional group diversity or ecological functional redundancy, and ecosystem resilience, resistance, and stability.

Srivastava and Vellend (2005) reviewed the relation between biodiversity and ecosystem function. They concluded that, although substantial evidence suggests that diversity affects function especially in plant communities, multiple stressors in large-scale systems complicate this affect, and that the effect might be most clearly defined for restoration. Managers striving to restore forest systems could identify reference conditions or conduct trial experiments to determine appropriate levels of species diversity needed to provide desired types and levels of redundancy of ecological functions (Moore et al., 1999).

Tenet. *More biodiverse systems include a wider array of rare species.*

The basis for this tenet follows from much work done on species-abundance curves that suggests that more species-rich communities have greater numbers of less-abundant species than do species-poor communities (Murray et al., 1999). Further, systems that are relatively more diverse may tend to be those that possess other rare elements (e.g., Cao et al., 2001) such as some rare plant communities, refugia, and endemics. Such relations may hold better for some taxa (e.g., birds; Bonn et al., 2002) than for others. Forest managers can maintain some rare and endemic species by conserving older-forest legacy elements and remnant patches (Godefroid and Koedam, 2003; Mazurek and Zielinski, 2004), although these do not provide for all rare and endemic species found in extensive older forests.

Tenet. *More biodiverse systems include a wider array of endemic species.*

The basis for this tenet is more tenuous than that for the previous tenet on rare species. Lamoreaux et al. (2006) reported that the correlation between global species richness and endemism is low, although areas with high endemism tend to be more species rich than random areas. Specific environmental conditions that contribute to high numbers of endemic species may not, however, necessarily also provide for highest overall species richness.

Tenet. *Rare or endemic species can provide important ecological functions.*

Empirical evidence is emerging that some rare or endemic species may play key ecological roles and ecosystem functions (Lyons and Schwartz, 2001; Lyons et al., 2005), and thus contribute to the functional dimension of biodiversity. Also, rare species may add to overall redundancy of some functions, and thus become important buffers for ecosystems in the face of disturbances (Andrén et al., 1995). Some endemic species may play narrow but important trophic roles, such as endemic cave invertebrate fauna critical in cave food webs. Such roles of endemics likely also exist in forest ecosystems, such as rare species associated with mycorrhizal-vascular plant associations (Dickie and Reich, 2005). In another example, red tree vole (*Arborimus longicaudus*) is an arboreal rodent, regionally endemic to western coastal United States, that serves the ecological roles of feeding exclusively on fir needles and serving as an important prey items for long-tailed weasels (*Mustela frenata*) and the threatened Northern Spotted Owl (*Strix occidentalis caurina*).

2.2.4. Parameters, estimators, and indicators (D)

Given all the above tenets of biodiversity relations, the difficult question arises as to what to measure, monitor, and manage. In general, management and monitoring can focus on surrogates or indicators that serve as estimators of the ultimate biodiversity variables of interest (Fig. 1, D).

Tenet. *Measuring surrogates or indicators serves as a reliable estimator of ultimate biodiversity parameters.*

The manager may need to proceed with some caution with this tenet. Some species–habitat relationships have been well established, such as bird species diversity being highly correlated with vegetation structural diversity (e.g., foliage height diversity, MacArthur and MacArthur, 1961), so that measures of habitat diversity can indicate faunal diversity. However, there are many examples where some management surrogate or set of indicator variables simply fail to represent a parameter of interest. This is true with the use of ecological indicator species intended to reflect the status of other species within a guild or ecological community. An example is use of ‘‘umbrella species’’ to represent the habitats, distribution, or ecological requirements of other species within an ecological community (Andelman and Fagan, 2000).

In some cases, however, empirical testing has identified appropriate use of ecological indicator species as estimators of some facets of biodiversity. One example is the use of number of endemic or frugivorous butterfly species that correlate with and can indicate number of endemic bird species (Schulze et al., 2004). Noss (1999) suggested that restoration of forest biodiversity can benefit from use of validated ecological indicators carefully selected to represent the specific conditions and trends of concern.

Lemma. *Composite indices of diversity may not be particularly useful to guide management.*

Composite diversity indices (e.g., Shannon-Weiner index, Simpson index) tend to combine multiple parameters such as species relative abundance and species richness, and thus, are not useful as ways to guide management of specific habitat components (Jost, 2006). Like leading economic indicators, they may summarize overall system performance in some general way, but would need to be decomposed into their constituent elements for the manager to determine what aspects of biodiversity contribute to the index value and what management should do for achieving specific biodiversity conservation or restoration objectives. Thus, a more useful approach may be to characterize ‘‘diversity’’ by its components (Table 1), such as forest overstory or understory flora or vegetation structure, or the composition and number of species of a particular taxonomic or functional category. In this way, the manager can then have a clearer understanding of what physical elements of a forest to manipulate or provide, and what may be the more specific response by the biota.

Tenet. *Estimators to biodiversity parameters can be identified and quantified that suggest critical thresholds and early warnings.*

The notion of easily identified threshold values in some signal is attractive to managers who need a simple way to determine if a system is in some acceptable condition. Groffman et al. (2006) noted that thresholds should be used with some caution because analysis of thresholds is complicated by nonlinear and multiple interacting factors across scales of time and space. Examples of thresholds of parameter values used in management include ''trigger points'' and early warning signals touted in adaptive management (Dunn, 2002; Read and Andersen, 2000; Lindenmayer et al., 2000), and species or ecosystem ''sentinels'' used to foretell impending system degradation or collapse (NRC, 1994; Jassby, 1998; Gaines et al., 2002). In some ecosystems, increasing variability is itself an early-warning indicator (Carpenter and Brock, 2006).

3. Conclusions and considerations for managing forest biodiversity

In this paper, I suggest one possible way to order our biodiversity-lexicon zoo, namely, as testable tenets and management hypotheses. I have addressed only some of the possible relations among many factors and processes that can influence, or that are influenced by, biodiversity. Other considerations pertain to effects of management *per se* on the various aspects of biodiversity. For example, managing for monocultures or altering forest types to non-native species may lead to greater probabilities of catastrophic loss from disturbance events such as wildfire, pathogens, and diseases.

Another consideration that may be critical to successful forest management is for managers to acknowledge that ecosystems tend to be in nonequilibrium conditions (Wallington et al., 2005) and to integrate such dynamics of forest ecosystems and disturbance regimes (natural and anthropogenic) into projections of stand growth and future levels of forest resources, ecosystem integrity, and forest ecosystem services. This provides a realistic expectation of how sustainable the production of forest resources and provision of forest ecosystems can be over time.

Another consideration is to treat management activities as experiments in the spirit of adaptive management. This means monitoring not just resource production levels but also other parameters of forest biodiversity and some of their dynamic relations with various factors discussed in this paper. For example, one can monitor the effect of various forest thinning and fire management prescriptions on economic value of future timber harvests (e.g., Adams and Latta, 2005), but also their effects on diversity of forest understory vegetation (Thomas et al., 1999), invertebrates (Yi and Moldenke, 2005; Peck and Niwa, 2005), wildlife (Converse et al., 2006; Suzuki and Hayes, 2003), and other ecosystem components (Sullivan et al., 2005) that in turn could affect or comprise elements of biodiversity.

There are some wonderful examples of research studies that have helped guide the correct use of empirically validated ecological indicators for managing forest biodiversity (Kremsater et al., 2003; Beese et al., 2001) and for monitoring (Kurtz et al., 2001). The manager could begin by posing a tentative relationship of an indicator, such as an umbrella species representing habitat conditions for a variety of other species, or some measure of habitat structural diversity indicating diversity of the biota. Then, research and management experiments can help determine the veracity and utility of such assumed relations (e.g., Pearman et al., 2006). The manager is further directed to useful reviews of use of ecological indicators by Niemi and McDonald (2004), and the use of ecological concepts for biodiversity conservation by Wallington et al. (2005).

Guidelines for managing forests for biodiversity can be found in several sources including Hunter (1999), Baydack et al. (1998), Lindenmayer and Franklin (2002), and Lindenmayer et al. (2006). The forest manager also may wish to review Fischer et al.'s (2006) 10 guiding principles for biodiversity conservation in commodity production landscapes. Their principles suggest that diverse systems enhance ecosystem function and resilience to disturbances. Their principles include provision of patches of native vegetation and linkage corridors, structural complexity in the managed matrix, and buffers around sensitive areas, and that management should maintain overall species diversity within and among functional groups, and keystone and threatened species.

Composite indices of diversity may mask complicated relationships between environmental conditions and species responses and between management activities and biodiversity response. I would advocate instead decomposing such indices into more specific and conventional measures. For example, diversity indices representing forest structure may be more usefully described as forest stand density, cover, basal area, and successional stages. Diversity indices representing community structure may be more usefully described as species composition, similarity, or richness in or among each structural layer of the forest. Other indices may prove useful for tracking community change, such as the Floristic Quality Index (Herman et al., 1997; Lopez and Fennessy, 2002; Rooney and Rogers, 2002) and the Index of Biotic Integrity for aquatic (Karr, 1991) and terrestrial (Karr and Kimberling, 2003) systems. Also, use of species functional groups is another useful approach (e.g., Conduit et al., 1996).

Another consideration is that managing for species richness (number of species) alone is likely to miss other dimensions of biodiversity (Wilsey et al., 2005). Richness by itself may not correlate with, or serve as a useful surrogate or indicator of, species composition, species relative abundance, and functional diversity of a community. The manager may wish to evaluate each of these dimensions separately, for example, taxonomic diversity (Shimatani, 2001).

A vital consideration for managers is that of scale, both spatial and temporal. For example, depicting disturbance regimes – such as their occurrence and location, and their modal or variation of intensity, duration, and spatial extent – is influenced by the span of time over which they are studied.

Large, infrequent disturbances might be ‘‘counted’’ only in the context of large areas studied over long time frames (Turner et al., 1998; Dale et al., 1998). Understanding life history characteristics of species (Bowyer and Kie, 2006) and accurately depicting their resource selection functions (Meyer and Thuiller, 2006), and classifying, modeling, monitoring, and restoring vegetation dynamics (Bestelmeyer et al., 2006) are all greatly influenced by geographic scale. Defining the appropriate scale is also important for studies of biodiversity (Beever et al., 2006). Ultimately, results of our research and management of forest biodiversity will tell us more about ourselves than it will about the environment on which we depend.

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