Biodiversity conservation in human-modified Amazonian forest landscapes

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ARTICLE INFO

ABSTRACT

Amazonia (*sensu lato*) is by far the largest tropical forest region, but has succumbed to the highest absolute rates of tropical deforestation and forest degradation, driven by rapid frontier expansion, road-building, and spontaneous or government-subsidized migration. The large area-through-time and paleoclimatic stability of Amazonian forests may help explain the high regional to local scale plant and animal species diversity of true forest specialists and high ecological sensitivity to contemporary land-use change. We describe the prevailing forms of anthropogenic disturbance that affect forest organisms in the context of the geographic and evolutionary background that has shaped the degree to which forest species may be resilient to environmental change. The fate of Amazonian biodiversity will partly depend upon the interaction between land-use and climate change, and the extent to which seasonally-dry forests can retain immunity against catastrophic recurrent wildfires. This review illustrates the importance of considering interactions between different forms of forest disturbance to develop effective conservation policy. We conclude with some considerations of the policy agenda necessary to protect forest cover and forest biodiversity at a meaningful scale across the Amazonian biome.

1. Introduction

Lowland and Andean Amazonia exhibit the greatest expression of tropical biodiversity on Earth and the highest absolute rates of tropical deforestation (Hansen et al., 2008). Amazonia (*sensu lato*) stretches from sea level to >6000 m across nine of the 12 South American countries and encompasses the world's largest river basin and most extensive unbroken tracts of tropical forests. The hydrological boundaries of the Amazon basin and neighbouring forested watersheds, including the Tocantins, Orinoco and smaller river basins across the Guianan Shields, amount to ~7.6 million km² (Goulding et al., 2003). This accounts for over 90% of remaining South American tropical forests, with Brazilian Amazonia alone comprising ~30% of the world's current primary tropical rainforests (FAO, 2006).

The Amazonian forest and freshwater biome contains some of the highest known levels of biological diversity including >50,000 terrestrial vascular plant species (e.g. Hubbell et al., 2008), although the spatial turnover of species assemblages at different scales remains poorly understood. Single localities of SW Amazonia can sustain the highest alpha-diversity documented to date anywhere on Earth for several taxonomic groups, including woody plants (Gentry, 1988), butterflies (Emmel and Austin, 1990), lizards (Dixon and Soini, 1986) and nonvolant mammals (Peres, 1999a). Lowland forests of central Amazonia can also rival or exceed levels of alpha-diversity of the upper Amazon (e.g. Cohn-Haft et al., 1997; Oliveira and Mori, 1999). Yet Amazonian biodiversity is not homogenous even at small to intermediate spatial scales for both forest (Tuomisto et al., 1995) and aquatic organisms (Fernandes et al., 2004). For example, adjacent seasonally flooded and unflooded forests exhibit high levels of species turnover for trees (ter Steege et al., 2003) and many faunal taxa including frogs (Gascon et al., 2000), small mammals (Malcolm et al., 2005) and large forest vertebrates (Haugaasen and Peres, 2005), as well as pronounced changes in community composition (Balslev et al., 1987; Pitman et al., 2008). Plant–animal interactions also match landscape-scale edaphic mosaics (Fine et al., 2004). Moreover, many habitat specialists are restricted to a small fraction of their hypothetical

geographic range and require large forest areas containing a sufficient number of minor habitat enclaves to maintain a viable (meta)population size.

Biotic diversity at all scales is increasingly threatened by a variety of human-induced structural impacts, ranging from small tree-fall gaps generated by highly diffuse logging operations to large-scale clear-cuts advancing into cheap or previously unclaimed public forestlands. Yet an integrative understanding of how arboreal, terrestrial and aquatic species in tropical forest biomes respond to different threat processes remains elusive. Forest loss can now be mapped for vast regions at a square-meter resolution, yet estimates of forest biodiversity loss – at the scale of species, populations or genes – at best remains an inexact science (e.g. Feeley and Silman, 2008). This review begins with a brief synopsis of the biogeographic history through which the Amazonian forest biota evolved. We then assess the degree to which natural and pre-Columbian human disturbance has played a role in shaping the comparative resilience of this biota to contemporary forms of anthropogenic disturbance. Next, we briefly review how forest biodiversity responds to a broad spectrum of disturbances currently affecting lowland and Andean Amazonia. Finally, we discuss the predicament of Amazonian forest biodiversity under rapidly changing climate and land-use scenarios, and the policy agenda required to address the daunting challenges of conservation in this region.

2. Geographic and paleoecological context

Since the breakup of Gondwanaland, much of northern South America emerged as the largest continuous expanse of closed-canopy tropical forest worldwide. Put simply, Amazonia is a colossal mid-domain basin close to sea-level in a major continent that is both widest just south of the Equator and flanked by a massive orographic wall of western uplifting mountains ensuring continuous precipitation recycling. Although ∼87% of the entire Amazon basin consists of lowland forest <500 masl, some 45% of the Andes within the Amazon watershed lies at submontane elevations (500–2000 masl) and the remainder between 2000 and 4000 masl (although several peaks in Peru extend much higher). The ∼623,000 km^2 Andean Amazon sources as much as 95% of the suspended sediments and nutrient solutes exported to the Amazonian floodplains (Meade et al., 1985). Indeed, the geochemistry and biophysical macromosaic of lowland Amazonia has been profoundly shaped by Andean erosion for over 10 million years (McClain and Naiman, 2008), creating significant basin-wide gradients of primary (Malhi et al., 2004) and secondary (Peres, 2008) forest productivity, thereby setting key preconditions to any large-scale plan for conserving basin-wide forest biodiversity.

Beyond the isolation and reconnection of South America, important geoclimatic events shaping Amazonia include the Andean uplift, the extensive marine incursions of the Miocene, the formation of the Orinoco and Amazon drainages, and the dry–wet climate cycles of the Plio–Pleistocene. However, the duration, magnitude and consequences of these events remain highly controversial (Hoorn, 2006). Largely unequivocal geological and paleobotanical evidence has shown that most of the Amazon lowlands has remained under forest throughout at least the last two glacial and interglacial cycles, rather than fragmented by open vegetation as postulated by the now widely discredited Pleistocene refugia hypothesis (Haberle and Maslin, 1999; Colinvaux et al., 2000). Sweeping conjectures of aridity and savanna climates are largely based on liberal interpretations of incomplete biogeographic evidence because of either circularity in the sampling effort of modern codistributions (Nelson et al., 1990) or evidence from fossil pollen from windblown grasses and herbs (e.g. van der Hammen and Absy, 1994), which would be expected from fringe Amazonian sites along ecotone boundaries that were dynamic on a millennial scale (Mayle et al., 2000). Large areas of arid savannas in core Amazonia are further questioned by carbon isotope ratios in fan deposits indicating that Hylean forests were never replaced by tropical grasslands (Kastner and Goñi, 2003). Forest stability since at least the early Miocene, which was further protected by regional-scale water cycling and the Andean rain-shadow, contributed to the generation of relatively high levels of local diversity and low extinction rates of forest species compared to more arid tropical landmasses (Bush, 1994; Morley, 2000; Stropp et al., 2009). In general, the larger area-through-time and paleo-climatic stability of Amazonian forests may explain their relatively high regional species diversity compared to Africa and Asia (Fine and Ree, 2006). This is not to deny frequent changes in landscape evolution, particularly in sedimentary processes that contributed to the Plio–Pleistocene to Holocene formation of fluvial systems that continue to mould the Amazonian biota (Rossetti et al., 2005). However, the evolutionary history of the vast majority of Amazonian species has been predominantly shaped by extensive closed-canopy moist forest cover, although evidence from molecular phylogenies and palynology suggest that lowland tropical deciduous forests may have waxed and waned in parts of Amazonia during glacial periods at the expense of evergreen forests (Pennington et al., 2000).

The historical dominance of forest in the neotropics, and particularly Amazonia, is supported by the extant vertebrate fauna, which exhibit the highest degree of morphological specialization to arboreality in forest environments dominated by a continuous canopy (Emmons and Gentry, 1983), and is relatively depauperate in terrestrial species when compared to paleotropical forest lineages (Cristoffer and Peres, 2003). For example, prehensile tails evolved independently at least five times in neotropical forest mammals, including primates (*Cebus* and all ateline genera), rodents (*Sphiggurus* and *Coendou*), carnivores (*Potos*), xenarthrans (*Tamandua* and *Cyclopes*) and all South American genera of marsupials. Different Amazonian forest localities also hold the highest global alpha-diversity of true forest specialists for many faunal taxa, including primates (Peres and Janson, 1999), birds (Stotz et al., 1996), frogs (Duellman, 2005), lizards (Pianka and Vitt, 2003), and many arthropod taxa that we have barely begun to document. These and many other intercontinental differences in faunal adaptation to a forest environment are likely due to the antiquity and sheer extent of closed-canopy Amazonian forests (Fjeldså, 1994; Richardson et al., 2001; de Vivo and Carmignotto, 2004).

3. Pre-Columbian forest disturbance

South America is the last major ice-free continent to be colonized by humans, and the overall impact of paleoindians—which in Amazonia may have numbered only fewer than 5 million prior to the diffusion of European epidemics and widespread population collapse—on forest integrity was at best modest (Meggers, 1954). The earliest pre-historic pottery excavated in Amazonia (Taperinha, lower Tapajós) dates from ∼7000 BP (Roosevelt et al., 1991), but densely-settled organized chiefdoms associated with elaborate material culture were small (20–50 ha, Heckenberger et al., 2008), few and far apart. Unlike parts of central-west Africa, most of Amazonia is not sufficiently nutrient-rich to support persistent game harvest by hunter–gatherers (Fa and Peres, 2001), who by necessity typically pursue a lifestyle characterized by recurrent nomadism and frequent resettlement. In fact, contrary to several interpretations of Balée's (1989) 'anthropogenic forest' hypothesis, >85% of Amazonia almost certainly did not sustain permanent settlements practicing perennial agriculture. Patches of black anthro-

pogenic soils (known as *terra preta*), albeit poorly mapped, are highly skewed geographically and likely restricted to <5% of the basin (Bechtold, 2009). Large-scale landscaping and enrichment of forest composition near sedentary settlements was therefore restricted to a relatively small part of seasonally-dry Amazonia, such as the Baures region of Bolivia (Erickson, 2000) and parts of the upper Xingú region (Heckenberger et al., 2008). For example, dense clusters of at least two tree species that are widely regarded as 'anthropogenic forest' indicators can be created by edaphic conditions combined with natural seed dispersal agents including agoutis (Brazil-nut tree *Bertholletia excelsa*: Peres and Baider, 1997) and tapirs (aguaje palm *Mauritia flexuosa*: Fragoso et al., 2003). In fact, there is no evidence suggesting that large areas away from major rivers, or more aseasonal parts of western Amazonia, were significantly altered by human disturbance (Bush and Silman, 2007). In any case, while some pre-historic sites were intensively modified, the spatiotemporal scale of the pre-Columbian human footprint in much of Amazonia, particularly in remote interfluvial regions, was virtually undetectable (cf. Gloor et al., 2009), thereby offering a poor historical analogue for the scale of human perturbation witnessed today.

4. Contemporary forest disturbance

Amazonian forests have been repeatedly subjected to millennial-scale natural disturbances including floodplain erosion through lateral river-channel migration (Salo et al., 1986), flood-pulses (Hess et al., 2003), windstorm-induced blowdowns causing large-scale tree mortality (Nelson et al., 1994) and episodic fires (Sanford et al., 1985). However, the spatiotemporal scale of this background disturbance regime bears little resemblance to present-day patterns of anthropogenic forest conversion/degradation, which have rapidly accelerated since the road-building and frontier-colonization projects of the 1970s. Considering all nine Amazonian countries, 63.8×10^6 ha of forest were lost to different land-uses between 1990 and 2007, but 76.1% of this deforestation occurred in Brazil alone, 95% of which in the Brazilian Amazon (Fig. 1). During the same period, however, the fastest relative deforestation rate was observed in Ecuador, which lost nearly 25% of its montane and lowland forest.

Clear-cutting from slash-and-burn agriculture, selective logging, large-scale forest conversion into cattle ranches, food crops, and exotic-tree monocultures, and the isolation and edge effects

associated with forest fragmentation processes are the most frequent forms of human disturbance, although the spatial extent of these perturbations remain highly skewed (Skole and Tucker, 1993; Asner et al., 2005). Natural and human-induced forms of forest-canopy disturbance differ markedly in their severity, total extent, grain size, periodicity, and permanence so that forest topologies that had been typically perforated by low-density fine-grained disturbance events on evolutionary timescales are now being exposed to large-scale 'shredding' and coarse-scale edge-effects resulting from fragmentation, shrinkage and attrition as forests succumb to other land-uses under varying scenarios of landscape configuration. Moreover, cryptic below-canopy disturbance, such as widespread overhunting of vertebrate game and over-harvesting of a range of other non-timber resources, alters the long-term dynamics of vast tracts of forests that otherwise remain undisturbed (Peres and Lake, 2003; Terborgh et al., 2008). Rarely these processes operate in isolation, so that interactions between spatially correlated patterns of habitat loss, habitat degradation and non-structural forest disturbance can accelerate or aggravate the rate of population declines and local extinctions of forest interior species (Laurance and Peres, 2006).

5. Biodiversity responses to land-use change

We compiled a total of 62 plant and animal community studies in forest landscapes of Amazonia and the tropical Andes that examined assemblage-wide ecological responses to different modes of structural forest conversion or degradation (see Table 1 and reference list in Supplementary Materials). The spatial extent of past research efforts is restricted to a negligible portion of this region (Fig. 2), with particular concentration of effort in a small number of well-studied localities, including the Biological Dynamics of Forest Fragmentation Project (PDBFF), north of Manaus, Brazil, the Bragantina region (eastern Pará), and more recently, a pulpwood forestry landscape in northeastern Pará (Jari Project). There is also a clear mismatch between the geographic distribution of forest conversion/degradation across Amazonian countries and the spatial allocation of ecological research effort. Furthermore, most studies have examined only a single taxonomic group, and cross-taxa landscape-scale studies sampling five or more taxa within the same sites are currently restricted to only five sites. Studies on the impact of forest replacement with cattle pasture and croplands on different taxa are largely lacking from vast areas of defor-
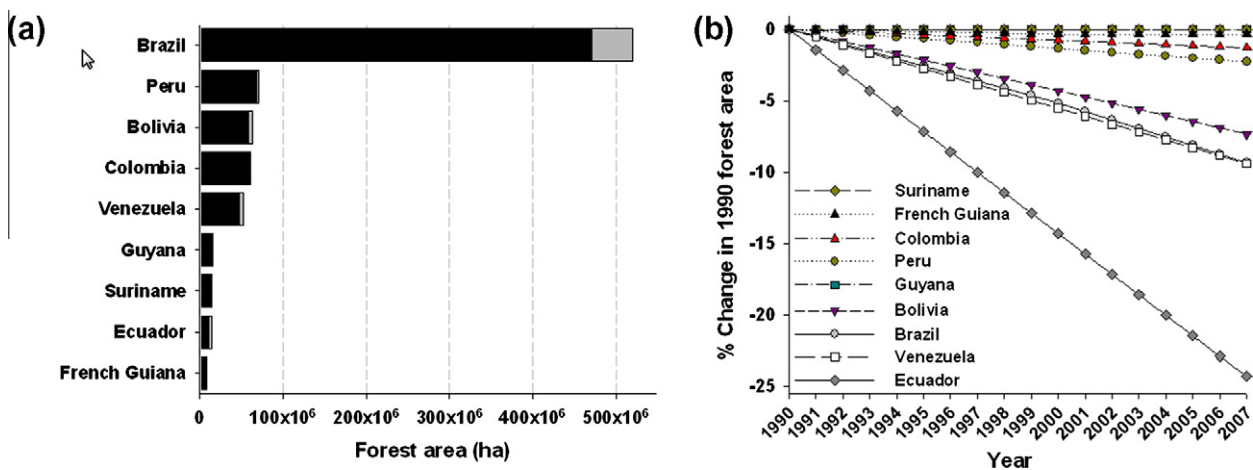

Fig. 1. Absolute and relative extent of forest loss across all nine Amazonian countries: (a) Horizontal bars represent the total forest cover in 1990; black bars indicate the amount of forest cover remaining by 2007. (b) Proportional forest loss over the same period calculated for different years in terms of the 1990 baseline. Countries are ordered by either (a) their total extent of 1990 forest cover, or (b) from the lowest to the highest proportional forest loss. Data from the UN's Food and Agriculture Organization (http://faostat.fao.org/default.aspx).

Table 1
List of biodiversity studies in human-modified forest landscapes of the lowland and Andean Amazon. Geographic coordinates were unavailable for some studies, but obtained from Google Earth on the basis of a published or unpublished map. References are listed in the Supplementary Materials.

Source	Nature of study			Taxonomic group	Land-uses other than primary forest	Biodiversity metric	Geographic location
	Taxonomic coverage	Land-use coverage	Primary forest				
Ackerman et al. (2009)	Single	Multiple	Yes	Termites	Palm-based agroforestry, home-garden agroforestry	Overall species richness, species diversity, community composition	02°31′04″S, 60°01′48″W
Adams (1997)	Single	Multiple	Yes	Bats	Forest fragments, secondary forest	Overall species richness, species diversity	01°11′S, 47°19′W
Andrade and Rubio-Torgler (1994)	Single	Single	Yes	Birds	Secondary forests	Overall species richness, community composition	01°08′S, 70°12′W
Armbrecht et al. (2005)	Single	Multiple	No	Ants	Forest, Polygeneric shaded coffee, Monogeneric shaded coffee, Sun coffee	Overall species richness, species diversity	05°08′–05°45′N, 75°45′–75°56′W
Barlow et al. (2007a, 2008)	Single	Multiple	Yes	Butterflies	Secondary forest, Eucalyptus plantation	Overall species richness, restricted species richness, community composition	00°27′00″–01°30′00″S, 51°40′00″–53°20′00″W
Barlow et al. (2007b)	Single	Multiple	Yes	Birds	Secondary forest, Eucalyptus plantation	Overall species richness, community composition	00°27′00″–01°30′00″S, 51°40′00″–53°20′00″W
Barlow et al. (2002)	Single	Single	Yes	Birds	Burnt forests	Overall species richness, community composition	02°44′S, 55°41′W
Bernard and Fenton (2002)	Single	Multiple	Yes	Bats	Forest fragments, Savannahs	Overall species richness, community composition	02°30′S, 54°57′W
Borges (2007)	Single	Single	Yes	Birds	Diverse secondary forests	Overall species richness, species diversity, community composition	01°54′S, 61°27′W
Borges and Stouffer (1999)	Single	Single	No	Birds	Secondary forest	Overall species richness, species diversity, community composition	02°20′S, 60°00′W
Carvalho and Vasconcelos (1999)	Single	Single	Yes	Ants	Edge habitat	Overall species richness, species diversity, community composition	02°20′S, 60°00′W
Cascante-Marín et al. (2006)	Single	Multiple	Yes	Epiphytes	Diverse secondary forests	Overall species richness, species diversity, community composition	10°17′10″N, 84°47′40″W
Castro-Arellano et al. (2007)	Single	Single	Yes	Bats	Logged forests	Overall species richness, species diversity, community composition	03°21′36″S, 54°57′00″W
Cochrane and Schulze (1999)	Single	Single	Yes	Woody plants	Burned forest	Overall species richness, species diversity	12.03°S, 44.03°W
Da Silva et al. (1996)	Single	Multiple	No	Birds	Secondary forests, Pastures	Overall species richness	02°59′S, 47°31′W
De Almeida et al. (2004)	Single	Multiple	No	Birds	Secondary forest, Eucalyptus plantation, Forest fragments	Overall species richness	04°59′05″–05°11′05″S, 47°39′29″–48°16′38″W
Dias et al. (2009)	Single	Single	Yes	Fish	Streams in logged forests	Overall species richness, community composition	02°57′N, 58°42′W
Fiedler et al. (2007)	Single	Single	Yes	Moths	Edge habitat	Overall species richness, species diversity, community composition	00°08′S, 113°40′W, 04°05′S, 79°10′W
Freitas (2008)	Single	Single	Yes	Mammals	Logged forests	Restricted species richness	02°43′–03°04′S, 58°31′–58°57′W
Gardner et al. (2008)	Single	Multiple	Yes	Dung beetles	Secondary forests, Eucalyptus plantations	Overall species richness, species diversity, community composition	00°27′–01°30′S, 51°40′–53°20′W
Gardner et al. (2007)	Multiple	Multiple	Yes	Amphibians, lizards	Secondary forests, Eucalyptus plantations	Overall species richness, community composition	00°27′–01°30′S, 51°40′–53°20′W
Haugaasen et al. (2003)	Multiple	Single	Yes	Birds, arthropods	Burnt forests	Overall species richness, community composition	02°44′S, 55°41′W
Hawes et al. (2009)	Single	Multiple	Yes	Moths	Secondary forest, Eucalyptus plantation	Overall species richness, species diversity, community composition	00°53′S, 52°36′W
Hung et al. (2008)	Single	Multiple	Yes	Arachnids	Secondary forest, Eucalyptus plantation	Overall species richness, species diversity, community composition	00°27′00″–01°30′00″S, 51°40′00″–53°20′00″W

Table 1 (continued)

Source	Nature of study			Taxonomic group	Land-uses other than primary forest	Biodiversity metric	Geographic location
	Taxonomic coverage	Land-use coverage	Primary forest				
Kattan et al. (1994)	Single	Single	Yes	Birds	Forest fragments	Overall species richness, community composition	10°19′43″N, 74°52′22″W
Klingbeil andWillig (2009)	Single	Single	Yes	Bats	Forest fragments	Overall species richness, species diversity, community composition	03°75′S, 73°24′W
Köster et al. (2009)	Single	Multiple	Yes	Epiphytes	Forest fragments, Secondary forests, Isolated remnant trees in pasture	Overall species richness, species diversity	00°25′S, 79°01′W
Laurance et al. (2006)	Single	Single	Yes	Trees	Forest fragments	Restricted species richness	02°30′S, 60°W
Leck 1979	Single	Single	No	Birds	Forest fragment	Overall species richness	0°35′S, 79°22′W
Lees and Peres (2006)	Single	Single	Yes	Birds	Forest fragments	Overall species richness, community composition	09°53′S, 56°28′W
Lees and Peres (2008)	Single	Single	Yes	Birds and Mammals	Riparian forest corridors	Overall species richness, community composition	09°53′S, 56°28′W
Lima et al. (2009)	Multiple	Multiple	Yes	Nitrogen-fixing bacteria	Secondary forest, agroforestry, subsistence crops, pastures	Overall species richness, community composition	4.41°S, 69.94°W
Martínez et al. (2006)	Single	Multiple	No	Earthworms	Mature forest, Pasture	Overall species richness, species diversity	02°42′–02°52′N, 76°30′–76°33′W
Mathieu et al. (2005)	Multiple	Multiple	Yes	Soil macrofauna	Rice crops, Fallows, Pastures	Overall species richness, species diversity, community composition	05°16′S, 49°50′W
Michalski et al. (2007)	Single	Single	Yes	Trees	Forest fragments	Overall species richness, community composition	09°53′S, 56°28′W
Michalski and Peres (2007)	Single	Single	Yes	Mammals	Forest fragments	Overall species richness	09°53′S, 56°28′W
Mitja et al. (2008)	Multiple	Multiple	No	Herbaceous, woody plants	Rice fields, pastures	Overall species richness, community composition	05°16′08″S, 49°50′29″W
Moreira et al. (unpublished data)	Multiple	Multiple	Yes	Soil meso and macrofauna, microbial communities	Secondary forest, agroforestry, subsistence crops, pastures	Overall species richness, community composition	4.41°S, 69.94°W
Muriel and Kattan (2009)	Single	Multiple	No	Butterflies	Shade coffee plantation, sun coffee plantation	Overall species richness, species diversity, community composition	05°45′–05°55′N, 75°36′–76°02′W
Nepstad et al. (1996)	Multiple	Multiple	Yes	Plants, ants, birds, bats	Secondary forest, abandoned pasture, active pasture	Overall species richness and composition	02°59′S, 47°31′W
Nöske et al. (2008)	Multiple	Multiple	Yes	Epiphytes, moths	Disturbed forest, Isolated trees in pasture	Overall species richness, species diversity, community composition	03°59′S, 79°04′W
Numa et al. (2005)	Single	Multiple	No	Bats	Forest fragments, Shaded coffee plantation, Associated coffee plantation	Overall species richness	04°10′–04°40′N, 75°35′–75°50′W
O'Dea and Whittaker (2007)	Single	Multiple	Yes	Birds	Secondary forest, Agricultural land	Overall species richness, species diversity, community composition	00°04′S–00°07′N, 78°36′–78°46′W
Parry et al. (2007)	Multiple	Single	Yes	Large mammals, large birds	Secondary forests	Overall species richness, community composition	00°53′S, 52°36′W
Peres et al. (2003)	Multiple	Single	Yes	Birds, mammals	Burnt forests	Overall species richness, community composition	02°59′58″S, 56°05′36″W
Presley et al. (2008)	Single	Single	Yes	Bats	Logged forests	Overall species richness, community composition	03°36′S, 54°95′W
Rondon et al. (2009)	Single	Single	Yes	Trees	Secondary forest	Overall species richness, community composition	04°54′S, 73°39′W
Rossi et al. (2006)	Multiple	Single	No	Soil macrofauna	Pastures	Overall species richness, species diversity	05°16′S, 49°50′W
Sampaio et al. (2003)	Single	Single	Yes	Bats	Forest fragments	Overall species richness, community composition	02°24′–02°25′S, 59°43′–59°45′W
Sampaio et al. (in revision)	Single	Multiple	Yes	Large mammals	Logged forest; Forest fragments isolated by scrub savannah	Overall species richness, community composition	2°34′S, 54°54′W; 2°8′S, 54°54′W

Reference				Taxa	Land-use types	Response measured	Coordinates
Scheffler (2005)	Single	Single	Multiple	Dung beetles	Selectively logged forest, Clear-cut forest, Pasture	Overall species richness, community composition	07°50′S, 50°16′W
Silva et al. (1996)	Single	Multiple	Yes	Birds	Secondary forest, abandoned pasture, active pasture	Overall species richness and composition	02°59′S, 47°31′W
Stone et al. (2009)	Single	Single	No	Mammals	Forest fragments	Overall species richness	01°11′–03°39′S, 47°19′–48°33′W
Vasconcelos et al. (2000)	Single	Single	Yes	Ants	Logged forests	Overall species richness, community composition	02°38′S, 60°11′W
Vasconcelos et al. (2006)	Single	Single	Yes	Ants	Forest fragments	Overall species richness, species diversity, community composition	02°30′S, 54°57′W
Vieira (1996)	Single	Single	Yes	Woody plants	Forest fragments, secondary forest	Overall species richness, species diversity, community composition	01°11′S, 47°19′W
Vulinec (2002)	Single	Single	Yes	Dung beetles	Secondary forest	Overall species richness, species diversity, community composition	10.34°S, 62.89°W
Vulinec et al. (2006)	Multiple	Single	Yes	Dung beetles, primates	Secondary forest	Abundance, functional community composition	3.36°S, 60.13°W
Werner and Gradstein (2009)	Single	Multiple	No	Epiphytes	Closed mixed forest, Closed acacia forest, Forest edge, Semi-closed secondary, Woodland, Isolated trees in grassland	Overall species richness, species diversity, community composition	00°00′S, 78°21′W
Willig et al. (2007)	Single	Multiple	Yes	Bats	Agriculture, Secondary forests	Overall species richness	03°74′S, 73°24′W
Wunderle et al. (2006)	Single	Single	Yes	Birds	Logged forests	Overall species richness, species diversity, community composition	03°21′S, 54°56′W

estation within the Brazilian states of Mato Grosso, Rondônia, and Pará, despite unprecedented agricultural expansion during the last two decades. In sum, all but a few human-modified Amazonian landscapes are yet to be investigated, and regardless of sampling intensity existing research effort has been heavily skewed towards a few localities.

Next, we review the prevailing patterns of land-use in Amazonia resulting in different consequences to landscape structure, and the ways in which existing research reveals how arboreal, terrestrial and aquatic species in forest environments respond to them.

5.1. Selectively logged forests

Timber is by far the most marketable extractive commodity in old-growth tropical forests and accounts for >90% of the revenues flowing from the nine Brazilian Amazonian states (IBGE, 2006). Selective logging in >30 Mha of Amazonian forests is a spatially diffuse activity—involving canopy perforation and fracture through large-tree thinning—that is notoriously difficult to distinguish remotely from space against the background natural treefall gap dynamics. The extent of logging disturbance in Amazonia has therefore been vastly underestimated, but often exceeds the total deforested area (Asner et al., 2005). Timber offtakes typically drive the process of frontier expansion by initially creating extensive networks of logging roads (Arima et al., 2008), and subsequently catalysing more intensive forms of land-use by increasing access and capitalizing rural enterprises (Rodrigues et al., 2009).

Yet in the context of other human-impacts such as agriculture, forest fragmentation and more cryptic disturbances such as surface fires, low-intensity logging is considered to be one of the least damaging forms of land-use for Amazonian biodiversity (Barlow et al., 2006). The direct biodiversity impacts of selective logging operate through changes in the structure and composition of forest habitat, typically resulting in the loss of forest interior specialists and proliferation of edge and gap tolerant species in clearings created by tree felling and roads (e.g. Vasconcelos et al., 2000). Conventional, unmanaged logging in the Amazon typically leads to severe structural damage to the forest and widespread canopy fracture. For example, Uhl et al. (1991) found that ~30 trees were damaged for every tree extracted in a logging frontier of eastern Pará. Aquatic systems embedded within logged forests may retain a relatively rich macroinvertebrate fauna, but their fish assemblages still become more depauperate and less functionally diverse (Nessimian et al., 2008). Reduced-impact logging (RIL) techniques—which are widely extolled as a promising sustainable extractive industry in Amazonia—greatly reduce this collateral damage and may result in only minor discernible impacts on biodiversity (e.g. Azevedo-Ramos et al., 2006; Wunderle et al., 2006). Nevertheless, some taxa appear to be sensitive to even low-intensity logging. For example, changes in canopy cover and understorey foliage density are detrimental for bats through knock-on effects on foraging and echolocation. Studies on bats at two separate RIL sites in the Brazilian Amazon (Tapajós and Kayapó reserves) have shown that while common species appear to be unaffected or even benefit from logging, certain guilds and rarer species are either absent or found in reduced abundances in RIL sites (Peters et al., 2006; Presley et al., 2008). Fish faunas can also be altered in forests subjected to RIL with changes in both habitat conditions and assemblage composition lagging for several years after logging has been discontinued (Dias et al., 2009).

Despite the relatively minor impacts of selective logging compared to other threats facing Amazonian biodiversity, it is difficult to draw reliable conclusions from existing studies for at least three inter-related reasons. First, with the exception of one short-term study (Azevedo-Ramos et al., 2006), all Amazonian biodiversity
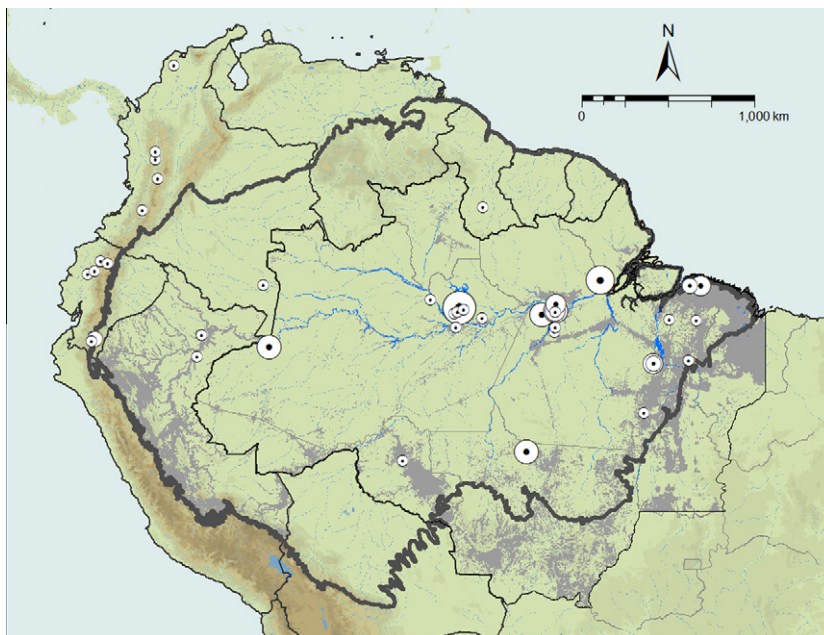
Fig. 2. Distribution of single taxon or multi-taxa studies on biodiversity responses to land-use change in lowland Amazonia and the tropical Andes (see Table 1 and references in Supplementary Materials). Gray areas indicate the extent of deforestation since the early 1970s to 2007 in Brazil and Peru. White circles are sized proportionally to the total number of plant, invertebrate and vertebrate taxonomic groups investigated at each site; e.g. a total of 22 taxa have been examined in the most studied site (Biological Dynamics of Forest Fragmentation Project, Manaus, Brazil). Thick dark-gray contour indicates the phytogeographic boundaries of Amazonia (*sensu lato*). Narrow black contour within Brazil indicates the political boundaries of 'Legal Amazonia'. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
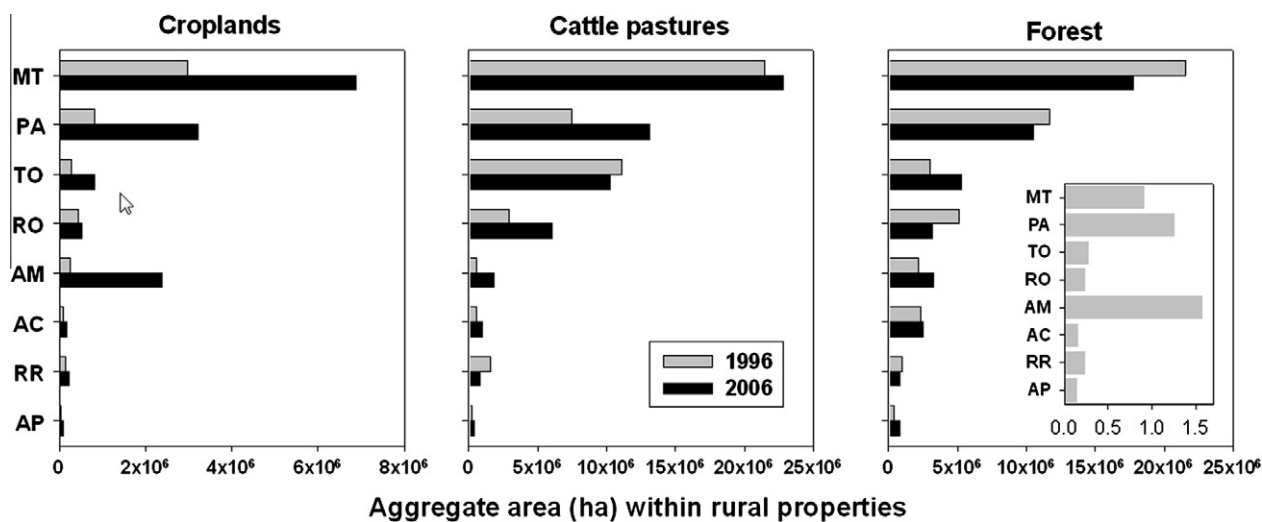
Fig. 3. Changes in total forest and non-forest cover recorded within private rural landholdings across different states of Brazilian Amazonia from 1996 to 2006; (MT) Mato Grosso, (PA) Pará, (TO) Tocantins, (RO) Rondônia, (AM) Amazonas, (AC) Acre, (RR) Roraima, and (AP) Amapá. Croplands include all types of subsistence and cash crops; cattle pastures include all managed and unmanaged pastoral lands, stocked primarily by varying densities of bovine cattle. Horizontal bars in inset graph indicate the total area (in 10^6 km^2) of each state. Data adapted from the Brazilian Agricultural Census (IBGE, 2006), which underestimates forest conversion to agriculture in the private sector because many legal or *de facto* properties are not captured by official census statistics.

studies on logging have not had access to pre-impact data, such that observations may be confounded by natural spatial heterogeneity in species distributions. Second, the potential impacts of logging may occur across temporal scales much longer than the duration of field studies. Finally, logging impacts usually interact with other human-induced disturbances such as fire and over-harvesting of non-timber resources (e.g. Nepstad et al., 2008). The challenge for future research will be to tease apart the relative importance of different management options, including differences in logging intensity, length of rotation cycle, road planning and the spatial distribution of no-take sites. The fact that many species responses to logging are dissipated across large areas and over long time-lags means that the development of minimum certification standards for ecologically responsible forest management requires a highly coordinated program of research and monitoring across a wide network of study sites.

5.2. Wildfire disturbance

Since Uhl and Buschbacher's (1985) seminal paper, it has become well established that human-induced forest degradation through logging and fragmentation can operate synergistically with abnormal climatic events to increase the frequency and severity of fires in Amazonian forests. Extreme supra-annual droughts triggered by ENSO events and elevated Atlantic sea-surface temperatures play a critical role in triggering extensive forest fires when combined with anthropogenic ignition sources from slash-and-burn agriculture and cattle ranching (Aragão et al., 2008). Indeed, fires can result in wholesale phase-shifts in the structure and composition of Amazonian forests (Barlow and Peres, 2008), comprising a key mechanism for a possible climate-mediated forest dieback (Malhi et al., 2009).

Even low-intensity fires often have a large impact on biodiversity, inducing high levels of tree mortality (up to 50% of trees ⩾10 cm DBH) and significant losses to faunal communities, including disturbance-sensitive birds and primates (e.g. Peres et al., 2003; Barlow and Peres, 2004a, b). Fires also lead to ecosystem instability and destabilising feedback cycles, as once-burned forests become more likely to burn again (Cochrane et al., 1999). These recurrent fires have much greater effects on forest biodiversity than initial fires, including a 100% turnover of bird species composition between twice-burned and unburned primary forest (Barlow and Peres, 2004b). Each subsequent fire appears to lead to both a dramatic shift in tree species composition (Barlow and Peres, 2008) and an associated collapse in forest biomass (Peres, 1999b; Cochrane et al., 1999; Barlow and Peres, 2004a).

Because fire occurrence is strongly linked to human activities, fires are likely to have a particularly important role in degrading the biodiversity value of fragmented landscapes. Surface-fire disturbance is a significant predictor of species richness in forest fragments for forest-dependent birds (Lees and Peres, 2006) and mammals (Michalski and Peres, 2007). In addition, burned fragments are unlikely to be recolonized by disturbance-sensitive species if entire, isolated fragments burn. However, the spatio-temporal variation in the causes and consequences of fires, and how fires interact with other forms of forest degradation and across different spatial scales remain poorly understood (Barlow and Silveira, 2009). This information is vital to better predict Amazon-wide implications of fires, identify vulnerability, and define and highlight potential tipping points beyond which the flora and fauna typical of closed-canopy Amazonian forest may be unable to recover.

5.3. Agro-pastoral matrix

Agricultural expansion for local, national and international markets is a major driver of Amazonian deforestation and land-use change. Extensive ranching of some ∼71 million head of cattle occupying 74 Mha of pastures is the dominant agro-pastoral activity in Brazilian Amazonia, accounting for ∼80% of the deforested area (Greenpeace, 2009). However, recent decades have witnessed a rapid northward expansion of mechanised monocultures, replacing both abandoned pastures (Simon and Garagorry, 2005) and primary and secondary forests (Morton et al., 2006). Major Amazonian agricultural commodities now include soybean, cassava, maize, bananas, beans, rice and coffee (Fearnside, 2001). In 2006, agricultural areas in private landholdings in Brazilian Amazonia had increased by ∼23 Mha within one decade to ∼69.7 Mha (79.5% as cattle pastures and 20.5% as croplands; Fig. 3). Yet ∼54.5 Mha was deforested in almost the same period (1998–2007), suggesting that over half of all deforestation occurred in previously unclaimed public lands.

Set against the scale of agro-pastoral expansion in the Amazon there has been relatively little research on the biodiversity impacts of the dominant production systems. Most work to date has been on cattle pastures, with few biodiversity studies in croplands outside small-scale slash-and-burn farming (see Table 1). Although cattle pastures encompass high levels of heterogeneity associated with age since deforestation, and the type and intensity of management (Dias-Filho and Ferreira, 2008), the replacement of closed-canopy forest with open farmland has predictably severe consequences for forest biodiversity. Compared to primary forest, pastures are invariably dominated by a highly impoverished subset of generalist or edge-tolerant forest species, open-area specialists or exotics. For example, of the 53 dung beetle species in an intact southeastern Amazonian forest site (Scheffler, 2005), only 13 were found in pastures, of which 87% of captures consisted of one species. In the central Amazon, native earthworms were either absent or rare in pastures, instead being replaced by large numbers of an exotic peregrine species (Decaens et al., 2004). Only three out of 47 frugivorous bird species forayed into active pasture from neighbouring secondary forests, whereas 18 species used a limited 80-m strip of scrubby pasture along the forest edge (Silva et al., 1996). Wholesale changes in aquatic habitats also occur in deforested areas, with streams becoming shallower, wider, hotter and sustaining lower primary productivity and less species-rich macroinvertebrate and fish assemblages, in which largely insectivorous ichthyofaunas shift to assemblages dominated by detritivores and periphytic algae–grazers (Bojsen and Barriga, 2002). Invasive allochthonous fish species from floodplain areas downriver may also become abundant (Nessimian et al., 2008).

Functional groups of soil organisms – including prokaryotes, nitrogen-fixing nodulating bacteria, arbuscular mycorrhizal fungi, pathogenic and antagonist fungi, earthworms, ants, beetles and termites – were compared across different land-uses in a heterogeneous landscape near Benjamin Constant, western Brazilian Amazonia, including primary forest, young secondary forests (<12 yrs-old) recovering from slash-and-burn plots, agroforestry home gardens, food crops, and pasture (Fidalgo et al., 2005). Under current conditions, slash-and-burn successional mosaics surrounded by large areas of primary forest retained the highest levels of soil fertility and species diversity for macro and mesofauna. However, soil microbial communities in cattle pastures and cropland were among the most diverse (Leal et al., 2009; Lima et al., 2009), showing that these land-uses did not deplete microbial diversity.

Despite the low intrinsic value of the agro-pastoral matrix for forest biodiversity, farm management decisions and land-use choices can have severe repercussions for conservation through their indirect influence on species persistence in adjacent forest remnants. Perhaps the most serious negative indirect effects of agriculture on forest biodiversity is the spread of forest wildfires originating from land-clearing or careless pasture management (Morton et al., 2008). Less well understood impacts come from the leakage into freshwater systems of the heavy cocktail of cropland pesticides and herbicides (Fearnside, 2001), particularly in the floodplain cultivation of annual crops. At the more local scale, agriculture and cattle ranching can detrimentally affect the integrity of forest fragments via spill-over and edge effects. For example, cattle overgrazing in remnant riparian forest strips can significantly reduce the species richness of forest birds (Lees and Peres, 2008).

A priority area of conservation research in Amazonian agricultural landscapes is the importance of land-use history and intensification on the prospects for regeneration and biodiversity recovery on abandoned farmland, and the potential for irreversible ecological change following intensive use. Andrade and Rubiotorgler (1994) suggested that shifting-agriculture can provide a sustainable form of land-use in the Colombian Amazon given that bird communities sampled in fields abandoned for only 10 years were indistinguishable from those in neighbouring forest areas.

However, this form of small-scale agriculture contrasts starkly with slow recovery trajectories such as those in eastern Brazilian Amazonia where degraded scrublands have often been subject to decades of non-forest land-use, such as intensive cattle grazing, and may be kilometres apart from the nearest patches of remaining forest (Uhl et al., 1988). The development of improved conservation strategies in Amazonian agricultural landscapes depends critically on understanding the extent to which the biodiversity benefits of local reforestation and biodiversity offset schemes and proposed low-impact farming techniques (e.g. silvopastoralism, Castro et al., 2008) are effective in the context of such regional and historical constraints.

5.4. Edge-dominated and fragmented forests

Forest fragmentation is an umbrella term for the simultaneous shrinkage of forest area, sub-division of large forest blocks, and proliferation of forest edges (Lindenmayer and Fischer, 2007). Edge habitats are expanding on a massive scale. For example, 6.4% of all remaining forest within a 1.12 million km^2 study area (covering >80% of the deforestation and selective logging in the Brazilian Amazon) falls within 100 m of a forest edge (Broadbent et al., 2008). The detrimental effects of forest fragmentation include elevated tree mortality (Laurance, 2000), changes in species composition and mutualistic or trophic interactions (Peres and Michalski, 2006; Cramer et al., 2007), and synergisms with other drivers of local extinctions such as wildfire susceptibility (Alencar et al., 2004), elevated hunting pressure (Peres, 2001) and conversion to agriculture (Morton et al., 2006). Land tenure dynamics also significantly affects forest retention. Although poorer smallholders tend to clear-cut a larger proportion of their landholdings, large properties (>100 ha) still account for 58% of overall deforestation in northern Mato Grosso, Brazil (Oliveira-Filho and Metzger, 2006).

Species richness in isolated forest fragments is primarily a function of fragment size, largely because many mammals (Michalski and Peres, 2007), birds (Stouffer and Bierregaard, 1995; Lees and Peres, 2006), and several arthropod taxa (Powell and Powell, 1987; Brown and Hutchings, 1997; Didham, 1997) are highly sensitive to the correlated effects of edges and forest patch area. Forest remnants contain a limited subset of any regional forest and aquatic biota. For example, aquatic macroinvertebrates in streams within ~10-ha forest fragments are just as species-poor as those coursing through completely deforested areas (Nessimian et al., 2008). This is partly because small patches inevitably sample fewer species and less habitat diversity than larger patches (Haila et al., 1993) which is aggravated by the intrinsic rarity of many tropical forest species. Post-disturbance faunal relaxation may take many decades until assemblages in fragments reach a quasi-equilibrium (Kattan, 1994; Ferraz et al., 2003). Such spatial and temporal sampling effects could be especially important for Amazonian species, which often have patchy distributions at varying spatial scales and complex patterns of endemism (e.g. Zimmerman and Bierregaard, 1986; Gentry, 1992; Didham et al., 1998). Negative edge effects on forest organisms include altered microclimates (Williams-Linera et al., 1998), fire damage (Cochrane and Laurance, 2002), elevated rates of tree mortality, and shifts in plant and animal community composition (Laurance et al., 2002). Finally, research on edge effects in the Amazon has been disproportionately concentrated within the PDBFF Project near Manaus (Lovejoy et al., 1986), so that the ecological impact of edges among different land-uses and land-use histories remains poorly understood (Fig. 2).

5.5. Secondary growth

Forest-replacing economic activities of varying patch sizes in the humid tropics are usually short-lived, resulting in highly variable secondary succession pathways, under multiple cycles of land-use abandonment and forest regrowth (e.g. Moran et al., 1996; Perz and Skole, 2003). Biodiversity recovery in Amazonian secondary forests is of potentially high conservation value, not least because of the vast fallow areas that are currently regenerating (Asner et al., 2009). On the basis of 26 Landsat scenes scattered across the most deforested region of Brazilian Amazonia, Almeida (2008) estimated that 19.4% of all forestland area that had been converted by 2006 (680,000 km^2) was second-growth under varying stages of regeneration. However, a 10-yr time-series of these images revealed that this second-growth was almost invariably short-lived, with a mean half-life shorter than 5 yrs, which is somewhat higher than previous estimates for 1978–2002 (Neeff et al., 2006).

Yet biodiversity recovery in tropical secondary forests critically accrues slow dividends (Chazdon et al., 2009). In lowland Amazonia, even relatively old secondary forests exhibit limited species accumulation. For example, relatively long-lived (20–40 yr-old) secondary forests of eastern Amazonia contained only 40.3–41.8% of the 268 tree species $\geqslant 5$ cm DBH of an adjacent primary forest, and those were largely regenerating vegetatively through resprouts (Vieira, 1996). Moreover, 84% of these primary forest tree species relied on animal seed-dispersal vectors, suggesting that their absence can thwart the influx of old-growth tree species into secondary forests (Vieira and Proctor, 2007). In the Jari landscape of northeastern Pará, where 15 vertebrate, invertebrate and plant taxa were sampled across five primary and five secondary forest (14–19 yr-old) sites, 59% of over 1000 species recorded in primary forest also occurred in secondary forests (Barlow et al., 2007). However, many of these species were recorded only once, and this figure fell to 46% when singletons were excluded from secondary forest samples. For a number of reasons, the data from Jari represent a best-case scenario of biodiversity recovery as most Amazonian secondary forests are much younger, farther removed from remnant patches of primary forest, more heavily disturbed, and carry the legacy of a less benign land-use and management history that is often exacerbated by additional biophysical constraints such as fire-mediated nutrient depletion and local extinction of animal seed-dispersal vectors.

6. Looming spectre of climate change

A potentially serious incipient threat to Amazonian biodiversity is global climate change. Over the past several decades temperatures in the Amazon have increased by approximately 0.025 °C yr^{-1} (Hansen et al., 2006; Malhi and Wright, 2004) but slightly faster in the Andes (Vuille and Bradley, 2000). Global Climate Models (GCMs) predict that temperatures in these regions will rise by 3–8 °C over the next century (Malhi et al., 2009). In response to changes in temperature and climate, species assemblages are predicted to respond with distributional shifts, predominantly by moving upslope towards colder climates (Colwell et al., 2008; Chen et al., 2009). Consequently, the amount of climatically suitable habitat available to many species will decrease, even if they are capable of perfect migration, possibly leading to local or even global extinction (Thomas et al., 2004). Habitat loss will be much greater if species are unable to migrate at the pace required by climate change, either due to limited dispersal or interactions with other abiotic and biotic factors (Malcolm et al., 2006). Forest conversion and fragmentation reduces habitat connectivity, thereby impeding geographic range readjustment. Likewise, human activities above the treeline, such as cattle grazing and burning in the Andes, may prevent upslope migration thereby hastening habitat loss and increasing extinction risk. If the number of species emigrating from an area exceeds the number immigrating there will be loss of local diversity or biotic attri-
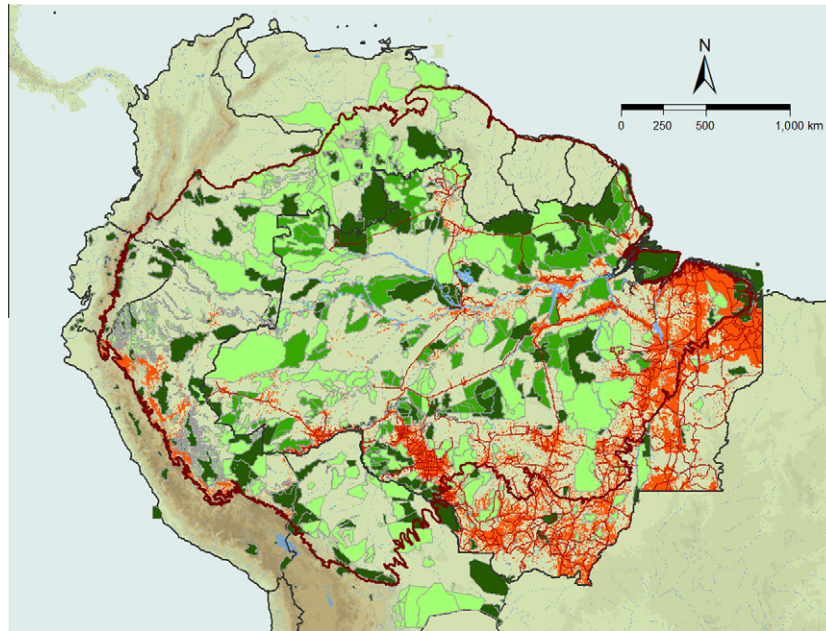
Fig. 4. Pan-Amazonian distribution of designated protected areas "on paper" under different denominations within and immediately outside the phytogeographic boundaries of the region (dark red line). Dark, intermediate and light green polygons indicate the boundaries of strictly protected areas, sustainable development reserves, and officially recognised indigenous territories, respectively. Deforested areas (by 2007) outside of parks and reserves are indicated in orange; deforestation within parks is not shown. Data are unavailable for Guyana, Suriname and French Guiana. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tion (Colwell et al., 2008; Feeley and Silman, 2009). This is a potentially serious threat to Amazonian–Andean biodiversity, since the lowland biota have few species to replace emigrating species along elevational gradients.

Unlike temperature, there is no clear consensus among GCMs as to how precipitation will change in the Amazon and tropical Andes. However, most models predict increased drying either due to lower total annual precipitation or longer and more severe dry seasons (Malhi et al., 2008). The sensitivity of tropical forests to water availability has been well demonstrated through both observational and experimental studies. Detailed Mesoamerican studies have shown that even relatively minor increases in dry season length/strength may lead to rapid declines in tree growth (Clark et al., 2009). The severe Amazonian drought of 2005 decreased tree growth and elevated tree mortality, resulting in lower forest biomass stocks and a net carbon emission (Phillips et al., 2009). These observations are supported by experimental rainfall exclusion from drought plots, which significantly increased large tree mortality (Nepstad et al., 2007). Rising temperatures coupled with decreased rainfall will likely trigger more frequent and more severe droughts in the Amazon. In some models, increased hydrological stress is predicted to trigger a large-scale forest dieback, followed by possible replacement by savannah-like habitat (Cox et al., 2004). While this has been questioned by several recent studies (see Cochrane and Barber, 2009), climate change in conjunction with other human disturbances has enormous potential to drive significant losses in forest biodiversity (Barlow and Peres, 2008; Malhi et al., 2008). Specifically, increased mortality of canopy trees due to dryer conditions may create large stocks of woody debris and open the canopy resulting in elevated flammability (Nepstad et al., 2004) which in turn will facilitate fire spread, especially if human access is enhanced through fragmentation and edge creation.

7. Conservation policy considerations

Although prioritizing biodiversity conservation across lowland Amazonia has been challenged on the grounds of putatively low

levels of endemism (Mares, 1992; Fjeldså and Rahbek, 1998), this largely reflects our disconcertingly large ignorance of fine- to broad-scale patterns of species distributions for even the best known vertebrate taxa such as birds and primates (see Table 1 in Peres, 2005). The Amazonian forest and freshwater biota remains severely undersampled, and its long evolutionary history has likely generated a yet-to-be-uncovered high level of cryptic diversity (Fjeldså, 1994). Concentrations of relatively archaic lowland species are in contrast with the relatively young species of the eastern slopes of the Andes. Priorities on any conservation agenda should include maximizing the protection of phylogenetic diversity (Crozier, 1997) and species-rich assemblages of disturbance-sensitive old-growth lowland forest specialists, especially in areas currently threatened by high levels of deforestation. Moreover, geologically older species exposed to long periods of geoclimatic stability are likely less preadapted to current environmental change and the buffeting effect of a fluctuating climate, as shown for ancient Southeast Asian forest vertebrate species, which are both more vulnerable to habitat degradation and have smaller geographic distributions (Meijaard et al., 2008).

Although the erosion of tropical forest biodiversity worldwide is most frequently associated with complete forest conversion to other land-uses, a myriad of additional processes have contributed to widespread population losses at local to regional scales, including surface fires, forest fragmentation, selective logging, and over-harvesting of non-timber resources such as game vertebrates (Laurance and Peres, 2006). The combination of these threats means that, one way or another, most of the Amazon can already be defined as "human-modified".

Drought sensitivity is a major determinant of species distributions of tropical forest trees (Engelbrecht et al., 2007; Butt et al., 2008) and other taxa, particularly in more aseasonal parts of lowland Amazonia and Andean cloud forests. Yet virtually the entire spectrum of forest disturbances highlighted in this review fractures or eliminates the protective structure provided by the forest canopy, driving increased incident radiation that desiccate the understorey. This is often followed by wholesale compositional

shifts in plant and animal communities at different stages of their life cycles as disturbance-sensitive species are replaced by gap-dependent and edge species under a novel microclimate. In the short-term, the consequences of this functional turnover to the overall impoverishment of old-growth forest assemblages depend largely on the extent, grain size, frequency and persistence of any pattern of disturbance. In the longer-term, the very hydrological viability of Amazonian forests could be put at risk as basin-wide water-cycling is weakened by the cumulative effects of large-scale deforestation, logging, and wildfire-mediated phytomass collapse (Sampaio et al., 2007; Malhi et al., 2008).

To protect Amazonian and Andean diversity from threats at the interface of land-use and climate change, decisive conservation measures are called for both at the global and regional scales (Killeen and Solorzano, 2008). At the global scale, elevated atmospheric concentrations of greenhouse gases must be reduced through both decreased emissions and increased sequestration, including the implementation of sustainable management, reforestation and other enhancements of carbon stocks included in Reduced Emissions from Deforestation and Degradation (REDD+) strategies (Butler and Laurance, 2008). At the regional scale, further agricultural expansion must be limited by increasing economic productivity of previously deforested areas. Concerted effort is needed to curb the threats of fire from profligate land-management, as well as depletion of functionally important vertebrate faunas through overhunting. Networks of public and private protected areas, supported by strategic ecological–economic zoning plans are needed to maintain habitat connectivity, ensure population viability in more isolated forest remnants and facilitate species migrations. Migrating species pose new challenges to conservation planning in that we need to protect not only the areas where species currently occur, but also the areas where they may occur in the future and the intervening areas through which they will move (Lee and Jetz, 2008).

As a final note of cautious optimism, unlike more densely settled parts of the tropics covered in this Special Issue, where forest reserves have become increasingly isolated (DeFries et al., 2005), Amazonia remains a relatively intact vast tropical wilderness with ample opportunities still available for expanding and strengthening the existing network of forest reserves of different denominations, which is already very substantial (see Fig. 4). Capitalizing on this narrow window of opportunity will require the dual-pronged approach of (1) designing and siting new reserves, which for now will have to rely on coarse-filter predictors of biodiversity distribution (e.g. Fearnside and Ferraz, 1995), but most importantly (2) effectively implementing the existing system of strictly protected, sustainable development and indigenous reserves 'on paper' (Peres, 2002). In the wider intervening matrix of unprotected areas, a range of socio-politically feasible deforestation-avoidance and reforestation strategies will need to be adopted, including strong incentive mechanisms that promote primary forest retention without strait-jacketing local economies and forest restoration of degraded pasturelands. The degree to which this can occur will rest critically on the political will of all tropical South American countries, the economically marginal Amazonian regions within those countries, and the leveraging of resources from corporations, multilateral banks, NGOs, universities, and international government agencies.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.01.021.

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