HOW BIG IS THE GLOBAL WEED PATCH?[1]

Clinton N. Jenkins[2] *and Stuart L. Pimm*[2,3]

Abstract

Invasive species are a major global threat to both biodiversity and agriculture and thus are a high priority for conservation science. Governments recognize this and are devoting increasing resources toward solving the problem. Even so, there is inadequate information on where invasives occur and thus where society can best use these resources. Disturbed areas tend to be very favorable to invasives, especially the weedy species. We map the world's disturbed areas, the global weed patch, using maps of original and current landcover. At least 29.4 million km^2 (ca. 23%) of the world's ice-free land area is disturbed and thus favorable for invasive species. This weed patch map corresponds well to known locations of some of the world's worst weeds, lending support to our approach. Our results should help in setting geographic priorities for actions against invasive species.

Key words: disturbance, global change, invasive species, landcover, weeds.

Organisms have moved—and been moved—around the planet for millennia, but never in the numbers and with such speed as today. Most are benign, but a dangerous few cause major environmental problems. Invasive species may thrive in their new environment and dramatically change the dynamics and composition of the ecosystem. Because of our lack of vigilance, we now suffer large economic losses in agriculture (Pimentel et al., 2000), suffer disrupted water supply and riverine transport (e.g., zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*), Pimentel et al., 2000), and witness the degradation or even replacement of entire ecosystems (e.g., purple loosestrife (*Lythrum salicaria* L.), Thompson et al., 1987; Pimentel et al., 2000). Growth of the global trade network results in a concomitant growth in the problem, and this is unlikely to change in the near future. As the problem is inherently global, we must develop a global strategy to solve it.

Much invasive species research focuses on identifying characteristics of species that enable them to invade. The idea is to identify who will invade and then restrict their movement around the world. That is certainly a vital approach to solving the problem, but it need not be the only one. This paper takes an alternative approach. We attempt to identify where they will invade rather than who the invaders will be.

Where Do Species Invade?

The simplest answer to this question is "everywhere"! Consider the flora of Britain: It includes *Polygonum amplexicaule* D. Don from the Himalayas, *Dianthus caryophyllus* L. from southern Europe, *Papaver somniferum* L. from western Asia, *Coronopus didymus* (L.) Sm. from South America, *Rubus spectabilis* Pursh from North America, and *Acaena novae-zelandiae* T. Kirk from New Zealand (Blamey & Grey-Wilson, 1989). These examples show that when a flora is well known it is likely to include species from around the world. Britain's species-poor native flora now accommodates a global flora. Species can be introduced from anywhere to anywhere, it would seem. That said, it is clear that some species are more likely to be introduced than others, and some areas are more likely to receive invasive species than others.

Our argument is that disturbed areas are the prime habitats for invasive species. Recognizing the absence of an ideal database, we selected a set of species from the World's Worst Invasive Alien Species list compiled by Lowe et al. (2001) to see if they occur predominantly in disturbed areas. The top three plants, and the number of countries in which they occur, were *Lantana camara* L. [51], *Chromolaena odorata* R. M. King & H. Rob. [38], and *Leucaena leucocephala* (Lam.) de Wit [37].

The counts of countries are a little misleading in

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[2] Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, Tennessee 37996, U.S.A. Present address: 13 Natural Resources, Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824-1222, U.S.A. jenkins@msu.edu.

[3] Nicholas School of the Environment and Earth Sciences, Duke University, Box 90328, Durham, North Carolina 27708, U.S.A. StuartPimm@aol.com.

that they are dominated by small, usually Pacific island nations. Nonetheless, all three species have invaded large areas. *Chromolaena odorata,* native to tropical America and the Caribbean (Holm et al., 1977: 212–216; Holm et al., 1979: 85), invades pastures and croplands in much of tropical Africa and Asia, the Southeast Asian island nations, and Australia. *Lantana camara,* native to Central and South America (Holm et al., 1977: 299–302; Holm et al., 1979: 207), is a widespread invader of pasturelands in Southeast Asia, Australia (where it is a Weed of National Significance), parts of southern Africa and Madagascar, the Mediterranean, and extreme southern parts of the United States. *Leucaena leucocephala* is native to tropical America (Holm et al., 1979: 214; Lowe et al., 2001), but in its nonnative range can form dense, almost monospecific stands that render large areas unusable. Currently it occurs in China, most of the Pacific Rim islands, and Australia.

All three species occur in heavily disturbed areas, as do many other widely distributed invasive species, such as *Mimosa pigra* L., various species of *Opuntia,* and *Ricinus communis* L. Another way to view this problem is to survey disturbed areas. Throughout the tropics, it is our experience that disturbed habitats will have at least one and often several of these listed species. Often they will be common; sometimes they will be the dominant species. Searching for "worst weeds" on the World Wide Web produces a list of repeat offenders that cause economic harm to croplands and pastures. Most are exotics, but not all.

In short, these and other examples suggest that invasive species occur predominantly in disturbed ecosystems. By "disturbed," we mean major ecosystem changes, such as conversion to croplands, grazing lands, urban areas, or anthropogenic ones, such as grasslands where there was once forest.

We will not further belabor this connection between invasive species and human-modified habitats, for it is well-established and not obviously controversial. Rather, we accept the connection and move to the problem of estimating how large a fraction of the Earth's land surface humans have modified. Since invasive species in these disturbed habitats are often deemed to be weeds, we can rephrase our question to: How big is the global weed patch?

We proceed by estimating the size of the weed patch at first global, then regional levels. Globally, the area of disturbed habitats is large. Regionally, we find that our global estimates are too small, for there is much disturbance that they miss. It is not surprising that invasive species are such an ecological problem.

A First Assessment of the Size of the Weed Patch

Global assessments of landcover change provide a series of somewhat overlapping estimates of disturbed habitats. A rough estimate of the size of the weed patch comes from combining the areas of (1) croplands, with (2) degraded grazing lands, and (3) the areas of cleared forests that are not in productive use.

(1) Of the ice-free land surface of about 129 million km^2, croplands cover about 15 million km^2 of the planet. All but 4 million km^2 were converted from naturally wooded or forested ecosystems (Pimm, 2001).

(2) The world's drylands cover roughly 61 million km^2—an estimate that includes deserts, grasslands, shrublands, and savannas. The area varies from author to author depending on what one means by "dry" (Pimm, 2001; Vitousek et al., 1986; Olson et al., 1983).

Most of the world's drylands suffer from desertification—a large portfolio of mostly human-caused problems that depress plant productivity. Some 23 million km^2 of the drylands have damaged vegetation (Dregne, 1986). This often means the spread or increase of unpalatable plant species following overgrazing by cattle, goats, and other livestock (Young & Longland, 1996; Archer, 1994; Bahre & Shelton, 1993; Van Auken, 2000). Those will sometimes be native species. For instance, mesquite (native *Prosopis* spp.) has dramatically increased in density over much of the southwestern United States (Bahre & Shelton, 1993; Archer, 1994; Van Auken, 2000). More often, the weeds will be exotic invasives such as *Opuntia* in Australia and Africa.

(3) Another 40 million km^2 of the land surface has forests or woodlands of one kind or another, another 8 million km^2 are tundras, and the remainder includes wetlands and urban areas (Olson et al., 1983).

The conversion of forests to other habitats is more complicated, since most of the world's croplands were once forests—and so have already been counted above as croplands. Most of the converted forests are in temperate regions. About 2 million km^2 of these forests have also been converted to grazing lands (Pimm, 2001).

Modern human actions have shrunk the world's tropical humid forests from an original area of from 14 to 18 million km^2 to about 7 million km^2 at present (Myers et al., 2000; Pimm, 2001). Again, the exact numbers depend somewhat on what one means by "humid." Yet only about 2 million km^2 of croplands are in what was formerly humid forests. Some 5–9 million km^2 of humid forests have been converted to nominally grazing land, though much of it has very low stocking rates (Pimm, 2001).

Summing these three pieces suggests that 15 million km^2 of present-day croplands, 23 million km^2 of drylands, 2 million km^2 of temperate forest converted to grazing lands, and from 5 to 9 million km^2 of additional forested land not producing crops have sustained sufficient changes to their vegetation to make them target areas for invasive species. The combined total is just under half the ice-free land surface. The potential weed patch is huge.

This approach is inevitably approximate and must miss many details. In particular, it does not map where these disturbed lands are. To both refine these estimates and provide a check on their accuracy, we will now explore detailed estimates of landcover. We do so first at a global scale, then at regional scales. Our analyses relate primarily to the once-forested half of the planet since the remote sensing imagery on which we rely does not so readily detect the damage to drylands.

A Spatially Explicit Global Assessment of Converted Forests

For the global analysis, we use a Geographic Information System (ERDAS Imagine v 8.5) to combine a map of presumed original vegetation with an estimate of current landcover. The result is a global map where each pixel has information about its original vegetation and if it has changed, or not changed, into a different type of landcover.

The original vegetation map is from the Integrated Model to Assess the Global Environment (IMAGE) project (Leemans & van den Born, 1994; Alcamo et al., 1998; IMAGE team, 2001). In their Terrestrial Vegetation Model, the IMAGE team uses a modified BIOME model to estimate potential natural vegetation using climate and soil characteristics. For a detailed description of this model, see Prentice et al. (1992) and Leemans and van den Born (1994). The resolution of this map is one-half degree of latitude and longitude. Color maps are available from Alcamo et al. (1998) and IMAGE team (2001).

The current landcover map is from the Global Land Cover Characterization (GLCC) (Loveland et al., 2000). A digital version is available at ⟨http://edcdaac.usgs.gov/glcc/glcc.html⟩. This project used a one-year sequence of AVHRR satellite imagery to identify landcover in ca. 1992. As the primary concern of our study is disturbance (i.e., areas vulnerable to invasion), we focus on the disturbed classes of the GLCC (croplands, mosaics of croplands and natural vegetation, and urban areas). The resolution of this map is approximately one km^2 at the equator.

We also identify areas that have changed landcover, but not necessarily into croplands or urban areas. For example, the conversion of forests into grasslands for grazing will not appear as disturbed, but it obviously is. (Grasslands are a natural type of vegetation, but not where the original vegetation was a humid tropical forest.) We do this to assess potential error causes and means of improving on our main analysis.

The current data sets are not adequate for a complete and detailed analysis of landcover changes of all ecosystem types. The BIOME and GLCC maps use different classification schemes for vegetation that make matching corresponding classes between them somewhat arbitrary. For example, the GLCC map has an "open shrubland" class that corresponds to some grassland in the BIOME map. However, open shrubland also includes areas that are obviously not grassland, such as central Australia, which the BIOME map classifies as hot desert. It is uncertain that these changes represent land degradation: more likely, they represent differences in classification schemes.

Results and Discussion

Not surprisingly, the global analysis confirms that humanity has disturbed a large fraction of the world (Fig. 1). Of the ca. 129 million km^2 of ice-free land, ca. 27 million km^2 appear to have been converted to croplands, mosaics of croplands and natural areas, and urban areas. Table 1 shows the total disturbed area originating from each vegetation type (rightmost column). Of the total disturbed area, 80% comes from just six vegetation types (bold numbers in Table 1) that originally covered 47% of the land. Disturbance concentrates in temperate climates (temperate forests, warm mixed forest, grassland/steppe) and the drier subtropical and tropical vegetation (scrubland, savanna). Again, not surprisingly, most of this disturbance coincides with the world's human population and croplands, mostly in the Northern Hemisphere.

Grasslands, scrublands, and savannas have lost from a fourth to a third of their original area (Table 1), but these numbers may be misleading. Disturbance from livestock grazing on such ecosystems is difficult to detect by satellite. Most of the very cold

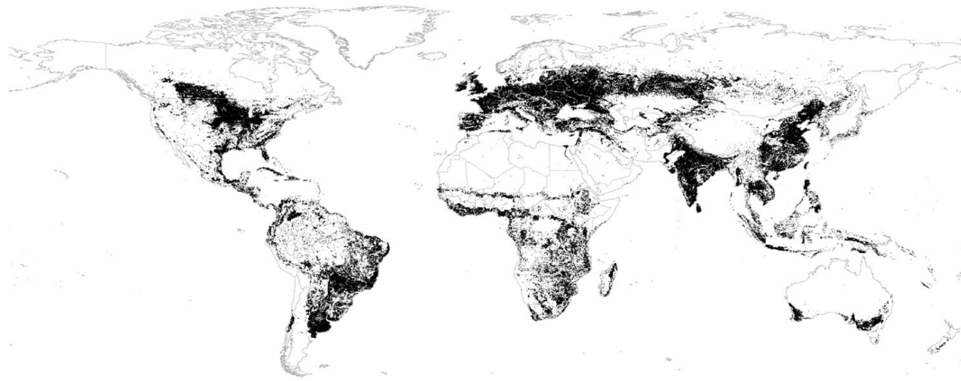

Figure 1. Map of global disturbed areas. Black areas include croplands, mosaics of croplands and natural vegetation, urban areas, and original tropical woodlands and forests that are now grassland, savanna, or woody savanna. Original vegetation is from the BIOME map and current landcover is from the GLCC map. This map uses a geographic projection and is not equal area.

areas (tundra and boreal forest) and the very dry (deserts) escape major disturbance.

Of the combined disturbed areas, 14.2 million km^2 are from once-forested areas (Table 1, sum of disturbed boreal forest, cool conifer, temp. mixed and decid. forest, warm mixed forest, and tropical woodland and forest). This seems to be a low estimate, for we should compare it with the 11 million km^2 of forests that are now croplands plus a further minimum estimate of 5 million km^2 of cleared tropical forests not converted to croplands (above and Pimm, 2001).

However, the GLCC data do not include separate categories for dry habitats (such as grasslands) that are purported to originally have been forest (Loveland et al., 2000). What happens if we assume that these are also converted landscapes? We approximate the area of forest to dryland conversion by identifying tropical woodlands and forests that are now grasslands, savannas, or woody savannas. The area is about 2.4 million km^2. Adding in this piece suggests that 16.6 million km^2 of forest have been converted. This is close to the lower estimate of 16 million km^2 based on combining independent es-

Table 1. Original area of each vegetation type, the area disturbed as croplands, mosaics of croplands and natural vegetation, and as urban areas. Drylands are areas that were originally tropical woodlands or tropical forests (BIOME map), but are now grasslands, savannas, or woody savannas (GLCC map). All areas are expressed as 1000s of square kilometers. Totals may be different from the sum of the parts because of rounding.

	Area (1000 sq. km.)					
Vegetation type	Original	Croplands	Mosaic	Urban	Drylands	Total disturbed*
Tundra	6096	7	13	0		20
Wooded tundra	2586	5	6	0		11
Boreal forest	16,144	399	119	6		523
Cool conifer	3809	686	378	10		1074
Temp. mixed forest	6471	2151	1706	67		**3924**
Temp. decid. forest	4677	1842	837	62		**2741**
Warm mixed forest	6189	1503	1185	31		**2719**
Grassland/steppe	17,800	1975	2078	32		**4085**
Hot desert	23,006	274	232	6		512
Scrubland	9745	2013	1356	19		**3387**
Savanna	15,926	2775	1962	11		**4748**
Tropical woodland	7485	830	842	10	1629	1682
Tropical forest	8893	718	843	7	767	1569
Total	128,824	15,178	11,556	260	2397	26,995

* Does not include drylands.

Table 2. Area disturbed through deforestation and through edge effects in the Amazon example. The area within 300 meters of an edge includes 4986 km² of "natural" edge forest (see text). All areas are expressed as square kilometers.

Year	Area of forest	Total area deforested	Area <300 m from edge	Total area disturbed
Original	112,919	0	4986	0
1992	100,974	11,945	17,801	24,760

timates of forest converted to croplands (11 million km²) and tropical forests converted to grazing lands (5 million km²); see above and Pimm (2001).

This broad agreement is encouraging, but it also points to the difficulty in translating landcover maps, with their inevitably arbitrary classifications of vegetation cover, into ecologically sensitive measurements of human impacts. That is a conclusion on which we now expand by considering two areas of forest conversion in more detail.

A Fine-Scale Analysis of Tropical Forests

We selected two tropical forest areas in Brazil with different disturbance histories to try to identify what the global analysis is missing.

The Amazon is relatively intact but has had high rates of recent deforestation (i.e., within the last 30 years, Skole & Tucker, 1993). Northern Mato Grosso state, in the southeastern Amazon Basin, is our example of such recent anthropogenic disturbance. In contrast, most of the Atlantic Forest was deforested more than 30 years ago (Fundação SOS Mata Atlântica, 1998). The state of Rio de Janeiro and the surrounding area is our example of such historic disturbance.

For the Amazon example, we calculate deforestation using forest cover maps from the Tropical Rain Forest Information Center (TRFIC, 2002). We use maps for 1992 to match the year of the GLCC map. We also simulate the undisturbed condition by replacing the deforested class in the 1992 map with forest.

Table 2 shows the deforestation statistics for the Amazon example. Comparison of TRFIC maps shows that as of 1992, 100,974 km² of the original 112,919 km² of forest remained, yielding 11,945 km² of deforested (disturbed) area.

The global analysis significantly underestimates disturbance in this region. According to the GLCC, the Amazon example shows just 3943 km² of disturbed area. That is only about a third of the regional estimate in the previous paragraph. Another 3582 km² is grassland, savanna, or woody savanna. Including these as disturbed brings the total to 7525 km², which is still less than two-thirds of the TRFIC estimate. Even after correcting the GLCC map for unnatural drylands, it still misses a third of the disturbed area.

For the Atlantic Forest example, we map forest cover in 1999 using Landsat 7 ETM+ satellite imagery. Using standard supervised classification techniques, we classify seven Landsat images into forest and non-forest classes. We do not distinguish between natural and plantation forests, but monospecific plantations (e.g., eucalyptus) are not a large proportion of remaining forest in this area (pers. obs.). The World Wildlife Fund ecoregion map provides an estimate of original forest cover (Olson & Dinerstein, 1998).

In the Atlantic Forest example, the analyses of Landsat imagery show that 91,993 km² of forest, of an original 127,850 km², has been lost to deforestation. The area of disturbed lands in the GLCC map is just 51,851 km², 56% of the Landsat-derived estimate. However, adding in forests converted to drylands increases the area to 111,000 km², an overestimate of disturbance.

In both examples, the best fit of estimates from GLCC data to detailed regional estimates comes only when we recognize the conversion of forests to obviously disturbed habitats (such as croplands) and less obvious categories (such as grasslands and savannas) that could be natural ecosystems, but are not.

Two factors contribute to these deficiencies of the GLCC map. One, the AVHRR imagery used in making the GLCC has limited ability to discriminate vegetation types. The AVHRR sensor's spectral bands are too wide and poorly positioned for mapping vegetation, yielding inevitable errors. This appears to contribute to the overestimation of deforestation in the Atlantic Forest example. The remaining forest is simply misclassified. The second factor is that the resolution of the regional analyses (0.0009 km²) is much finer than the GLCC data (1 km²) in the global analysis. This finer resolution enables better detection of small areas of deforestation. This likely contributes to the underestimate in the Amazon example, where there are many small patches of deforestation.

We do not know if these error rates are general for the global analysis. These are only two examples from relatively small areas. What they do indicate is a need for better global mapping of landcover. At the time of writing, the GLCC was the best global data set available, but good prospects exist for refining our results. Efforts are under way using

MODIS ⟨http://geography.bu.edu/landcover/index.html⟩ and Landsat ⟨http://www.geocover.com⟩ satellite imagery to map the world at 250-meter and 30-meter resolutions, respectively. Vegetation mapping is a primary consideration in these sensor's designs, so the resulting maps should better discriminate vegetation types and their level of disturbance. The improved spatial resolution should also better detect small areas of disturbance.

The Missing Edges

We have mapped disturbed areas as best possible using current data sets, but another part of the weed patch is still missing from our estimates. Laurance (1997) found forest edges to be vulnerable to invasives because of "edge effects" disturbing the forest community. Although we cannot assess how much edge forest contributes to the global weed patch, the one km^2 resolution is too coarse; we can estimate it for the Amazon and Atlantic Forest examples.

The regional forest maps have some errors that we must first correct. They have small gaps of non-forest, some of which may be natural, but many of which are small classification errors. These are insignificant for the earlier analyses, but can cause large areas of forest to appear to be near an edge, even if that edge is a single 30-m pixel. To account for this, we replace patches of non-forest smaller than 2 hectares with forest. The use of 2 hectares is conservative. It is larger than the presumed classification errors, but may also include some truly deforested areas and natural gaps. The result is a probable underestimate of edge forest.

In the Amazon example, 17,801 km^2 of forest is within 300 meters of an edge (Table 2), the distance that Laurance et al. (1998, 2000) detected community changes in Amazonian forest fragments. However, in the original state this region already had 4986 km^2 of natural edge forest due to rivers and savannas. Adding the edge forest, minus natural edge, to the earlier estimate of disturbed area yields 24,760 km^2 of disturbed area (Table 2), approximately twice the original estimate.

In the Atlantic Forest example, 29,373 km^2 of the remaining forest is within 300 meters of an edge. Adding this to the deforested area yields 121,366 km^2 of disturbed area, leaving just 6484 km^2 of undisturbed forest. The map of original forest (WWF ecoregion) is too general to reliably calculate a "natural" amount of edge as done for the Amazon.

When we incorporate these regional estimates of edges into the calculations of disturbed area, then the GLCC estimates are both too small. In short, much disturbance—and much habitat for invasive species—occurs on a scale too small to detect with global landcover maps.

Conclusions

Invasive species are a growing problem for the world, both ecologically and economically. In response to the problem, governments are devoting increasing amounts of resources toward the prevention, control, and eradication of invasives in many parts of the world. To enable efficient use of these resources, the scientific community needs to identify where invasives are likely to be a problem or become a problem in the future.

Disturbed ecosystems are often favorable for invasives, a conclusion confirmed by comparing our map of disturbed areas with the distributions of some of the worst invaders. These disturbed areas, the global weed patch, occupy at least 29.4 million km^2 (23%) of the ice-free land surface. Other than the overgrazed drylands, which our analyses are unable to detect, the numbers broadly agree with independent estimates of disturbed area.

The advantage of our approach is that it shows where those disturbed areas are and thus where the invaders are likely to be. Combining this with information on who the invaders are likely to be should help in efficiently allocating resources to solve the invasive species problem.

Literature Cited

Alcamo, J., R. Leemans & E. Kreileman. 1998. Global Change Scenarios of the 21st Century: Results from the IMAGE 2.1 Model. Pergamon & Elsevier Science, Oxford, U.K.

Archer, S. 1994. Woody plant encroachment in southwestern grasslands and savannas: Rates, patterns and proximate causes. Pp. 39–45 *in* M. Vavra, W. A. Laycock & R. D. Pieper (editors), Ecological Implications of Livestock Herbivory in the West. The Society for Range Management.

Bahre, C. J. & M. L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. J. Biogeogr. 20: 489–504.

Blamey, M. & C. Grey-Wilson. 1989. The Illustrated Flora of Britain and Northern Europe. Hodder & Stoughton, London.

Dregne, H. E. 1986. Desertification of arid lands. P. 12 *in* F. El-Baz & M. H. A. Hassan (editors), Physics of Desertification. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Fundação SOS Mata Atlântica/INPE/Instituto Socioambiental. 1998. Atlas da Evolução dos Remanescentes Florestais da Mata Atlântica e Ecossistemas Associados no Período de 1990–1995. São Paulo, Brasil.

Holm, L. G., D. L. Plucknett, J. V. Pancho & J. P. Herberger. 1977. The World's Worst Weeds: Distribution and Biology. Univ. Press of Hawaii, Honolulu.

———, J. V. Pancho, J. P. Herberger & D. L. Plucknett. 1979. A Geographical Atlas of World Weeds. John Wiley & Sons, New York.

IMAGE team. 2001. The IMAGE 2.2 Implementation of the SRES Scenarios: A comprehensive analysis of emissions, climate change and impacts in the 21st century. RIVM CD-ROM publication 481508018, National Institute for Public Health and the Environment, Bilthoven, The Netherlands.

Laurance, W. F. 1997. Hyper-disturbed parks: Edge effects and the ecology of isolated rainforest reserves in tropical Australia. Pp. 71–83 *in* W. F. Laurance & R. O. Bierregaard, Jr. (editors), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Univ. Chicago Press, Chicago.

———, L. V. Ferreira, J. M. Rankin-de Merona & S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79: 2032–2040.

———, H. L. Vasconcelos & T. E. Lovejoy. 2000. Forest loss and fragmentation in the Amazon: Implications for wildlife conservation. Oryx 34: 39–45.

Leemans, R. & G. J. van den Born. 1994. Determining the potential global distribution of natural vegetation, crops, and agricultural productivity. Water Air Soil Pollut. 76: 133–161.

Loveland, T. R., B. C. Reed, J. F. Brown, D. O. Ohlen, Z. Zhu, L. Yang & J. W. Merchant. 2000. Development of a global land cover characteristics database and IGBP DISCover from 1-km AVHRR data. Int. J. Remote Sensing 21: 1303–1330.

Lowe, S., M. Browne & S. Boudjelas. 2001. 100 of the World's Worst Invasive Alien Species. Invasive Species Specialist Group, IUCN/SSC GISP.

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

Olson, D. M. & E. Dinerstein. 1998. The global 200: A representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biol. 12: 502–515.

Olson, J. S., J. A. Watts & L. J. Allison. 1983. Carbon in Live Vegetation of Major World Ecosystems. ORNL publication no. 5862. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Pimentel, D., L. Lach, R. Zuniga & D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53–65.

Pimm, S. L. 2001. The World According to Pimm: A Scientist Audits the Earth. McGraw-Hill, New York.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud & A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19: 117–134.

Skole, D. & C. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. Science 260: 1905–1910.

Thompson, D. G., R. L. Stuckey & E. B. Thompson. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. Fish and Wildlife Research Report no. 2. U.S. Fish and Wildlife Service, Washington, D.C.

TRFIC. 2002. Tropical Rain Forest Information Center. Available at: ⟨http://www.bsrsi.msu.edu/trfic/⟩ (accessed on 28 October 2002).

Van Auken, O. W. 2000. Shrub invasions of North American grasslands. Annual Rev. Ecol. Syst. 31: 197–215.

Vitousek, P. M., P. R. Ehrlich, A. H. Ehrlich & P. A. Matson. 1986. Human appropriation of the products of photosynthesis. Bioscience 36: 368–373.

Young, J. A. & W. S. Longland. 1996. Impact of alien plants on Grant Basin rangelands. Weed Technol. 10: 384–391.