Genes, Species, Ecosystems: Is Surrogacy Meaningful?

Jim Pojar
British Columbia Ministry of Forests
Postal Bag 5000, Smithers, BC, V0J 2N0, Canada
Jim.Pojar@gems3.gov.bc.ca

ABSTRACT

Biological diversity encompasses genes, species, and ecosystems. Some suggest dispensing with the habitat or ecosystem level of biodiversity, for a variety of reasons—which I will explore. They choose species diversity as a surrogate for biodiversity. The focus on species, indeed on only certain groups of species, is ill-advised, and will inevitably result in negative consequences for some taxonomic groups. Making biological diversity synonymous with species diversity trivializes the broader meaning of biodiversity and promotes misconceptions of conservation issues. Thorough sampling, inventory, and monitoring of species, populations, and gene frequencies require far too much time and effort to underpin a practical conservation strategy. Management for biodiversity must concentrate on the ecosystem and landscape levels of organization; in other words, must employ a "coarse-filter" strategy, with tactical application of the "fine filter."

Keywords: biological diversity, coarse filter, communities, ecosystems, fine filter, species diversity.

This is a talk I should not have to give. I will present little that most of you have not read or heard before. Much of it falls in the category of "what should be self-evident, at least to biologists." But judging from some recent public and academic discourse, and recent trends in resource management in British Columbia, this material bears repeating. Please note that many of my points are in the context of terrestrial environments, in particular of forests and forestry.

COMMUNITIES AND ECOSYSTEMS: REAL OR ILLUSORY?

Some biologists maintain that we should not use communities or ecosystems as measurable, operational targets in managing for biodiversity because: a) communities/ecosystems are conceptual, not very concrete units; and b) they are naturally unstable, continually moving targets (Bunnell et al. 1998, Simberloff 1998*a*). Bunnell et al. (1998) pointedly exclude habitat or ecosystem diversity as a component of biodiversity, which becomes the "diversity of genes, populations, and species."

Communities and ecosystems are concepts, but so too are the gene and the species. In particular, there continues to be much discussion in biology about what exactly a species is (Mallet 1995). Certainly communities and ecosystems are less discrete (I would not say they are less concrete—these assemblages do exist) and repeatably identifiable than are genes or species, which is what one would expect for a higher level of generalization, a higher level of biological organization. One can argue that the generality of the ecosystem concept is one of its chief strengths (Burns 1992, Kay and Schneider 1994). Note also that the ecosystem is still considered the most influential idea in ecology, judging by recent textbooks of ecology and surveys of professional opinion, such as Cherrett (1989).

Most certainly ecosystems change; no one could legitimately argue otherwise. But change includes rate and extent, and depends on scale, both in time and space. Individual forest ecosystems (or developmental stages of a given forest stand) continually change, but some change faster than others. In some old forests, especially in humid forests dominated by gap dynamics, the system can be characterized as a "shifting mosaic–steady state" (after Bormann and Likens 1979), with little evidence of change at the landscape scale for hundreds and even thousands of years (Lertzman et al. 1996). Lertzman and colleagues now have data from Clayoquot Sound (Gavin et al. 1997) and elsewhere demonstrating that some such forests have gone for several thousand years between stand-destroying disturbances. Paleobotanists tell us that extant, wet coastal forests have not changed all that much in the last 3–4,000 years, although in the past 10–12,000 years they have changed considerably (Hebda and Whitlock 1997).

But there are deeper undercurrents here. The objections (especially from within the cloister of academic ecologists) that communities and ecosystems are not real, reflect the persistent debate about the individualistic vs. the typic concept

L. M. Darling, editor. 2000. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb.,1999. Volume Two.
B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 520pp.

of ecological communities. Barbour (1996) provides a revealing analysis of this debate in a case study of a revolutionary shift in the plant community paradigm during the 1950s, a shift that suggests that culture can lead science, rather than the other way around. The shift was from the Clementsian organismic concept to the Gleasonian individualistic concept of the plant association, from plant communities as discrete units (organic entities) to the continuum theory of vegetation. From a broader perspective, what happened represents yet another example of holism yielding to reductionism, a common theme in the history of science.

The cultural interpretation: post–World War II U.S.A. was disaffected with socialism; holism in ecology and culture became unfashionable; individualism and existentialism rose to prominence (individual self-absorption over social involvement), as did the themes of antiestablishmentarianism (beatniks) and social fragmentation—themes that still resonate in contemporary American society. "It could be that ecologists consciously or subconsciously swam with the currents of their surrounding culture to change some fundamental opinions, to take new research directions, and to view nature in a reductionist, rather than a holistic way" (Barbour 1996).

In North America, the debate has been largely one-sided (the Gleason, individualistic side) for the past 40 or 50 years. Interestingly, some North American ecologists are beginning to think what was unthinkable—or at least unpublishable—until recently. Namely, that there is more to the organization of communities than mere chance, interference, and species individualism (Callaway 1997). In addition to the manifold organizing impacts of parasites and pathogens (Dobson and Hudson 1986), there is increasing empirical evidence of positive interactions (facilitation) among the primary producers themselves, as well as mutualisms between trophic levels (for example, mycorrhizae, nitrogen fixation, pollination, fungi, and fungivores): see Boucher et al. (1982), Bronstein (1994), Callaway (1995), Kareiva and Bertness (1997), Wilkinson (1998). One can discern the emergence of some qualified support for the concept of communities as organic entities, or at least for the notion that communities represent a combined and structured expression of positive and negative interactions among their constituent species.

So the debate continues (Palmer and White 1994) after all these years—Clements and Gleason worked back around the 1920s. Keddy (1993) maintains that the debate over existence of communities is an ontological and epistemological game that is peripheral and perhaps harmful to scientific progress. After becoming involved in this issue in the late 1960s and early 1970s, and after doing considerable fieldwork, I concluded that it was trivial. Trivial in the sense that vegetation and communities and ecosystems have elements of both discreteness and continuity; often boundaries are indistinct but sometimes they are very sharp, depending on the underlying physical gradients; dominant trees behave differently than understory vegetation; discreteness/continuity vary among different regions and vegetation types; and so forth. O'Neill (1996) expresses this duality very cogently: "The dichotomy between the thermodynamic, biogeochemical paradigm of ecosystems and the evolutionary, competitive paradigm of species is the most basic, though seldom discussed, problem in ecology. The situation is fully analogous to the old wave and particle dichotomy in physics." So it is, but why are ecologists still debating this?

Well, partly because they can still make considerable academic hay by attacking or defending one or the other of these views. As Barbour points out, another reason is cultural; it is a bit like asking why the National Rifle Association is still so powerful in the United States. Furthermore, there are nontrivial consequences for measuring/monitoring/conserving biodiversity if you believe that communities and ecosystems do not exist, or, if they do, cannot be delineated. Simberloff (1998*a*) suggests that if one is primarily concerned with the services provided by ecosystems and communities, and particularly if one holds the individualistic view, a large degree of species loss and of substitution of 1 species for another could be perfectly acceptable. Some foresters and range managers readily warm to this world view.

Breathing life into what should be a moribund issue also provides a venue for revisionist ideologues. The mechanistic, constant change, chaos-plus-contingency approach to ecosystem organization and function underlies the revisionist view of Nature, conservation, protected areas, landscape corridors, and so forth. This outlook has intellectual ties to "post-modern deconstruction" theory of the humanities (Soulé and Lease 1995), which asserts (among other things) that definitions of Nature are culturally based, that what biologists perceive as the reality of Nature is actually a construct of First World, largely white, male scientists, and has no more validity than competing constructs. Competing constructs could be: Nature as what you struggle with to survive; Nature as capital to be liquidated, or wilderness to be industrialized; Nature as a shamanistic vision; Nature as a Disney-esque theme park or a plastic diorama. Nature does not really exist—it is a subjective, culturally constructed concept, an artifact of human desires. Many so-called natural areas were in fact modified and managed by indigenous peoples prior to European settlement; every corner of the globe today has been affected by human activity; everything changes constantly; the "natural" state cannot be objectively defined. Therefore, the deconstructionists argue, it is meaningless to speak of preserving or restoring Nature.

O'Neill (1996) clearly proclaims a somewhat related, mechanistic view of the ecosystem: "After all, the ecosystem is merely the localized, transient experiment in species interaction. It is mostly designed to support life under the temporary local conditions. When it collapses, due to disturbance or changing conditions, no great tragedy. The species, the enduring, stable entities, simply reassemble a new, more appropriate ecosystem."

Some well-known ecologists, such as Botkin and Simberloff, seem to subscribe to this view, or at least some of their work has been interpreted to support it, often by interests that are advanced by such an interpretation. Some other, equally well-known ecologists have a very different view of the value of natural ecosystems and the tragedy of their demise. More importantly, such views have as much to do with the individual ecologist's philosophy of science and cultural conditioning, as they do with objective truth or scientific credibility.

This could appear like a lot of fuss over a simple decision. But it is important to appreciate the intellectual and cultural antecedents of certain "schools of thought" (perhaps better termed "systems of belief"). Regardless of their belief system, biologists should not dismiss the coarse-filter, ecosystem-based approach to conservation of biodiversity so briefly and conveniently, or at least should be very clear about the reasons for dismissal.

One must also confront management issues. In practice, it is very difficult to manage a gradient; regulatory structures and operating procedures virtually impose compartmentalization. But even ecologists who (like me) believe that "most communities intergrade continuously along environmental gradients, rather than forming distinct, clearly separated zones" (Whittaker 1975) can, if pressed, describe, classify, and map communities, ecosystems, and landscapes. As long as they acknowledge that any classification (including that of species) is an abstraction, a human construct devised for convenience and communication, no harm done and usually something useful accomplished.

GENES, SPECIES, OR ECOSYSTEMS?

I agree with Bunnell et al. (1998) that "genetic variation cannot be a measurable, operational target" in forest management. But we must not forget that the diversity found within species is the ultimate source of biodiversity at higher levels, and that understanding forest biology and ecology requires at least a rudimentary understanding of the system of genetic variability of forest species. Describing the genetic architecture and monitoring the genetic diversity of certain species of management concern, like commercial tree species, Vancouver Island marmot, devil's club, and pine mushroom, certainly should be part of the stewardship of forest land.

Unfortunately, many people think that biodiversity is synonymous with species diversity, or is sort of a new-age version of species diversity. Even some biologists still conflate species diversity with biological diversity. Hence, we encounter a continuing preoccupation with species, and with ways to quantify their diversity. This preoccupation spawned an academic industry in the 1960s and 1970s (e.g., Whittaker 1972), an industry that shows few signs of abating (e.g., Magurran 1988, Ricklefs and Schluter 1993, Huston 1994, Brouard and John 1997, among many others).

Species-based approaches still have an important role to play in biological conservation (Simberloff 1998*b*), and we certainly need to know more about genetic diversity and about the genetic variation of feature species. But I agree with Franklin (1993) that "larger-scale approaches—at the levels of ecosystems and landscapes—are the only way to conserve the overwhelming mass—the millions of species—of existing biodiversity." Franklin specifically had in mind the "physically smaller but overwhelmingly more numerous elements of diversity" (invertebrates, fungi, bacteria) that perform critical ecosystem functions, such as decomposition, nitrogen fixation, and nutrient cycling—"the little things that run the world."

Some ecologists contend that a strategy for conserving biodiversity would best be organized around the central concept of ecology: the ecosystem (Franklin 1993, Noss 1996). The ecosystem concept unites the abiotic and biotic realms, includes processes as well as entities, and is fuzzy, elastic, and inclusive enough to be applied at different scales and to very different habitats (Noss 1996). Furthermore, most terrestrial ecosystems can be characterized, classified, and mapped—which means that they and the structural elements they contain can be "measurable, operational" targets.

SCALE

Suppose for the sake of argument we decided that species were the "enduring, stable entities," that they and their interactions were paramount, and, therefore, that managing for sustained biological diversity should focus on the species level of organization. We would then confront the problem of scale. Scale in space, time, and organization is a fundamental issue in ecology (Levin 1992).

Consider the concept of levels of biological organization (after Rowe 1961). Biological diversity is more comprehensive than species diversity, so we must specify the biological hierarchy (genetic, taxonomic, or ecological) and the organizational level under consideration. Biologists could try to inventory all the genetic elements, all the taxonomic elements, all the ecological elements of a particular area. Even if we knew all the elements present, "no accepted calculus permits integration of counts of elements across levels within a hierarchy (e.g., phyla and species) or across hierarchies (e.g., species and genes). Arguably, no such calculus should be sought" (Angermeier and Karr 1994). We must seek simpler assessments, but I maintain that a focus on the species level of the taxonomic hierarchy is misplaced.

COGNITIVE DISSONANCE

Failure to conceptually integrate the multiple aspects of biodiversity results in narrowly conceived and incomplete comparisons (Angermeier and Karr 1994), like between-habitat species richness of vertebrates, or indices of taxonomic diversity based on cladistics and distinctness of taxa (Humphries et al. 1995). Such analyses are interesting and valuable, but not comprehensive or even representative assessments of biodiversity—because they ignore genetic and ecological hierarchies. Making biological diversity synonymous with species diversity trivializes the broader meaning of biodiversity, and promotes misconceptions of conservation issues. Loss of biodiversity is much more than species extinctions, which often represent the endpoint of a process of population extinctions resulting from habitat destruction and modification. In many cases, species do not go extinct but are lost from much of their former range, (e.g., grizzly bears). Conversion of huge areas of old-growth forest to short-rotation managed forest, extensive overgrazing of grasslands, declines in hundreds of genetically distinct salmonid stocks, and the loss of distinct populations from portions of a species' range, all represent significant losses of biodiversity, regardless of whether any species become extinct. Addition of species of invasive aliens, often with cascading negative effects on native biota, is another, often-neglected issue (Hobbs and Mooney 1998).

Furthermore, one could conclude from a hierarchical analysis of scale (e.g., Jensen et al. 1996) that for most metabiota (multicellular macroscopic life) except probably arthropods, sampling, inventory, and monitoring at any scale less than 10s or 100s of thousands of hectares, and for less than 10s of thousands of years, would involve assessing changes in populations (dynamics, demographics) or in gene frequencies—not in speciation or extinction, for the most part. One can think of specific exceptions to this generalization, like the Dawson caribou or Vancouver Island marmot or sticklebacks or narrowly endemic plants. Studies of the dynamics of populations and gene frequencies are valuable, but they give us only part of the picture. To provide more than a sketch of what is happening to species (our "enduring, stable entities") would require enormous effort over daunting time, even for a handful of "indicator" species (Niemi et al. 1997). Meanwhile, the ecological face of British Columbia is changing literally before our eyes. Logging proceeds apace (about 200,000 ha per year over the last decade), to say nothing of landscape alteration by agriculture, hydroelectric developments, and urbanization. I am not reassured that logging has apparently not yet caused the extinction of any vertebrate species in British Columbia. We haven't been at it very long (2 rotations at most). The Swedes have been, and almost 2,000 organisms—mostly non-vertebrates—are currently Red-listed (Östlund et al. 1997). In this respect, vertebrate species are decidedly not a good surrogate for "species" in general; if logging causes species extinctions in British Columbia, they are unlikely to occur among the vertebrates (e.g., Winchester and Ring 1996).

VERTEBRATE SURROGATES?

Vertebrates are indeed useful (though partial) indicators of species diversity. Vertebrate species diversity could be an acceptable surrogate for biological diversity if:

1. species are an acceptable surrogate for biological diversity;
2. vertebrate species and their biology and habitat relationships represent well other taxonomic groups and their ecologies; and
3. a focus on vertebrate species does not result in negative consequences for other taxonomic groups.

None of these conditions holds. Forests are not merely woody substrates or growth media for vertebrates. Forests are assemblages of organisms (communities) dominated aboveground by plants (the primary producers) and arthropods, and belowground by soil fauna, microbes, and fungi. Taxonomically and in terms of biomass, vertebrates constitute much less than 1% of British Columbia's living organisms. With respect to biomass and energetics, vertebrates are largely incidental in forest ecosystems—although they (e.g., keystone herbivores) can play disproportionately large roles in ecosystem organization and dynamics.

I strongly disagree that "the sustained presence of terrestrial vertebrates is a credible indicator of the state of other components of biological diversity" (Bunnell et al. 1998). I certainly would not rely on amphibians, shrews, and rodents as indicators of the state of the soil fauna, which is megadiverse in temperate forests. Nor are rodents reliable indicators of fungi. The sustained presence of terrestrial vertebrates cannot tell us much about the state of plant diversity. However, I am not too worried about most species of vascular plants with respect to forest management (but see Jules 1998), or at least am much less concerned about species than about certain forested and nonforested plant communities (Pojar 1980).

Cryptogamic plants are another matter. In particular, forest management threatens some epixylic species that rely on decaying wood for substrate (Berg et al. 1994), and threatens certain epiphytes—especially late-successional lichens (Lesica et al. 1991; Rose 1992; Goward 1993, 1994; Esseen et al. 1996; Sillett and Neitlich 1996). Goward and Arsenault have more to say about lichens and forests elsewhere in these proceedings. I merely emphasize that maintaining the epiphytic lichen component of biodiversity requires maintaining forests in all age classes, including very old stands. Widespread short-rotation forestry reduces such diversity (Fig. 1). To assess the state of epiphytic lichens in forests, it makes more sense to monitor the lichens themselves, or the status of the old forests in which the threatened lichens thrive, than to monitor caribou and flying squirrels.

Lichens are peculiar organisms, but it is unlikely that epiphytic lichens are unique in their relationships with humid forests. I suspect that epiphytes in general behave in a somewhat similar fashion, and perhaps also groups like canopy arthropods. Lowman and Nadkarni (1995), Pettersson et al. (1995), Shaw et al. (1996), and Humble et al. (2000) address these issues.

One could argue that lichens and other epiphytes are not that important in the scheme of things, or that there is a lot of redundancy in the epiphytic guild. But the sheer biomass of epiphytes in some old forests, and the role of epiphytes in nutrient cycling and as habitat for other creatures, suggest ecological significance (see also Rhoades 1995). Moreover, functional redundancy does not necessarily imply ecological dispensability (Naeem et al. 1998, especially their Fig. 1).

CONCLUSIONS

In summary and in my opinion:

- Species diversity is not an acceptable surrogate for biological diversity.
- Vertebrates are not acceptable indicators of species diversity of all biota.
- More attention must be paid to loss of populations (and genotypes) through ecosystem modification and habitat loss, and to gain of species via invasions.
- Management for biodiversity must concentrate on ecosystem and landscape levels of organization.

This is the essence of the “coarse-filter” conservation strategy, which the United States Nature Conservancy estimates could protect 85–90% of species by conserving samples of natural ecosystems without separate inventory and management of each species (Noss et al. 1995). The conventional “fine filter” of individual-species inventory and protection can address species not dealt with adequately by the coarse filter. Such species of management concern could include rare/endangered and narrow endemic species, large carnivores, and commercially important or culturally significant species. Nevertheless, we must not forsake research at species, population, and genetic levels. We need to know more about the autecology and genecology of selected species at all trophic levels, and we must continue to validate assumptions and test hypotheses about the way biological systems work and how they are affected by human activities and changing environments.

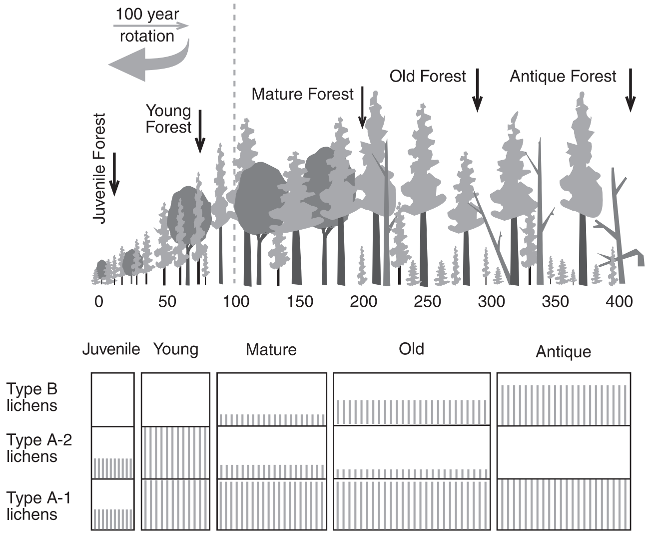

Figure 1. Stand age, development stage, and relative abundance of epiphytic macrolichens in toe-position, western-hemlock-dominated forests of the Kispiox Valley, west-central British Columbia. Type A-1 (terminology of Goward 1994) lichens are widespread generalists that occur in forests of all ages and developmental stages. Type A-2 lichens are also widespread species, but are restricted primarily to younger forests. Type B lichens are specialists restricted primarily to old-growth forests.

ACKNOWLEDGEMENTS

T. Goward and A. MacKinnon helped formulate some of these thoughts.

LITERATURE CITED

Angermeier, P. L., and J. R. Karr. 1994. Biological integrity versus biological diversity as policy directives. BioScience 44:690–697.

Barbour, M. 1996. American ecology and American culture in the 1950s: who led whom? Bull. of Ecol. Soc. of Amer. 77:44–51.

Berg, Å., B. Ehnström, L. Gustafsson, T. Hallingbäck, M. Jonsell, and J. Weslien. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8:718–731.

Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. Amer. Sci. 67:660–669.

Boucher, D. H., S. James, and K. H. Keeler. 1982. The ecology of mutualism. Annu. Rev. of Ecol. and Systematics 13:315–347.

Bronstein, J. L. 1994. Our current understanding of mutualism. Q. Rev. of Biol. 69:31–51.

Brouard, J. S., and S. E. John. 1997. Biodiversity measurement: where are we? Appendix 1, Pp. 1–50 *in* G. Namkoong, G. G. Scudder, J. Smith, and F. L. Bunnell, eds.

Developing a strategy for biodiversity measurement in British Columbia: workshop proc. 19–20 Feb. 1997, Univ. B.C., Vancouver, BC.

Burns, T. P. 1992. Ecosystem: a powerful concept and paradigm for ecology. Bull. of Ecol. Soc. of Amer. 73:39–43.

Bunnell, F. L., L. L. Kremsater, and M. Boyland. 1998. An ecological rationale for changing forest management on MacMillan Bloedel's forest tenure. Centre for Appl. Conserv. Biol., Univ. B.C., Vancouver, BC. Unpubl. rep.

Callaway, R. M. 1995. Positive interactions among plants. Bot. Rev. 61:306–349.

_____. 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112:143–149.

Cherrett, J. M. 1989. Key concepts: the results of a survey of our members' opinions. Pp. 1–16 *in* J. M. Cherrett, ed. Ecological concepts: the contribution of ecology to our understanding of the natural world. Blackwell, Oxford, England.

Dobson, A. P., and P. J. Hudson. 1986. Parasites, disease and the structure of ecological communities. Trends in Ecol. and Evol. 1:11–15.

Esseen, P. A., K. E. Renhorn, and R. B. Pettersson. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecol. Appl. 6:228–238.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecol. Appl. 3:202–205.

Gavin, D. G., K. P. Lertzman, L. B. Brubaker, and E. Nelson. 1997. Holocene fire size and frequency in a coastal temperate rainforest. Bull. of Ecol. Soc. of Amer. 78:93.

Goward, T. 1993. Epiphytic lichens: going down with the trees. Pp. 153–158 *in* S. Rautio, ed. Community action for endangered species: a public symposium on B.C.'s threatened and endangered species and their habitats. Fed. of B.C. Nat./Northwest Wildl. Preservation Soc., Vancouver, BC.

_____. 1994. Notes on oldgrowth-dependent epiphytic lichens in inland British Columbia, Canada. Acta Bot. Fennica 150:31–38.

Hebda, R. J., and C. Whitlock. 1997. Environmental history. Pp. 227–254 *in* P. K. Schoonmaker, B. von Hagen, and E. C. Wolf, eds. The rain forests of home: profile of a North American bioregion. Island Press, Washington, DC.

Hobbs, R. J., and H. A. Mooney. 1998. Broadening the extinction debate: population deletions and additions in California and Western Australia. Conserv. Biol. 12:271–283.

Humble, L. M., N. N. Winchester, and R. A. Ring. 2000. The potentially rare and endangered terrestrial arthropods in British Columbia: revisiting British Columbia's biodiversity. Pp. 101–108 *in* L. M. Darling, ed. Proc. Conf. Biology and Management of Species and Habitats at Risk, Kamloops, BC, 15-19 Feb. 1999. Vol. One. B.C. Minist. Environ., Lands and Parks, Victoria, BC, and Univ. College of the Cariboo, Kamloops, BC. 490pp.

Humphries, C. J., P. H. Williams, and R. I. Vane-Wright. 1995. Measuring biodiversity value for conservation. Annu. Rev. of Ecol. and Systematics 26:93–111.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, England.

Jensen, M. E., P. Bourgeron, R. Everett, and I. Goodman. 1996. Ecosystem management: a landscape ecology perspective. Water Resour. Bull. 32:203–216.

Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: *Trillium* in old-growth forest. Ecology 79:1645–1656.

Kareiva, P. M., and M. D. Bertness, eds. 1997. Special feature: re-examining the role of positive interactions in communities. Ecology 78:1945–2024.

Kay, J. J., and E. Schneider. 1994. Embracing complexity: the challenge of the ecosystem approach. Alternatives 20:32–39.

Keddy, P. 1993. Do ecological communities exist? A reply to Bastow Wilson. J. Vegetation Sci. 4:135–136.

Lertzman, K. P., G. D. Sutherland, A. Inselberg, and S. C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77:1254–1270.

Lesica, P., B. McCune, S. V. Cooper, and W. S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Can. J. Bot. 69:1745–1755.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lowman, M. D., and N. M. Nadkarni, eds. 1995. Forest canopies. Academic Press, San Diego, CA.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

Mallet, J. 1995. A species definition for the modern synthesis. Trends in Ecol. and Evol. 10:294–299.

Naeem, S., Z. Kawabata, and M. Loreau. 1998. Transcending boundaries in biodiversity research. Trends in Ecol. and Evol. 13:134–135.

Niemi, G. J., J. M. Hanowski, A. R. Lima, T. Nicholls, and N. Weiland. 1997. A critical analysis on the use of indicator species in management. J. Wildl. Manage. 61:1240–1252.

Noss, R. F. 1996. Ecosystems as conservation targets. Trends in Ecol. and Evol. 11:351.

_____, E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. U.S. Dep. Int., Natl. Biol. Serv., Laurel, MD. Biol. Rep. 28.

O'Neill, R. V. 1996. Review of Patten and Jorgensen. "Complex ecology: The part-whole relation in ecosystems." Ecology 77:659–660.

Östlund, L., O. Zackrisson, and A.-L. Axelsson. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Can. J. For. Res. 27:1198–1206.

Palmer, M. W., and P. S. White. 1994. On the existence of ecological communities. J. Vegetation Sci. 5:279–282.

Pettersson, R. B., J. P. Ball, K. E. Renhorn, P. A. Esseen, and K. Sjoberg. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. Biol. Conserv. 74:57–63.

Pojar, J. 1980. Threatened forest ecosystems of British Columbia. Pp. 28–39; [and] Threatened habitats of rare vascular plants in British Columbia. Pp. 40–48 *in* R. Stace-Smith, L. Johns, and P. Joslin, eds. Threatened and rare species and habitats in British Columbia and the Yukon: symposium proc., B.C. Minist. Environ., Victoria, BC.

Rhoades, F. 1995. Nonvascular epiphytes in forest canopies: worldwide distribution, abundance, and ecological roles. Pp. 353–408 *in* M. D. Lowman, and N. M. Nadkarni, eds. Forest canopies. Academic Press, San Diego, CA.

Ricklefs, R. E., and D. Schluter, eds. 1993. Species diversity in ecological communities. Historical and geographical perspectives. University of Chicago Press, Chicago, IL.

Rose, F. 1992. Temperate forest management: its effects on bryophyte and lichen floras and habitats. Pp. 211–233 *in* J. W. Bates, and A. M. Farmer, eds. Bryophytes and lichens in a changing environment. Oxford University Press, Oxford, England.

Rowe, J. S. 1961. The level-of-integration concept and ecology. Ecology 42:420–427.

Shaw, D. C., C. L. Rose, S. C. Sillett, and A. B. Carey, eds. 1996. Special issue on northwest forest canopies. Northwest Sci. 70:1–108.

Sillett, S. C., and P. Neitlich. 1996. Emerging themes in epiphyte research in westside forests with special reference to cyanolichens. Northwest Sci. 70:54–60.

Simberloff, D. 1998*a*. Measuring diversity of communities and ecosystems with special reference to forests. Pp. 66–81 *in* F. L. Bunnell, and J. F. Johnson, eds. Policy and practices for biodiversity in managed forests: the living dance. University of British Columbia Press, Vancouver, BC.

_____. 1998*b*. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. 83:247–257.

Soulé, M. E., and G. Lease, eds. 1995. Reinventing nature? Responses to postmodern deconstruction. Island Press, Washington, DC.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

_____. 1975. Communities and ecosystems. Second ed. Macmillan, New York, NY.

Wilkinson, D. M. 1998. The evolutionary ecology of mycorrhizal networks. Oikos 82:407–410.

Winchester, N.N., and R. A. Ring. 1996. Centinelan extinctions: extirpation of northern temperate old-growth rainforest arthropod communities. Selbyana 17:50–57.