Questionable Utility of the Frontier Forest Concept

JOHN L. INNES AND KENNETH B. H. ER

International concern over the continual loss of natural forests has increased considerably over the last decade (McNeely and Miller 1983, WCED 1987, WRI 1994). The World Resources Institute (WRI) in Washington, DC, has estimated that almost half of the world's original forests have been cleared over the past 8000 years. Of the remaining forests, 22% are relatively undisturbed by anthropogenic forces and remain intact, while the rest have been highly altered and fragmented (Bryant et al. 1997). The large number of organisms that forests contain helps to sustain many environmental functions upon which humanity is dependent. These functions include photosynthesis, provision of food and other renewable resources, soil generation and preservation, nutrient recycling, filtering of pollution and waste assimilation, climate moderation, maintenance of the hydrological cycle, and regulation of the greenhouse gases in the atmosphere. The protection of natural forests is therefore important in the global landscape, where the human population continues to grow and impinge upon the condition and amount of forest (Ehrlich and Ehrlich 1992, Sisk et al. 1994, Folke et al. 1996).

Given the clear importance of forests, an obvious way to prevent further loss would be to increase the area of protected forests. However, such a policy is beset with the problems of conflicting land use and limited resources. There has been much debate over the criteria used to identify areas of high conservation priority and the standards by which conservation resources are dispensed (e.g., Dinerstein and Wikramanayake 1993, Mittermeier et al. 1998). Forests with high conservation priority are identified through a process that identifies ecoregions of high conservation priority. Examples of this process include the use of biodiversity hotspots or the Global 200 initiative (Myers 1988, Olson and Dinerstein 1998), where the focus has been on ecosystems rather than strictly on forests.

Recently, WRI introduced the concept of "frontier forest" to identify large, intact, and relatively undisturbed natural forests on a global scale (Bryant et al. 1997). The term, however, is not widely used in the scientific literature. A search of the online databases CAB Abstracts® and Current Contents® (from 1973 and 1996, respectively, to November 2000) revealed that the term has not been used in the title or abstract of any publication other than those of WRI. Nevertheless, the term has been adopted by a number of environmental nongovernmental organizations, including the World Conservation Monitoring Centre, World Wildlife Fund, the Natural Resources Defense Council, and the Rainforest Alliance, and has been adopted also by a number of large funding bodies, including the MacArthur Foundation.

> THE CONCEPT OF FRONTIER FORESTS HAS VERY LIMITED VALUE WHEN IDENTIFYING GLOBAL CONSERVATION PRIORITIES FOR FORESTS

Bryant and colleagues (1997) defined frontier forests thus:

- They are of sufficient size to support ecologically viable populations of the largest carnivores and herbivores associated with that particular forest ecosystem, although they may not actually contain these species.
- They are of sufficient size to support ecologically viable populations of these species in the face of a major natural disturbance episode, such as typically occurs once in a century within the ecosystem in question.
- They exhibit a structure and composition shaped largely by natural events, as well as by limited human disturbance from traditional activities such as shifting cultivation.
- They are relatively unmanaged, which allows natural disturbances (such as fire) to occur across most of the area in question.

John L. Innes (e-mail: innes@interchange.ubc.ca) is the FRBC chair of Forest Management and director of the Centre for Applied Conservation Research, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada V6T 1Z4. Kenneth B. H. Er is a graduate student at the Faculty of Forestry, University of British Columbia.

- They contain mosaics of forest patches representing a range of seral stages, in areas where such landscape heterogeneity would be expected to occur under natural conditions.
- They contain most, if not all, of the species associated with that ecosystem type.
- Finally, they are dominated by indigenous species associated with that ecosystem type.

On the basis of this definition, frontier forests were identified and a frontier forest index (FFI) was proposed to prioritize the conservation of forests (Bryant et al. 1997). This index ranked countries according to the percentage of frontier forest lost and the percentage of the remaining frontier forest that is moderately or highly threatened by human activities. Countries with a high FFI would have the highest percentage of frontier forest lost and the highest risk of losing all of their remaining frontier forests, which would therefore be of high conservation priority. The following ideas underlie the use of the frontier forest concept for prioritizing the conservation of forests: Pristine and relatively undisturbed forests are distinct in their compositional, structural, and functional diversity, as compared with forests that are disturbed by humans; the protection of pristine and relatively undisturbed forests is vital, given the current global trends in forest loss; and large tracts of pristine and relatively undisturbed forests are biologically more important than smaller remnants of the same forest type.

In this article, we examine these ideas underlying the frontier forest concept and evaluate the utility of the frontier forest index as a means to achieving the overall goal of conservation of forest biodiversity.

How natural should a forest worthy of conservation be?

This question revolves around whether pristine and relatively undisturbed forests are distinct in their compositional, structural, and functional diversity, as compared with forests that are disturbed by humans. The idea that forest ecosystems will develop toward climax systems, which are relatively stable (Clements 1936), has given way to the more recent views that forest ecosystems are dynamic and in a constant state of change as a result of large- and small-scale disturbances (Botkin 1990, Attiwill 1994). The rationale for restricting the criterion of frontier forest to those forests that are relatively undisturbed by humans assumes that human disturbance results in changes in the forest that are different from changes induced by natural disturbances. However, there is a scale of human disturbance, just as there is one for natural disturbance. Among harvesting systems, single-tree selection appears to cause considerably less disturbance than large-scale industrial clearcutting, especially if the former is done by helicopter extraction without felling the tree onto the forest floor. Most harvesting systems used today fall between these extremes, and a gradient of responses might therefore be expected. Within certain thresholds, we can expect that a forest will be able to recover from the effects of human-induced disturbance, such that there will not be any significant changes to the forest composition, function, and structure (Hobbs and Norton 1996).

The resilience of forests in recovering from varying degrees of human disturbance is best illustrated by studies in the tropical rain forests of South America. Research from these forests has shown that traditional shifting cultivation ("slash and burn") does not significantly change the soil nutrient status or physical structure, and the forest is able to recover and return to mature primary rain forest in a space of about 190 years, with little discernible change in biomass, productivity, nutrient cycling, and species composition (Uhl 1987). However, the more intensive disturbance that results from the use of fertilizers, fire, bulldozers, or ploughing, which are associated with the conversion of tropical rain forests to pasture, may involve a time-scale for recovery as long as 1000 years or more (Buschbacher et al. 1988, Uhl et al. 1988).

Although there has been much emphasis on the degree of human disturbance, the level of resilience may differ among forest types and thus result in different thresholds to the intensity of human disturbance. Working in the montane ash *(Eucalyptus regnans)* forests of Victoria, Australia, Lindenmayer and colleagues (1990) found that the spatial distributions of large-diameter trees (i.e., hollow-bearing trees) were typically regularly distributed in unlogged old-growth stands, whereas after clearcutting, the spatial distributions of large-diameter trees tended to be clustered in stands that had regenerated. On the other hand, in a study of unlogged and logged jarrah *(Eucalyptus marginata)* forest stands in Western Australia, Abbott (1984) did not find any difference in the spatial distribution of large-diameter trees. Unfortunately, there are no published studies that compare the impacts of different intensities of harvesting under fully replicated conditions and across all scales appropriate to biodiversity, although projects such as EMEND (Ecosystem Management Emulating Natural Disturbance) in Alberta, Canada, may help provide answers (Spence and Volney 1999).

Some forests with a history of human disturbance may still develop structural, compositional, and functional characteristics that are similar to those of relatively undisturbed forests. Whether a forest can recover to some semblance of an undisturbed state is determined by two factors: the degree of human disturbance and the resilience of the forest type. Any criterion used to prioritize the conservation of forests according to its "naturalness" must first identify the threshold at which a logged forest is deemed to have recovered to a state that is indistinguishable from the natural state. Failing this, such a criterion may be of limited value in landscapes where truly pristine forests are rare. The use of the frontier forest criterion will exclude forests that have been relatively disturbed by humans and but that may still be of conservation value.

How much forestland should we protect?

The issue here is the importance of protecting pristine and relatively undisturbed forests, given the current global trends in forest loss. The arguments for the protection of forests often transcend science. Much depends upon the value that soci-

Table 1. Ranking of conservation priority in countries with frontier forests.

Country	Percentage of original frontier forest lost	Percentage of current frontier forest threatened by human activities	Frontier forest index
Countries that risk losing their remaining frontier forest, unless they act immediately			
Nigeria	99	100	99
Finland	99	100	99
Vietnam	98	100	98
Laos	98	100	98
Guatemala	98	100	98
Côte d'Ivoire	98	100	98
Taiwan	98	100	98
Sweden	97	100	97
Bangladesh	96	100	96
Central African Republic	96	100	96
Thailand	95	100	95
Countries that, without any further conservation action, will continue to lose their frontier forests			
Argentina	94	100	94
New Zealand	91	100	91
China	98	93	91
Costa Rica	90	100	90
Cambodia	90	100	90
Cameroon	92	97	90
Brunei	89	100	89
Honduras	84	100	84
United States	94	85	79
Nicaragua	78	100	78
Bhutan	76	100	76
Mexico	92	77	71
Gabon	68	100	68
Sri Lanka	88	76	67
Panama	65	100	65
Ecuador	63	99	63
Democratic Republic of the Congo (formerly Zaire)	84	70	59
India	99	57	56
Bolivia	56	97	55
Burma	94	56	52
Australia	82	63	52
Papua New Guinea	60	84	50
Congo	71	65	46
Belize	65	66	43
Malaysia	85	48	41
Peru	43	95	41
Indonesia	72	54	39
Chile	45	76	35
Countries that have a real chance, with careful forest stewardship, of keeping most of their frontier forests			
Brazil	58	48	28
Venezuela	41	37	15
Russia	71	19	13
Colombia	64	19	12
Canada	42	21	8
Guyana	18	41	7
Suriname	8	22	2
French Guiana	8	0	0

Source: Adapted from Bryant and colleagues (1997).

ety places on forests and the political will to protect such forests (Cairns 1993). As such, we doubt that all forests identified by the frontier forest criterion will be completely protected. It would be of greater value to determine the amount of relatively undisturbed forests that should be protected. This is not addressed by the frontier forest criterion.

Currently, many countries aim to conserve at least 12% of their forest cover. This level of conservation follows recommendations in the Brundtland report, which called for the protection of at least 12% of the natural habitat (including forests) in each country (WCED 1987). The 12% figure was based on an *ad hoc* calculation by McNeely and Miller (1983)

Table 2. Biodiversity indicators for countries identified as having frontier forests.

Country	Annual percentage rate of forest cover change (1990–2000)	Percentage of mammal species threatened with extinction	Percentage of bird species threatened with extinction	Percentage of plant species threatened with extinction
Countries that risk losing their remaining frontier forest, unless they act immediately				
Nigeria	–2.6	9.1	1.3	2.5
Finland	0	10.0	1.2	0.1
Vietnam	0.5	17.4	6.5	1.2
Laos	–0.4	15.7	3.9	NA
Guatemala	–1.7	2.4	1.3	0.9
Côte d'Ivoire	–3.1	7.4	2.2	2.8
Taiwan	NA	NA	NA	NA
Sweden	0	13.3	0.8	0.2
Bangladesh	1.3	19.3	7.8	0.2
Central African Republic	–0.1	5.7	0.6	0.3
Thailand	–0.7	12.8	6.0	0.7
Countries that will continue to lose their frontier forests without any further conservation action				
Argentina	–0.8	10.0	4.3	0.4
New Zealand	0.5	80.0	41.3	0.9
China	1.2	19.3	7.6	0.5
Costa Rica	–0.8	6.8	2.2	0.9
Cambodia	–0.6	17.1	6.2	NA
Cameroon	–0.9	9.0	2.2	1.9
Brunei	–0.2	5.7	3.4	3.3
Honduras	–1.0	5.2	1.2	1.9
United States	0.2	8.6	8.5	0.9
Nicaragua	0	3.0	1.0	0.5
Bhutan	0	20.2	2.7	0.1
Mexico	–1.1	14.1	5.1	0.6
Gabon	0	.9	1.3	1.1
Sri Lanka	–1.6	22.7	5.6	8.4
Panama	–1.6	9.2	2.2	1.9
Ecuador	–1.2	10.3	4.5	1.0
Democratic Republic of the Congo (formerly Zaire)	–0.4	8.9	3.0	0.5
India	0.1	27.2	7.6	1.5
Bolivia	–0.3	7.3	2.1	0.4
Burma	–1.4	14.3	4.0	0.5
Australia	0	24.2	5.4	0.2
Papua New Guinea	–0.4	26.1	4.9	1.2
Congo	–0.1	6.0	0.9	0.6
Belize	0	3.2	0.6	1.0
Malaysia	–1.2	15.7	7.3	4.4
Peru	–0.4	10.2	4.7	1.5
Indonesia	–1.2	30.6	7.4	1.3
Chile	–0.1	23.1	7.1	0.8
Countries that have a real chance, with careful forest stewardship, of keeping most of their frontier forests				
Brazil	–0.4	18.9	7.5	0.6
Venezuela	–0.4	7.7	1.8	0.3
Russia	0	15.6	6.1	0.0
Colombia	–0.4	10.0	4.5	0.4
Canada	0	7.3	1.9	0.0
Guyana	–0.3	4.7	0.3	0.4
Suriname	0	6.1	0.2	0.5
French Guiana	0	6.0	0.0	0.3

NA, not available.

Note: The percentage of species threatened with extinction is expressed as the number of threatened species versus the total number of species in each taxon.

Source: Data on forest cover are from FAO (2001). Data on the total number of mammal, bird, and plant species are from UNDP and others (2000) for all countries except Brunei, French Guiana, and Bolivia (birds only), the data for which are from WRI (1994). Data on the number of mammal, bird, and plant species threatened with extinction are based on the species listed under the IUCN criteria of critically endangered, endangered, and vulnerable for each country (IUCN 2000).

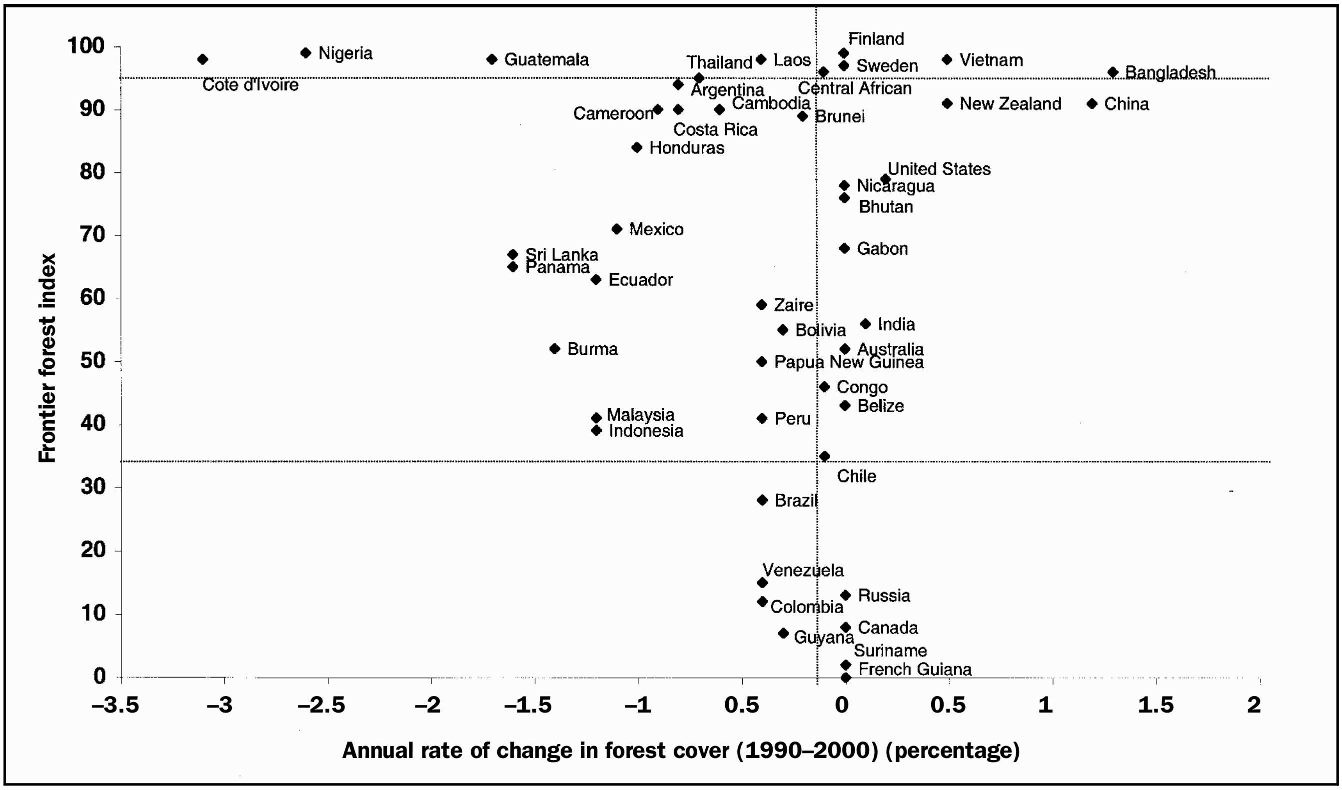

Figure 1. Plot of the frontier forest index (FFI) against the annual rate of change (percentage) in forest cover (1990–2000) for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on forest cover are from FAO (2001) (which excludes Taiwan, n *= 46). Vertical dotted line represents the global mean annual rate of change in forest cover, –0.127%,* n *= 203. The global mean of the annual rate of change of forest cover was calculated by averaging across all countries in the world that have available data.*

that, because the percentage of habitat protected globally at that time was approximately 4%, the ultimate aim would be to conserve three times that amount. There is no scientific basis to this figure. More significantly, it paints the misleading picture that, once the 12% ceiling is reached, any form of human-induced extinction in species will be averted, a view that can lead to public complacency and political denial (Soulé and Sanjayan 1998).

Various estimates of the amount of habitat that must be protected have been proposed as an alternative, although these estimates vary according to ecoregion and habitat type. For example, Margules and colleagues (1988) showed that approximately 45% of the total wetland area in coastal northern New South Wales, Australia, would have to be protected to ensure that all plant species were represented. On the other hand, Saettersdal and colleagues (1993) suggested that at least 75% of the total area of deciduous forest in Norway must be protected to ensure that all plant species were protected. Estimating the amount of habitat that should be protected becomes increasingly difficult in species-rich habitats, such as tropical rain forests, because of difficulties in measuring biodiversity, a lack of survey and monitoring information, and our lack of understanding of density packing in these habitats (Boyle and Sayer 1995). These difficulties are further compounded by continental and local variability in rain forest species richness. For example, Gentry (1992) showed that the rain forests of tropical America contain at least three times more vascular plant species than the rain forests of Malesia (the region encompassing peninsular Malaysia, Singapore, Borneo, Indonesia, the Philippines, and Papua New Guinea). In contrast, the vascular plant species richness of the rain forests of Africa tends to be poorer than that of the rain forests of tropical America and Malesia. At the same time, high local variation in plant species richness was observed in the rain forests of tropical America and Africa.

In determining the amount of forest to protect, one often ignores the fact that forests are constantly being renewed through reforestation efforts and natural regeneration, and they also constantly decay or deteriorate through human activities and natural succession. On a global basis, the current rate of decay of forests as a result of human activities far surpasses the rate of natural decay (i.e., natural succession) and the rate at which forests can be renewed (i.e., regeneration through natural succession and reforestation). Recognizing this situation, Sinclair and colleagues (1995) proposed that the amount of forest to be protected should be such that the rate of forest decline is balanced by the rate of forest renewal. They illustrated this idea with a habitat decay–renewal equilibrium model and argued that the designation of natural habitat as reserves can help buy time for habitat renewal. This

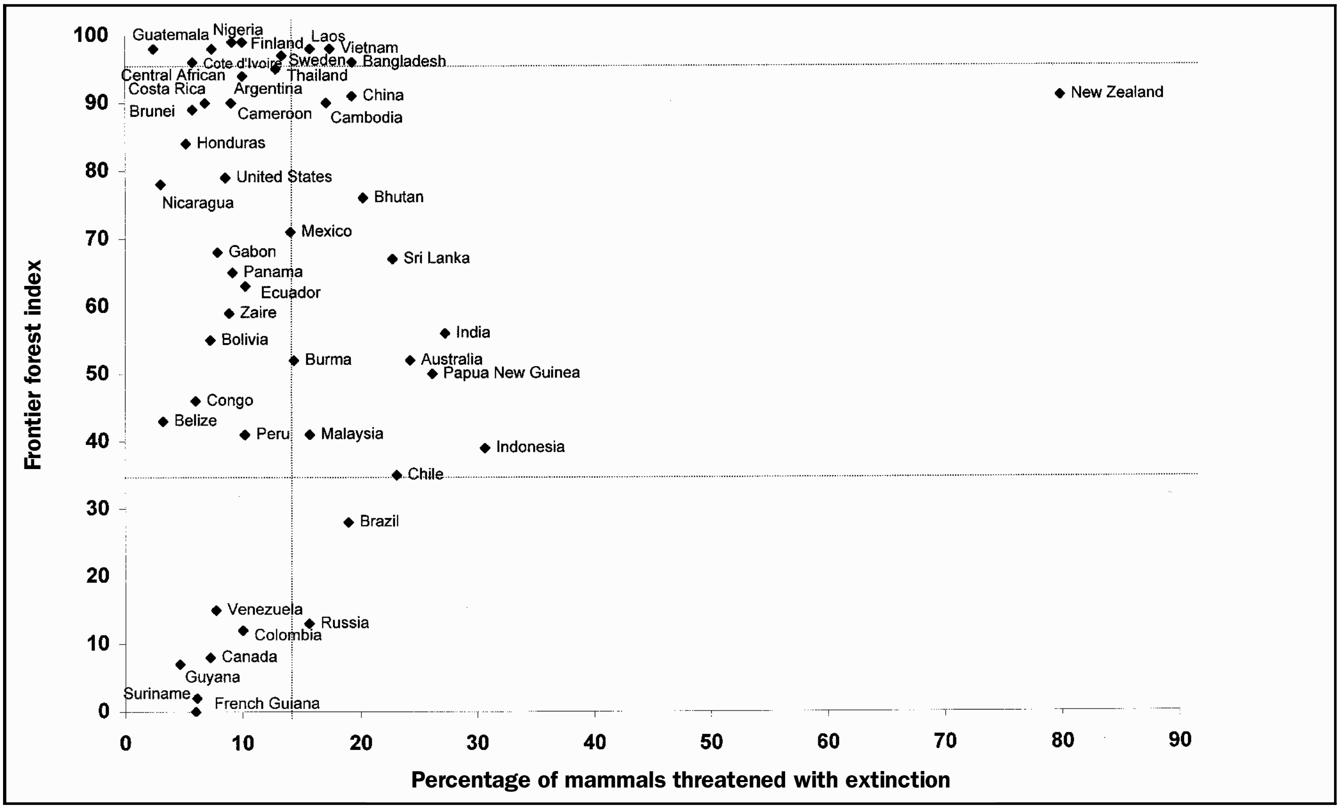

Figure 2. Plot of the frontier forest index (FFI) against the percentage of mammal species that are threatened with extinction (number of threatened versus the total number of mammal species in the respective country) for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on the total number of mammal species are from UNDP and others (2000) for all countries except Brunei and French Guiana, the data for which are from WRI (1994). Data on the number of threatened mammal species are based on mammal species that are listed under the IUCN criteria of critically endangered, endangered, and vulnerable for each country (IUCN 2000) (which excludes Taiwan,* n *= 46). Vertical dotted line represents the global mean percentage of threatened mammal species, 14.5%,* n *= 154. The global mean of the percentage of threatened mammal species was calculated by averaging across all countries in the world that have available data.

model is appealing because it provides a justifiable and reasonable basis for determining the amount of relatively undisturbed forests that can be protected, as long as the world eventually achieves a consensus on the proportion of natural habitat to be maintained at equilibrium.

Much research is urgently required to determine the amount of forest that the world needs to protect. The frontier forest concept does little to address this situation, but it amplifies this need.

How large should a forest worthy of conservation be?

This issue centers on whether large tracts of pristine and relatively undisturbed forests are biologically more important than are smaller remnants of the same forest type.

Use of umbrella species. One measure used to identify relatively undisturbed forests that may be deemed worthy of conservation is whether the size of the forest will allow it to sustain wide-ranging umbrella species (e.g., brown bears *[Ursus arctos]* or spotted owls *[Strix occidentalis])*. The justification for using this measure is that by protecting forest areas large enough to accommodate these umbrella species, the protection of a higher number of indigenous species will automatically follow (Bryant et al. 1997). This idea is appealing to land managers because such umbrella species serve as coarse filters for the ecosystem, thereby reducing the need to consider the habitat requirements of all species in the community. However, the use of umbrella species does not guarantee that all species in the community will automatically fall under the umbrella. Although use of the concept of umbrella species may appear to conserve large tracts of habitat, often the microhabitat requirements of the umbrella species do not coincide with the requirements of other endangered species within the community (Simberloff 1998).

A good example is the case of the spotted owl in the Pacific Northwest of the United States. It was hoped that by conserving the spotted owl, which requires approximately 800 hectares (ha) of old-growth forest per pair (Forsman et al. 1984), a large suite of species would also be saved. While this appears to be true, many species that occur in old-growth forest are not dependent on or closely associated with old-

Table 3. Socioeconomic indicators for countries identified as having frontier forests.

Country	Percentage of forests in protected areas	GNP per capita (US $)	Annual rate of population growth, 1995–2000 (percentage)
Countries that risk losing their remaining frontier forest, unless they act immediately			
Nigeria	7	239	2.4
Finland	7	26,020	0.3
Vietnam	6	299	1.6
Laos	20	414	2.6
Guatemala	35	1481	2.7
Côte d'Ivoire	10	727	1.8
Taiwan	NA	NA	NA
Sweden	8	25,685	0.2
Bangladesh	14	352	1.7
Central African Republic	15	341	1.9
Thailand	23	2821	0.9
Countries that will continue to lose their frontier forests without any further conservation action			
Argentina	7	8755	1.3
New Zealand	3	15,233	1.0
China	3	668	0.9
Costa Rica	36	2626	2.5
Cambodia	24	303	2.3
Cameroon	11	587	2.7
Brunei	22	NA	2.2
Honduras	5	723	2.8
United States	40	28,310	0.8
Nicaragua	23	408	2.8
Bhutan	25	406	2.8
Mexico	4	3304	1.6
Gabon	16	3985	2.6
Sri Lanka	18	770	1.0
Panama	35	2993	1.7
Ecuador	20	1531	2.0
Democratic Republic of the Congo (formerly Zaire)	9	114	2.6
India	8	392	1.7
Bolivia	31	912	2.4
Burma	5	NA	1.2
Australia	13	19,689	1.0
Papua New Guinea	9	931	2.2
Congo	14	633	2.8
Belize	37	2547	2.4
Malaysia	9	4469	2.0
Peru	10	2580	1.7
Indonesia	16	1096	1.4
Chile	14	4478	1.4
Countries that have a real chance, with careful forest stewardship, of keeping most of their frontier forests			
Brazil	17	4514	1.3
Venezuela	66	3499	2.0
Russia	3	2235	–0.2
Colombia	24	2039	1.9
Canada	5	19,267	1.0
Guyana	1	766	0.7
Suriname	4	940	0.4
French Guiana	7	NA	4.3

NA, not available.

Source: Data on the percentages of forests in protected areas, GNP per capita, and annual rate of population growth are from FAO (2001).

growth forests, as is the spotted owl. Ruggiero and colleagues (1991) classified a total of 198 species: 47 fungi species, 47 vascular plant species, 61 bird species, 25 mammal species, and 18 amphibian and reptile species, in terms of their association with old-growth forests in various regions of the Pacific Northwest. Of these 198 species, only 15 were closely associated with old-growth (i.e., significantly more abundant in numbers in old-growth as compared with other seral stages), and another 39 were deemed to be associated with old-growth forests (i.e., numerically but not significantly more

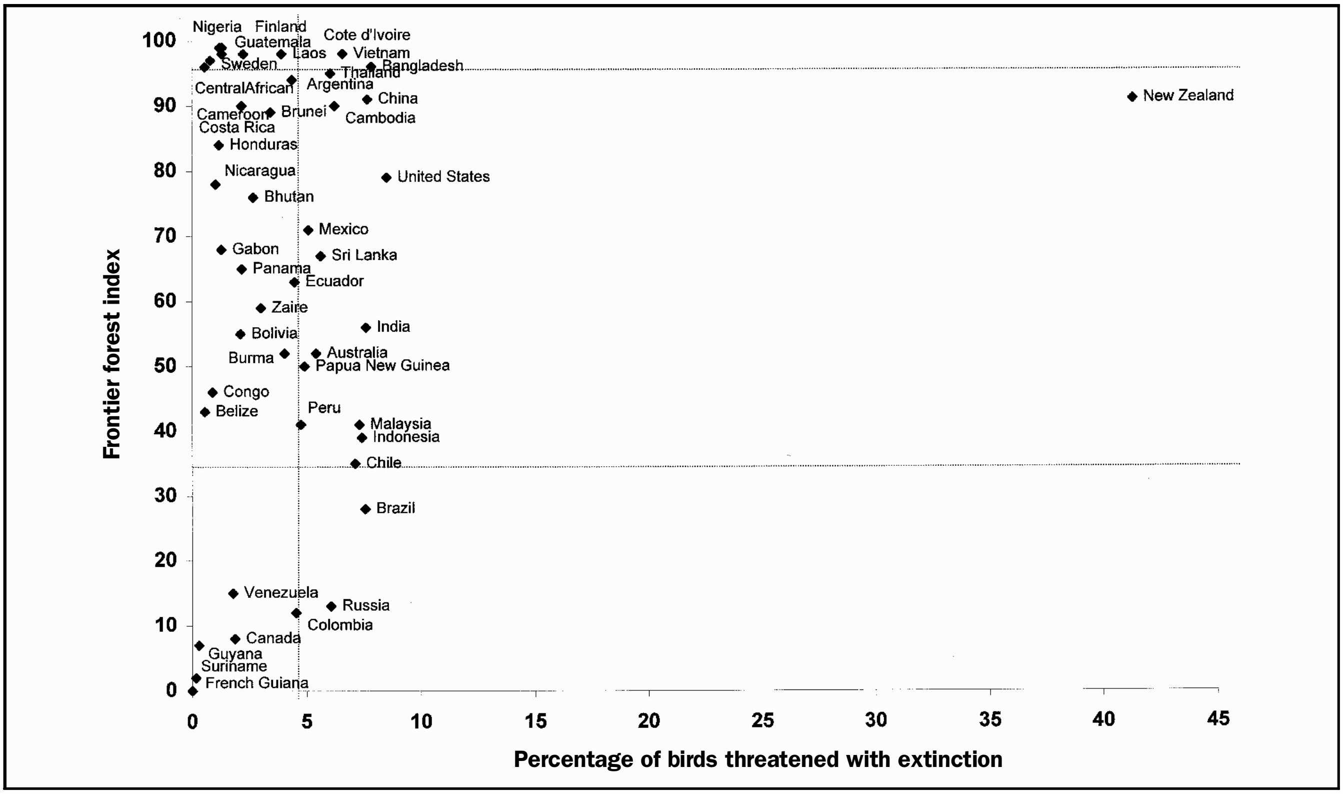

Figure 3. Plot of the frontier forest index (FFI) against the percentage of bird species that are threatened with extinction (number of threatened versus the total number of bird species in the respective country) for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on the total number of bird species are from UNDP and others (2000) for all countries except Brunei, Bolivia, and French Guiana, the data for which are from WRI (1994). Data on the number of threatened bird species are based on bird species listed under the IUCN criteria of critically endangered, endangered, and vulnerable for each country (IUCN 2000) (which excludes Taiwan, $n = 46$). Vertical dotted line represents the global mean percentage of threatened bird species, 4.6%, $n = 149$. The global mean of the percentage of threatened bird species was calculated by averaging across all countries in the world that have available data.

abundant in old-growth as compared with other seral stages). In contrast, 129 species were found in lower abundance in old-growth, as compared with the other seral stages. In a more extensive review of species that are dependent on old-growth forests in the Pacific Northwest, Thomas and colleagues (1993) found that 312 of 700 plant species, 149 of hundreds of invertebrate species, 112 of 214 stocks of anadromous salmonids, 4 resident fish species, and 90 of 224 terrestrial vertebrate species were closely associated with old-growth forests.

The use of the frontier forest criterion to prioritize forest for conservation may not necessarily result in the conservation of all species threatened with extinction if the concept of umbrella species is used to delineate the size of a natural forest worthy of conservation. We suggest that the umbrella concept be broadened to include a suite of focal species, each of which is used to define spatial and compositional attributes that must be present in the landscape (Lambeck 1997). Emphasis should be given to conserving species that are closely linked to the functioning of the ecosystem (Folke et al. 1996).

Extent of natural disturbance as a determinant.

Pickett and Thompson (1976) first highlighted the need to consider the ability of a habitat patch to buffer the effects of natural disturbance within the patch so that extinction rates would be minimized. This idea has been well received and is often incorporated into the design of reserves. This is also another measure of the frontier forest criterion to delineate the size of a natural forest that is worthy of conservation. While Pickett and Thompson (1976) perceived this buffering effect as important, they also put forth two cautions in the application of the idea. The first pertains to knowledge of the size and timing of rare, extensive disturbance events, and the second pertains to the fact that disturbance regimes will differ among regions as a function of climate, geomorphology, and biota. Even within the same region, this can differ, depending on the terrain and isolation by water. For example, in the boreal region of Canada, large fires (over 400 ha) were found to be regular, and fires exceeding 100,000 ha were occasional in flat and unbroken expanses of forest, compared with the much smaller fires in mountainous terrain and in places that

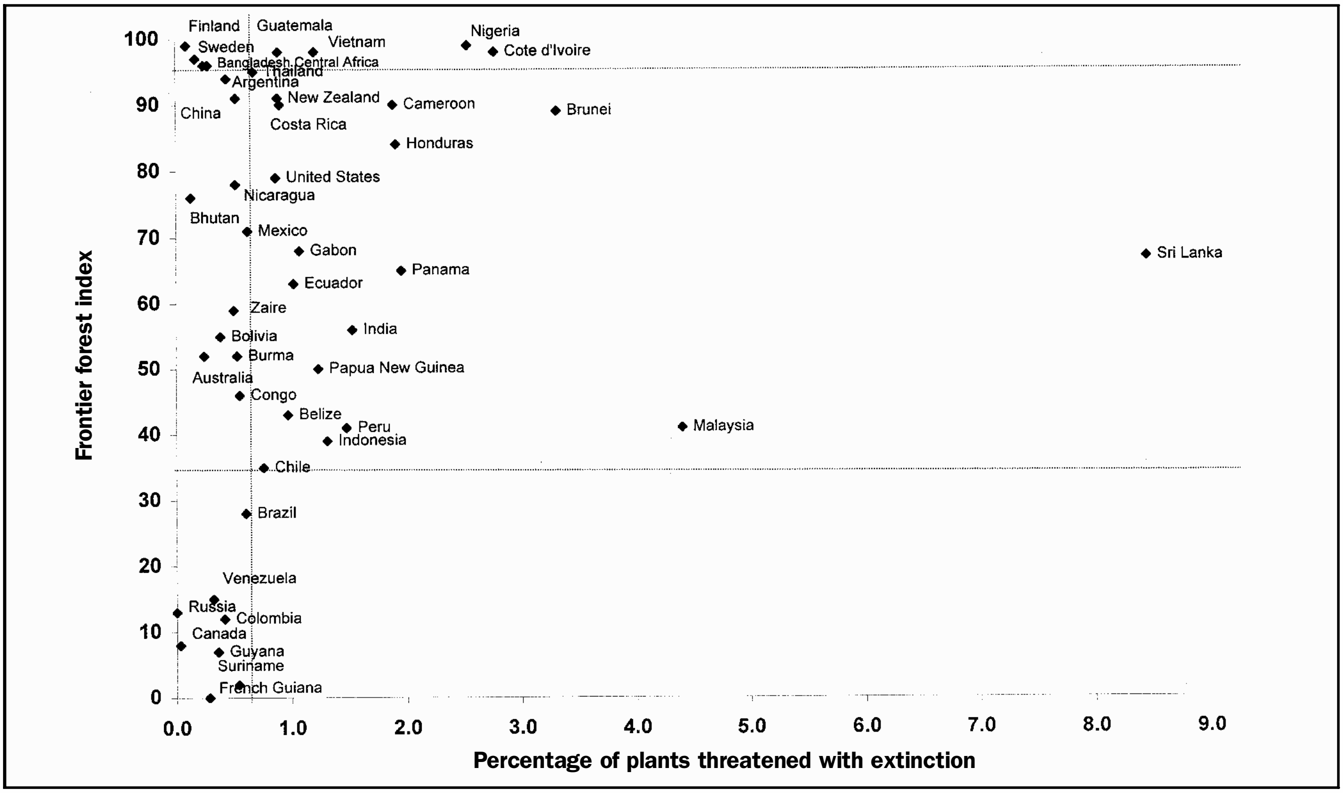

Figure 4. Plot of the frontier forest index (FFI) against the percentage of higher plant species that are threatened with extinction (number of threatened versus the total number of higher plant species in the respective country)for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on the total number of higher plant species are from UNDP and others (2000) for all countries except Brunei and French Guiana, the data for which are from WRI (1994). Data on the number of threatened higher plant species are based on plant species listed under the IUCN criteria of critically endangered, endangered, and vulnerable for each country (IUCN 2000) (which excludes Taiwan, Laos, and Cambodia, n = 44). Vertical dotted line represents the global mean percentage of threatened higher plant species, 0.673%, n = 143. The global mean of the percentage of threatened higher plant species was calculated by averaging across all countries in the world that have available data.

are bounded by water (Kilgore 1981, Foster 1983). Recent use of spatially explicit and stochastic simulation models of fire disturbance in the forest landscape of the state of Wisconsin showed that the probabilities of more severe fires can also change as the landscape ages (He and Mladenoff 1999). Given the spatial and temporal variation, it is difficult to determine what size forest is required to buffer a natural disturbance.

More important, the upper limit of the size of forest required to buffer natural disturbances may be extremely large (e.g., approximately 10,000 ha or more for boreal forests). It may not be feasible to find a forest of such size in highly fragmented landscapes. In such a scenario, it may be better to have several forest patches of smaller areas extending within the same landscape, so that some insurance against the effects of natural disturbance can be secured. If the frontier forest criterion were applied strictly in terms of the size of the forest required to buffer the rare or occasional large-scale natural disturbance, it would be inevitable that the criterion would be strongly biased toward forests that still occur in large tracts. The value of smaller remnants of natural forests would be ignored. As few countries in the world have large tracts of relatively natural forest, this criterion is of limited utility in many countries.

Role of small forest remnants. Although not specifically part of the frontier forest criterion, it is generally accepted that between two patches of forest in a fragmented landscape, the larger patch would have higher species richness because of a lower extinction rate and higher habitat diversity and less exposure to edge effects in terms of microclimatic changes and increased predation (Saunders et al. 1991). It is with these reasons that many forest conservation plans emphasize the importance of conserving large tracts or patches of forest, at the expense of the smaller forest patches.

In recent years, some authors have argued that remnants of forest as small as 150 ha may still contain a high number of species and that the time lag between forest loss and extinction in these remnants may be longer than previously thought. For example, the tropical rain forest in Bukit Timah Nature Reserve in Singapore, which is about 164 ha in size and

Table 4. Global ranks accorded to species by the Network of Natural Heritage Programs and Conservation Data Centers, indicating their conservation status and urgency for conservation or management actions.

Global rank	Definition
G1	Critically imperiled (typically 5 or fewer occurrences or 1000 or fewer individuals)
G2	Imperiled (typically 6 to 20 occurrences or 1000 to 3000 individuals)
G3	Vulnerable; rare or uncommon but not imperiled (typically 21 to 100 occurrences or 3000 to 10,000 individuals)
G4	Apparently secure; uncommon but not rare, with some cause for long-term concern (usually more than 100 occurrences and 10,000 individuals)
G5	Demonstrably secure; common, widespread, and abundant
GH	Of historical occurrence (possibly extinct, still searching with the expectation that it may be rediscovered)
GX	Presumed extinct throughout the range
G#–G#	Range of ranks, insufficient information to rank more precisely
G?	Not yet ranked

Note: By "occurrence," the Natural Heritage Network is referring to all of the individuals in a species at a particular site.

has been isolated for about 200 years, still maintains a distinct primary rain forest structure and plant species composition (Turner and Corlett 1996). While studying birds in tropical rain forest remnants in Kenya, Brooks and colleagues (1999) showed that remnants of approximately 1000 ha in size would most likely suffer half the total number of forest bird extinctions within the first 50 years after isolation. This lends support to the suggestion that small tropical rain forest remnants can retain a relatively large proportion of their biodiversity after decades of isolation.

In a review of the current knowledge on the effects of fragmentation on biodiversity, especially the effect of area on species richness, Zuidema and colleagues (1996) pointed out that much of what we know is based mainly on studies in small forest fragments (i.e., less than 10 ha in size). They argued that such studies cannot be extrapolated to larger-sized, protected forests and do not therefore necessarily support the case for large, protected forest reserves. More recently, a review of 20 long-term fragmentation studies (those studies lasting longer than 3 years) showed that not all of the studies found that species richness increased with increasing fragment size. The observed species–area relationship may depend on the taxon and spatial scale under consideration and may also be influenced by edge effects and interspecies interactions in the habitat fragments (Debinski and Holt 2000). Developments in spatially realistic metapopulation models have indicated just how complex such relationships are (Hanski and Simberloff 1997).

The relevance of this observed species–area relationship is that the frontier forest criterion appears to be highly biased toward large, continuous tracts of forests. Such a criterion may have limited utility in landscapes that are highly fragmented.

Interactions between frontier forests and socioeconomic factors

Using the frontier forest index, Bryant and colleagues (1997) identified 47 countries where frontier forests are still present (see table 1). They further ranked the countries according to the risk they ran of losing all their frontier forests and by conservation priority (i.e., countries with high FFI would have the highest risk of losing all their frontier forests and would be of high conservation priority). They identified 11 countries that must act immediately because they are likely to lose most of their frontier forests (FFI ≥ 95). Another 28 countries were identified as having not much time left to protect their remaining frontier forests (FFI ≥ 35 but < 95). Finally, 8 countries, Brazil, Suriname, Guyana, Canada, Colombia, Venezuela, Russia, and French Guiana (an overseas territory of France) were identified as having a chance—with careful forest stewardship—of retaining most of their frontier forest (FFI < 35).

Two questions are of interest, if countries with high FFI are to be accorded greater conservation priority and the goal of conservation is to maintain high biodiversity: Is the ranking of countries on the basis of the FFI consistent with the amount of biodiversity threatened with extinction in these countries? Is the use of the FFI to prioritize the conservation of forests feasible in view of the varying socioeconomic factors in these countries?

Matching the frontier forest index with biodiversity indicators. Two indicators can approximate the amount of biodiversity threatened with extinction: the annual rate of change in forest cover over time (decadal scale) and the percentage of threatened mammal, bird, and higher plant species in these countries. Data used to calculate these indicators were obtained from WRI (1994), UNDP and others (2000), and FAO (2001) for the period 1990–2000. Data on the number of bird, mammal, and higher plant species threatened with extinction in each of these countries came from IUCN (2000); threatened species—those categorized as critically endangered, endangered, or vulnerable—are expressed as percentages of the total number of species in each taxon (see table 2). In all figures and tables, it should be noted that the data for some

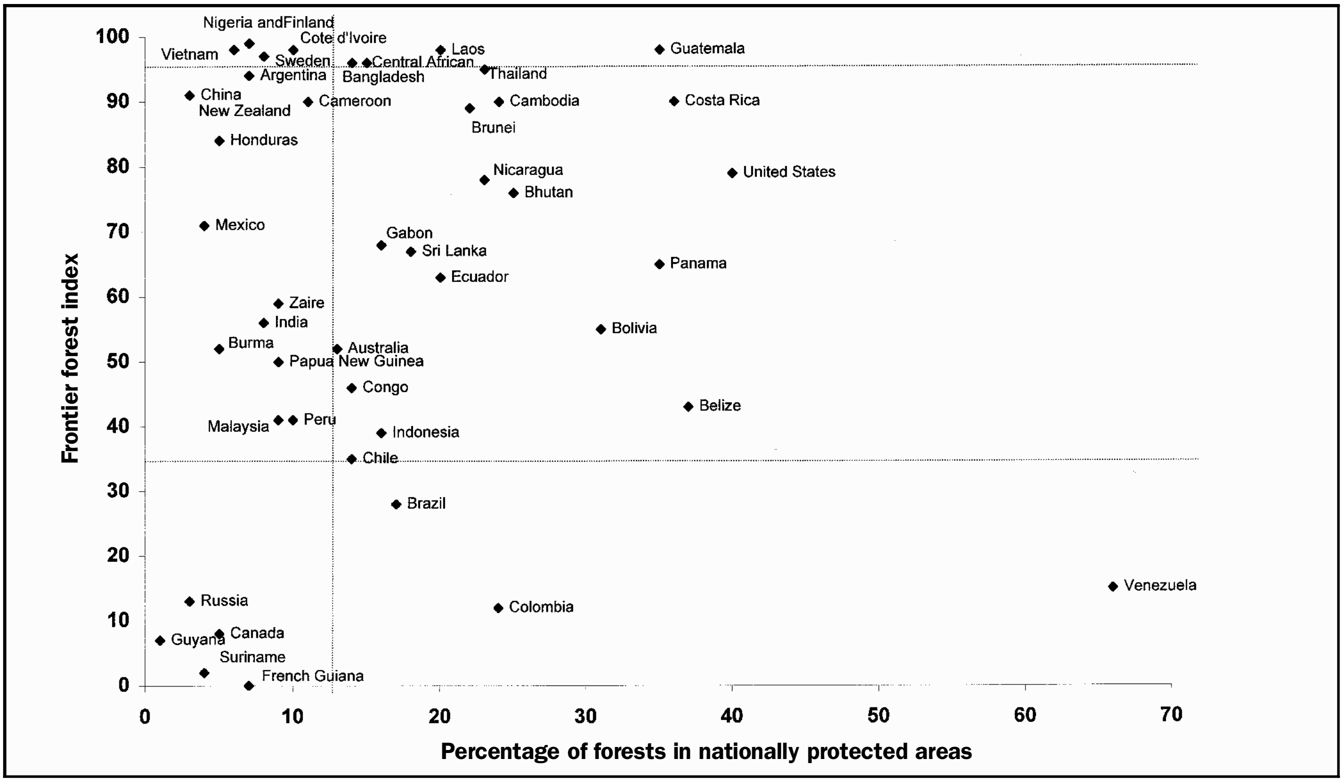

Figure 5. Plot of the frontier forest index (FFI) against the percentage of forests in nationally protected areas for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on forests in protected areas are from FAO (2001) (which excludes Taiwan, n *= 46). Vertical dotted line represents the global mean percentage of forests in protected areas, 12.6%,* n *= 165. The global mean of the percentage of forest currently under protection was calculated by averaging across all countries in the world that have available data.*

countries are more reliable than data for others. Global means of the annual rate of forest cover change and the percentage of threatened species in each taxon were calculated by averaging across all countries that have available data (mean annual rate of forest cover change = –0.127%, $n = 203$; mean percentage of threatened mammal species = 14.5%, $n = 154$; mean percentage of threatened bird species = 4.6%, $n = 149$; mean percentage of threatened higher plant species = 0.673%, $n = 143$). The FFI was plotted separately against the annual rate of change of forest cover and the percentages of threatened mammal, bird, and higher plant species for countries where frontier forests are present (figures 1 through 4, respectively).

Conservation priorities attached to countries on the basis of FFI were not entirely consistent with the annual rate of change in forest cover in these countries. Not all countries with high FFI (≥ 95) had high negative rates of change of forest cover. The annual rate of change in forest cover ranged from –3.1% to 1.3%, with 5 of the 10 countries having rates lower than the global mean. Similarly, there was no appreciable trend for countries with moderate FFI (FFI ≥ 35 but < 95). The annual rate of change in forest cover ranged from –1.6% to 1.2%, with 17 of 28 countries having rates lower than the global mean. Countries that had low FFI (< 35) also did not have high positive annual rates of change in forest cover, as would have been expected if low FFI represents lower risk of losing frontier forests and lower conservation priority. In fact, they had rates less than or equal to 0%, with 4 of the 8 countries having rates lower than the global mean (figure 1). An important observation was that the range in the annual rate of change in forest cover (i.e., spread) was larger across countries with high FFI than in countries with low FFI. This suggests that the deforestation situation in countries that still have larger amounts of frontier forests is more stable than in countries that have very little frontier forests left. In this respect, the FFI may be of some utility in conservation planning.

As with the change in forest cover, the trends in the percentages of mammal, bird, and higher plant species that are threatened with extinction in countries with frontier forests did not appear to be entirely consistent with the conservation priorities established by FFI. The expected trend—countries with high FFI will have higher percentages of these threatened species than will countries with low FFI—was not always observed. Less than half the number of countries with high FFI (≥ 95) had percentages of threatened mammal and bird species greater than the global mean (3 of 10 countries for mammals and 4 of 10 countries for birds). At the same time, 6 of 8 countries with low FFI (< 35) had percentages of threatened mammals and bird species below the global mean (figures 2 and 3). The trends for higher plant species did not

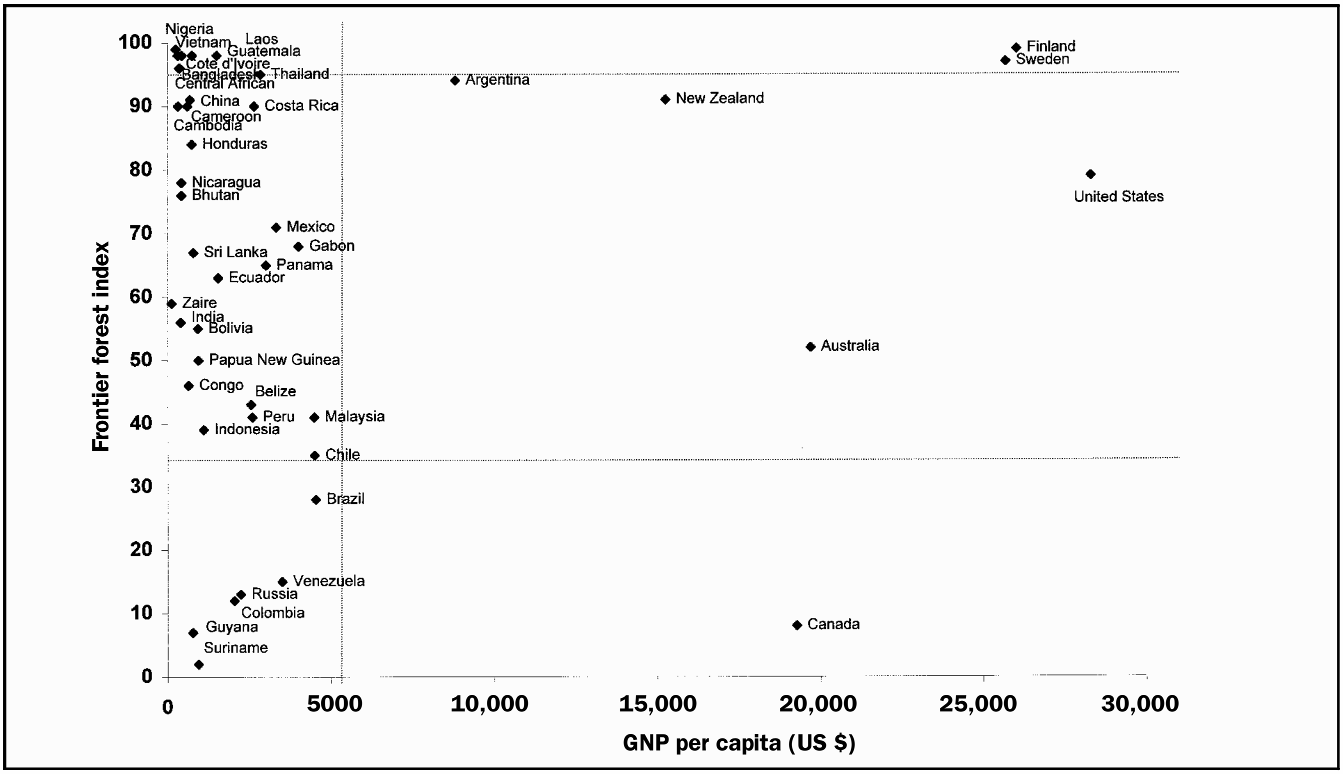

Figure 6. Plot of the frontier forest index (FFI) against GNP per capita (US dollars) for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on GNP per capita are from FAO (2001) (which excludes Taiwan, Brunei, Burma, and French Guiana,* n *= 43). Vertical dotted line represents the global mean GNP per capita, $5226,* n *= 159. The global mean of GNP per capita was calculated by averaging across all countries in the world that have available data.

differ considerably from those of mammal and bird species. However, a higher percentage of countries with high FFI (≥ 95) had percentages of threatened higher plant species that exceeded the global mean (5 of 9 countries), and all countries with low FFI (< 35) had percentages of threatened higher plant species less than the global mean (figure 4). It appears that the amount of frontier forests may be reflective of the percentages of mammal, bird, and higher plant species that are threatened with extinction only in countries where there are large tracts of frontier forests.

Matching the frontier forest index with socioeconomic indicators. It is important to place forest conservation needs within the context of population pressure and other anthropogenic forces (Sisk et al. 1994). The socioeconomic conditions of countries were approximated by the percentage of forest in protected areas, the GNP per capita, and the annual rate of population growth. Information on these indicators was obtained from FAO (2001) for countries that were identified as having frontier forests (table 3). Global means were also calculated for these variables by averaging across all countries in the world with available data (mean percentage of forest currently under protection = 12.6%, $n = 165$; mean GNP per capita = $5226, $n = 159$; mean annual rate of population growth = 1.6%, $n = 212$). The FFI was then plotted separately against the percentage of forest in protected areas, the GNP per capita, and annual rate of population growth for countries where frontier forests are present (figures 5, 6, and 7).

The results revealed that the percentage of forest in protected areas exceeded the global mean in approximately half or more of the countries with high and moderate FFI (5 of 10 countries with FFI ≥ 95 and 16 of 28 countries with FFI ≥ 35 but < 95). On the other hand, only 3 of 8 countries with low FFI (< 35) had exceeded the global mean in terms of the percentage of forest in protected areas (figure 5). Contrary to the priority ranking based on FFI, the percentage of forests in protected areas suggests that there is a greater need for conservation of forests in countries with low FFI than in countries with high FFI.

Even more startling is the fact that more than three-quarters of the countries with frontier forests had GNP per capita less than the global mean (36 of 43 countries), and slightly more than half of the countries with frontier forests had annual rates of population growth that were greater than the global mean (27 of 46 countries) (figures 6 and 7). This suggests that a global forest conservation prioritization initiative based wholly on the frontier forest criterion will be met with difficulties in terms of socioeconomic issues and the political expediency of implementation.

This simple analysis echoes the view of many other authors who have emphasized the importance of considering the

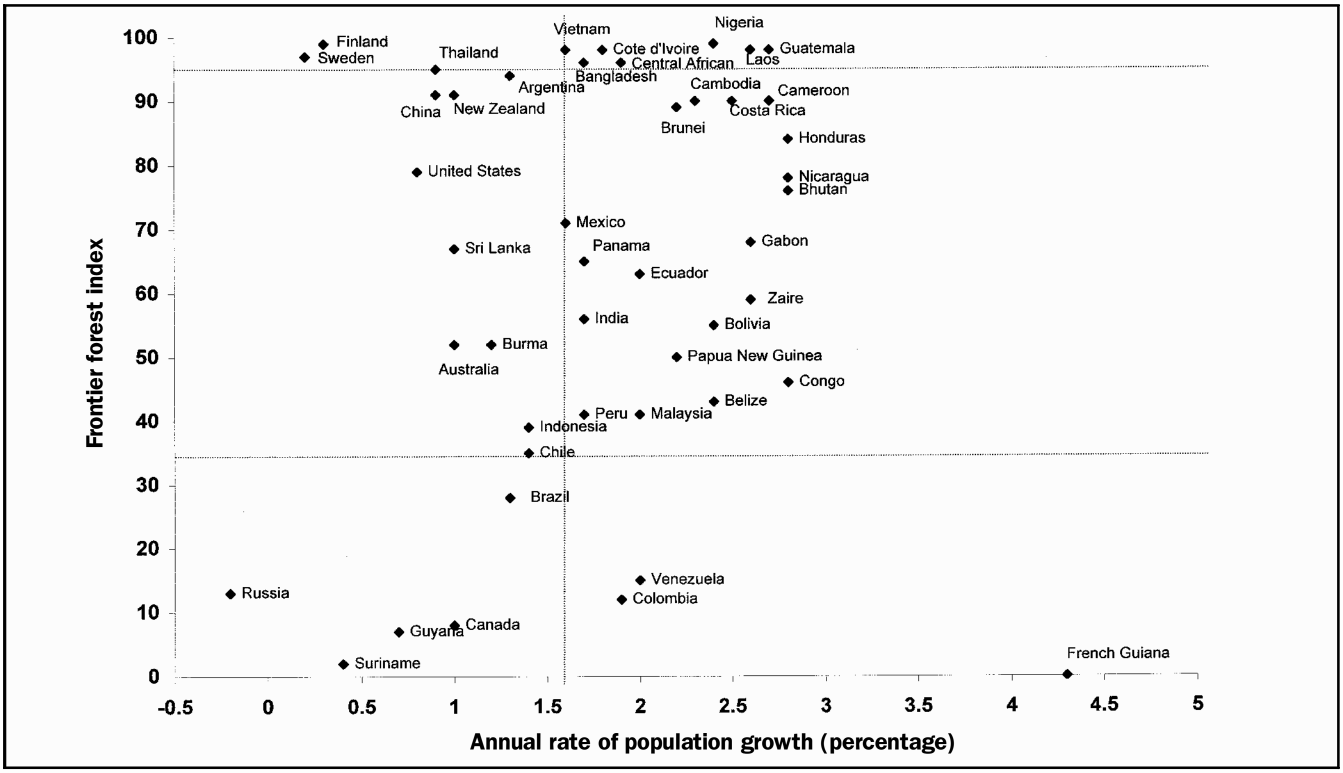

Figure 7. Plot of the frontier forest index (FFI) against the annual rate of percentage population change (1995–2000) for countries that have frontier forests. FFI data are from Bryant and colleagues (1997). Data on population change are from FAO (2001) (which excludes Taiwan, n = 46). Vertical dotted line represents the global mean annual rate of population change, 1.6%, n = 212. The global mean of the annual rate of population change was calculated by averaging across all countries in the world that have available data.

socioeconomic context when prioritizing the conservation of forests on a global scale (Dinerstein and Wikramanayake 1993, Sisk et al. 1994, Myers 1998). Both the frontier forest concept and the resultant frontier forest index are deficient in this respect. Full success in prioritizing forest conservation on a global scale cannot be achieved through such a criterion alone.

Where do we go from here?

Any scheme that attempts to prioritize the conservation of forests must first and foremost determine whether a forest type or community is truly endangered. The mapping and development of terrestrial ecoregions that accurately reflect the past and present distributions of natural communities at global and regional scales is a first step in this direction (WCMC 1997, Olson et al. 2001). This should be followed by the development of indicators of endangerment, which are specific to forests. Noss and colleagues (1995) assessed the endangerment of ecosystems in the United States according to the extent of decline in the ecosystem's historical distribution (i.e., areal loss) and the level of ecological degradation. In addition, the authors highlighted the need to determine the relative risks of further decline of or losses to an ecosystem. They further suggested that the current framework used by the US Fish and Wildlife Service to identify and prioritize the conservation and recovery of endangered species in the United States be adapted for endangered ecosystems.

In a similar vein, a biodiversity element ranking system was developed and has been used for more than 10 years by the network of Natural Heritage Programs and Conservation Data Centers to identify and prioritize the conservation of endangered species in the United States, Canada, and Latin America (Master 1991). Species are assessed according to the indicators of habitat specificity (estimated number, quality, and condition of occurrences), local population size (estimated number of individuals), geographic range (restriction of range and habitat), trends of decline (in populations and habitat), immediate threats (including human activities and protection, as well as socioeconomic and political factors), and fragility. On the basis of these indicators, species are accorded a global rank that will indicate the conservation status and urgency for conservation or management actions (table 4; Master 1991). We propose that this existing biodiversity element ranking system and indicators used to identify and prioritize the conservation of endangered species be adapted and developed for use with forest ecosystems.

The use of an analogous ranking system for elements of biodiversity and indicators to assess the endangerment of forest ecosystems is attractive, because forest ecosystems could be ranked not only according to the extent of decline but also according to the existing condition of the forest, as well as the amount of forest in protection. Moreover, such a system would address rarity, an indicator that is distinguishable according to geographic range at regional and global scales. More important, this system would be flexible to allow for adaptation and modification to meet the requirements for assessing the endangerment of forest ecosystems. The indicators could be ranked in accordance to their relative importance in identifying endangered forest ecosystems. Immediate threats to the forest ecosystem, which include human activities (e.g., logging or clearing of land for agriculture) and underlying socioeconomic and political factors that may hinder conservation (e.g., political strife and civil war, population growth, economic debt, and poverty) could also be identified. The need to understand and resolve many of the underlying socioeconomic and political problems affecting many developing countries and local communities is key to the successful conservation of forest ecosystems.

Conclusion

Although the intentions behind the frontier forest concept are good in that they reflect concerns about continuing high rates of deforestation worldwide, the use of this concept to develop a prioritization scheme for the conservation of forests is unrealistic. The frontier forest criterion considers only the conservation of forests that are relatively undisturbed, but it falls short of defining the acceptance level of human disturbance. It also does not address the problem of determining the amount of forest to protect and is biased toward large tracts of forests. Although the latter may be ecologically justifiable, it is of little relevance in many parts of the world where forest landscapes are highly fragmented. A prioritization scheme resulting from the frontier forest concept does not reflect the status of forest cover change, biodiversity loss, and socioeconomic conditions in the countries identified as having frontier forests. Taking these deficiencies into consideration, we propose that the existing biodiversity element ranking system and indicators used by the Network of Natural Heritage Programs and Conservation Data Centers to identify and prioritize the conservation of endangered species in the United States, Canada, and Latin America be adapted and developed for use with forest ecosystems. This measure, coupled with existing efforts to map the past and present distributions of forest ecosystems, will facilitate the identification of forests that are truly endangered.

Acknowledgments

We are grateful to Victor Teplyakov, Jeff Sayer, and two anonymous referees for comments on an earlier version of this manuscript. While working on this article, Kenneth Er was supported by a Canadian Commonwealth Scholarship and granted study leave by the National Parks Board of Singapore.

References cited

Abbott I. 1984. Comparisons of spatial pattern, structure and tree composition between virgin and cut-over jarrah forest in Western Australia. Forest Ecology and Management 9: 101–126.

Attiwill PM. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. Forest Ecology and Management 63: 247–300.

Botkin DB. 1990. Discordant Harmonies. New York: Oxford University Press.

Boyle TJB, Sayer JA. 1995. Measuring, monitoring and conserving biodiversity in managed tropical forests. Commonwealth Forestry Review 74: 20–25.

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

Bryant D, Nielsen D, Tangley L. 1997. The Last Frontier Forests: Ecosystems and Economies on the Edge. Washington (DC): World Resources Institute.

Buschbacher R, Uhl C, Serrao EAS. 1988. Abandoned pastures in eastern Amazonia, II: Nutrient stocks in the soil and vegetation. Journal of Ecology 76: 682–699.

Cairns J. 1993. Ecological restoration: Replenishing our national and global ecological capital. Pages 193–208 in Saunders DA, Hobbs RJ, Ehrlich PR, eds. Nature Conservation 3: Reconstruction of Fragmented Ecosystems. Chipping Norton (Australia): Surrey Beatty and Sons.

Clements FE. 1936. Nature and structure of the climax. Journal of Ecology 24: 252–284.

Debinski DM, Holt RD. 2000. A survey and overview of habitat fragmentation. Conservation Biology 14: 342–355.

Dinerstein E, Wikramanayake ED. 1993. Beyond "hotspots": How to prioritize investments to conserve biodiversity in the Indo-Pacific region. Conservation Biology 7: 53–65.

Ehrlich PR, Ehrlich AE. 1992. The value of biodiversity. Ambio 21: 219–226.

[FAO] Food and Agriculture Organization of the United Nations. 2001. Global Forest Resources Assessment 2000. (11 October 2002; *www.fao.org/forestry/fo/fra/main)*

Folke C, Holling CS, Perrings C. 1996. Biological diversity, ecosystems and the human scale. Ecological Applications 6: 1018–1024.

Forsman ED, Meslow EC, Wright HM. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs 87: 1–64.

Foster DR. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Canadian Journal of Botany 61: 2459–2471.

Gentry AH. 1992. Tropical forest biodiversity: Distribution patterns. Oikos 63: 19–28.

Hanski IA, Simberloff D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in Hanski IA, Gilpin ME, eds. Metapopulation Biology: Ecology, Genetics, and Evolution. San Diego: Academic Press.

He HS, Mladenoff DJ. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology 80: 81–99.

Hobbs RJ, Norton DA. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4: 93–110.

[IUCN] International Union for Conservation of Nature and Natural Resources. 2000. The 2000 IUCN Red List of Threatened Species. Gland (Switzerland): IUCN.

Kilgore BM. 1981. Fire in ecosystem distribution and structure: Western forests and scrublands. Pages 58–89 in Mooney HA, Bonnicksen TM, Christensen NL, Lotan JF, Reiners WA, eds. Fire Regimes and Ecosystem Properties. Washington (DC): US Department of Agriculture, Forest Service. General Technical Report WO-26.

Lambeck RJ. 1997. Focal species: A multi-species umbrella for nature conservation. Conservation Biology 11: 849–856.

Lindenmayer DB, Norton TW, Tanton MT. 1990. Differences between wildfire and clearfelling on the structure of montane ash forests of Victoria and their implications for fauna dependent on tree hollows. Australian Forestry 53: 61–68.

Margules CR, Nicholls AO, Pressey RL. 1988. Selecting networks of reserves to maximise biological diversity. Biological Conservation 43: 63–76.

Master LL. 1991. Assessing threats and setting priorities for conservation. Conservation Biology 5: 559–563.

McNeely JA, Miller KR. 1983. National Parks and Protected Areas. Bangkok (Thailand): United Nations Economic and Social Commission for Asia and the Pacific.

Mittermeier RA, Myers N, Thomsen JB, da Fonseca GAB, Olivieri S. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conservation Biology 12: 516–520.

Myers N. 1988. Threatened biotas: "Hotspots" in tropical forests. The Environmentalist 8: 178–208.

Myers N. 1998. Global biodiversity priorities and expanded conservation policies. Pages 273–285 in Mace GM, Balmford A, Ginsberg JR, eds. Conservation in a Changing World. Cambridge (United Kingdom): Cambridge University Press.

Noss RF, LaRoe ET III, Scott JM. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Washington (DC): US Department of the Interior, National Biological Service. Biological Report 28.

Olson DM, Dinerstein E. 1998. The Global 200: A representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology 12: 502–515.

Olson DM, et al. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. BioScience 51: 933–938.

Pickett STA, Thompson JN. 1976. Patch dynamics and the design of nature reserves. Biological Conservation 13: 27–37.

Ruggiero LF, Jones LC, Aubry KB. 1991. Plant and animal habitat associations in Douglas-fir forests of the Pacific Northwest: An overview. Pages 447– 462 in Ruggiero LF, Aubry KB, Carey AB, Huff MH, eds. Wildlife and Vegetation of Unmanaged Douglas-fir Forests. Portland (OR): US Department of Agriculture, Forest Service. General Technical Report PNW-GTR-285.

Saettersdal M, Line JM, Birks HJB. 1993. How to maximize biological diversity in nature reserve selection: Vascular plants and breeding birds in deciduous woodlands, western Norway. Biological Conservation 66: 131–138.

Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5: 18–32.

Simberloff D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation 83: 247–257.

Sinclair ARE, Hik DS, Schmitz OJ, Scudder GGE, Turpin DH, Larter NC. 1995. Biodiversity and the need for habitat renewal. Ecological Applications 5: 579–587.

Sisk TD, Launer AE, Switky KR, Ehrlich PR. 1994. Identifying extinction threats: Global analyses of the distribution of biodiversity and the expansion of the human enterprise. BioScience 44: 592–604.

Soulé ME, Sanjayan MA. 1998. Conservation targets: Do they help. Science 279: 2060–2061.

Spence JR, Volney WJA. 1999. EMEND. Ecosystem Management Emulating Natural Disturbance. Edmonton, Alberta (Canada): Sustainable Forest Management Network. Project Report 1999-14. (11 October 2002; *http://sfm-1.biology.ualberta.ca/english/pubs/PDF/PR_1999-14.pdf*)

Thomas JW, Raphael MG, Anthony RG, Forsman ED, Gunderson AG, Holthausen RS, Marcot BG, Reeves GH, Sedell JR, Solis DM. 1993. Viability Assessments and Management Considerations for Species Associated with Late-Successional and Old-Growth Forests of the Pacific Northwest. Portland (Oregon): US Department of Agriculture, Forest Service.

Turner IM, Corlett RT. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology and Evolution 11: 330–333.

Uhl C. 1987. Factors controlling succession following slash-and-burn agriculture in the Amazon. Journal of Ecology 75: 377–407.

Uhl C, Buschbacher R, Serrao EAS. 1988. Abandoned pastures in eastern Amazonia, I: Patterns of plant succession. Journal of Ecology 76: 663–681.

[UNDP et al.] UN Development Programme, UN Environment Programme, World Bank, World Resources Institute. 2000. World Resources 2000–2001—People and Ecosystems: The Fraying Web of Life. Washington (DC): World Resources Institute.

[WCED] World Commission on Environment and Development. 1987. Our Common Future. Oxford (United Kingdom): Oxford University Press.

[WCMC] UN Environment Programme World Conservation Monitoring Centre, Center for International Forestry Research. 1997. Statistical Analysis of Global Forest Conservation. (11 October 2002; *http://www.wcmc.org.uk/forest/data/cdrom2/stat1.htm/*)

[WRI] World Resources Institute, UN Environment Programme, UN Development Programme. 1994. World Resources 1994–1995. New York: Oxford University Press.

Zuidema PA, Sayer JA, Dijkman W. 1996. Forest fragmentation and biodiversity: The case for intermediate-sized conservation areas. Environmental Conservation 23: 290–297.