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Remaining natural vegetation in the global biodiversity hotspots

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ABSTRACT

The biodiversity hotspots are 35 biogeographical regions that have both exceptional endemism and extreme threats to their vegetation integrity, and as such are global conservation priorities. Nonetheless, prior estimates of natural intact vegetation (NIV) in the hotspots are generally imprecise, indirect, coarse, and/or dated. Using moderate- and high-resolution satellite imagery as well as maps of roads, settlements, and fires, we estimate the current extent of NIV for the hotspots. Our analysis indicates that hotspots retain 14.9% of their total area as NIV (~3,546,975 km^2). Most hotspots have much less NIV than previously estimated, with half now having ⩽10% NIV by area, a threshold beneath which mean NIV patch area declines precipitously below 1000 ha. Hotspots with the greatest previous NIV estimates suffered the greatest apparent losses. The paucity of NIV is most pronounced in biomes dominated by dry forests, open woodlands, and grasslands, reflecting their historic affinities with agriculture, such that NIV tends to concentrate in select biomes. Low and declining levels of NIV in the hotspots underscore the need for an urgent focus of limited conservation resources on these biologically crucial regions.

1. Introduction

The biodiversity hotspots are 35 biogeographic regions that cover 17.3% of the Earth's land surface (excluding Antarctica) and are characterized by both exceptional biodiversity and acute land-cover disturbance (Mittermeier et al., 2004; Myers et al., 2000). They are, in short, where human settlement, biological richness, and environmental degradation converge (Williams, 2013). Within the hotspots are over 2 billion people (Landscan, 2006; Mittermeier et al., 2011, 2004) increasing at higher-than-average rates (Cincotta et al., 2000; Williams, 2013), and an estimated 85% human-modified landscapes by area (Mittermeier et al., 2004). Hotspots sustain ~77% of all mammal, bird, reptile and amphibian species, including 50% of all plant species and 42% of terrestrial vertebrate species as endemics (Mittermeier et al., 2004), as well as three-quarters of all endangered terrestrial vertebrates (Brooks et al., 2002; Mittermeier et al., 1998, 2004). Cultural diversity is also high in the hotspots, with half of all indigenous languages found therein (Gorenflo et al., 2012).

Since the seminal publication of Myers et al. (2000) the concept of hotspots as focal points for global conservation action has become one of the foremost global conservation-prioritisation paradigms (Mittermeier et al., 2011). The concept has attracted over $1 billion in conservation investment from entities like the Critical Ecosystem Partnership Fund (i.e., World Bank, Global Environment Facility, and The Governments of Japan, France and Europe), The MacArthur Foundation, The Global Conservation Fund (i.e., Moore Foundation), Conservation International and its affiliated TEAM Program and Centers for Biodiversity Conservation, among many others (Dalton, 2000; Mittermeier et al., 2011, 1998, 2004; Myers, 2003; Myers and Mittermeier, 2003). These entities have explicitly adopted the hotspot concept as a central conservation-investment strategy. Whether or not the concept has garnered the "largest [monetary] sum ever assigned to a single conservation strategy" (Myers, 2003), its global traction and legacy are indisputable.

While it is accepted that primary vegetation has been widely disturbed in the hotspots and globally (Vitousek et al., 1997), precise estimates of remaining intact remnant vegetation at very large spatial scales have proven challenging and elusive. Global land-cover maps derived from moderate- or coarse-resolution satellite imagery have existed since the early 1990s (Bontemps et al., 2011; Dong et al., 2012; Friedl et al., 2010; Loveland et al., 2000) but afford only broad nominal classifications of vegetation reflectance, structure, and phenology and do not therefore readily distinguish *disturbed* covers from natural, primary, intact covers *per se*, particularly in environments that are naturally unforested or

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semi-forested, such as savannas. As illustrated below, an uncritical interpretation of such classifications in efforts to estimate the area of remaining natural intact vegetation is prone to significant error (Hoekstra et al., 2005). Global land-cover change analyses using satellite imagery are more promising insofar as they may exclude areas known to have undergone certain land-cover conversions (Hansen and DeFries, 2004; Hansen et al., 2013, 2008). Yet they remain similarly unable to address the integrity of supposedly ‘unchanged’ areas, which in a great many cases will be disturbed, and which in any case are observable at large spatial scales only at very coarse resolutions since the 1980s and at finer resolutions only since ca. 2000 with the advent of moderate-resolution imagery. While recent advances now provide relatively nuanced finer-scale measures of ‘percent tree cover’ and changes thereof since ca. 2000 (Hansen et al., 2003, 2013; Sexton et al., 2013), it has not been possible, nor will it likely be possible, to determine reliable thresholds identifying disturbed and thus undisturbed forest across large and varied regions, to say nothing of undisturbed vegetation in naturally semi-forested or unforested environments.

Two sets of relatively-derived estimates of remaining natural intact vegetation over large spatial scales have arisen in light of such issues. The first are those of Myers (1988, 1990), Myers et al. (2000), and Mittermeier et al. (1999, 2004), which entailed expert assessments of existing vegetation atlases, satellite-image classifications and similar secondary data for the hotspots. These estimates are now dated, difficult to replicate, and prone to inconsistency and approximation. The second set of estimates are those of Sanderson et al. (2002), Schmitt et al. (2009), Potapov et al. (2008), and Bryant et al. (1997), among others, which variously mapped intact areas with reference to criteria such as land-cover class, forest patch size, proximity to infrastructure, and accessibility. These estimates are problematic because they are either particular to closed-forest biomes, very large vegetation patches, or tree cover generally, or optimistically equate an absence of evidence of human disturbance with evidence of its absence. These are key limitations where habitats that are structurally and compositionally varied, heavily fragmented and under intense, proximate human pressure.

Updated and improved estimates of remaining natural intact vegetation (NIV) area in the hotspots are crucial for appropriate global conservation planning. Prior estimates have been used to prioritize hotspots for conservation action (Myers et al., 2000), determine their species-extinction susceptibility (Brooks et al., 2002; Malcolm et al., 2006), and calculate the costs their conservation (Pimm et al., 2001). In light of the uncertainties surrounding prior NIV estimates, such derivations are similarly subject to revision. A revision of hotspot conservation priority and attendant conservation action could have significant implications for future biodiversity loss and particularly its attenuation considering that biodiversity loss becomes increasingly exponential as the final vestiges of intact habitat are destroyed (Rybicki and Hanski, 2013; Turner, 1996). Rigorously updated NIV estimates for the hotspots are a matter of improved measurement for improved management.

Here we present updated, transparent, comprehensive and consistent estimates of NIV area and fragmentation for the world's biodiversity hotspots. The following section briefly reviews the hotspot concept and previous natural-area estimates. Section 3 discusses our methodology, and the subsequent sections present our estimates and highlight their implications for global conservation planning.

2. Hotspots and remaining natural vegetation

2.1. The hotspot approach and expert estimates

The hotspot concept prioritises the conservation of biologically-exceptional and highly-threatened regions with the explicit goal of stemming species extinction, as per the irreplaceability-vulnerability conservation framework articulated by Margules and Pressey (2000). Myers (1988) first encapsulated this concept globally by delimiting 10 largely tropical biogeographical regions of exceptional biodiversity and habitat destruction (Table 1) – the first ‘hotspots’, e.g., Madagascar, New Caledonia. Myers (1990) later added eight largely semi-arid hotspots to this list, e.g., Southwest Australia (Table 1). Conservation International adopted the hotspot concept as its central global conservation strategy in 1989 (Conservation International, 1990a,b; Mittermeier et al., 2004), and the concept has since become a major conceptual template among conservation scientists (Redford et al., 2003; Roberts et al., 2002; Sechrest et al., 2002; Turner et al., 2012; Willis et al., 2006). Myers, Conservation International, and collaborators later revised estimates of remaining primary habitat and defined the hotspots formally as biogeographic regions with >1500 endemic vascular plant species and $\leqslant$30% of original primary habitat (Mittermeier et al., 1999; Myers et al., 2000). Species endemism, rather than biodiversity *per se*, became a key definitional criterion given concern over extinction rates (Brooks et al., 2002; Mittermeier et al., 1998). This revision saw the hotspots expand in area as well as in number, to 25. A second global revision and update in 2004 (Mittermeier et al., 2004) expanded this count to 34 and adjusted hotspot boundaries to concord with the ecoregions of Olson et al. (2001). Recently, a 35th hotspot was added, the Forests of East Australia (Williams et al., 2011) (Fig. 1).

Mittermeier et al. (1999, 2004), Myers et al. (2000) and Myers (1988, 1990) present areal estimates of remaining natural intact habitat for the hotspots (Table 1). Their approach entailed first consulting estimates of vegetation cover and loss for those counties and/or regions within each hotspot, including vegetation atlases (e.g., Harcourt and Sayer, 1996), satellite forest-cover inventories (e.g., CCT/CIEDES, 1998), national environmental overviews (e.g., FWI/GFW, 2002), and occasionally the 1990 FAO Forest Resource Assessment (FAO, 1993). "Digitised forest cover data" from the World Conservation Monitoring Centre were also consulted (Mittermeier et al., 1998) (these data were uncited but are likely UNEP-WCMC (1996) or UNEP-WCMC (1998)). These estimates were then adjusted on the basis of expert opinion and unpublished data to estimate the area of "primary" or "more or less pristine" vegetation per hotspot (Mittermeier et al., 2004). Such adjustments sometimes reduced initial estimates by as much as 50%. Many of the source data were derived prior to the widespread use of GIS and satellite imagery at large scales, and no attempt was made to map primary vegetation in the hotspots.

The final estimates – hereafter termed *Expert Estimates* – while groundbreaking and widely adopted, are difficult to scrutinize and replicate. Expert adjustments of the initial estimates were not well documented and, in the absence of greater transparency, uncertainties tend to become generalized. The Expert Estimates derived from sources that were not necessarily comparable and occasionally had little explicit bearing on ‘primary’ versus ‘perturbed’ land covers. Further, many sources pertained to individual countries and it is unclear how these were adjusted to concord with the irregular biogeographic boundaries of hotspots (Fig. 1).

Perhaps more importantly, the Expert Estimates are increasingly dated. Even in the most recent update (Mittermeier et al., 2004) many of the data consulted span the 1980s and early 1990s, and habitat loss in the hotspots is certain to have advanced since (Balmford et al., 2002; Butchart et al., 2010; FAO, 2010; Hassan et al., 2005) as, among other drivers of habitat loss, increasing demand for agricultural products has been met in large part via continued habitat conversion (Gibbs et al., 2010; Laurance et al., 2014; Rudel et al., 2009). More recent global surveys of naturally vegetated areas have since been undertaken but, as argued below, these do not offer ready and reliable estimates for the hotspots.

Table 1
Natural vegetation area as percentages of originally-vegetated area, by hotspot and study.

		EXPERT ESTIMATES				INDEPENDENT ESTIMATES							NIV
Hotspot	Total Area (km^2)	Myers (1988) *Primary Forest*	Myers (1990) *Primary Forest*	Myers et al. (2000) & Mittermeier et al. (1999) *Primary Vegetation*	Mittermeier et al. (2004) *Primary Habitat*	McCloskey and Spalding (1989) *Wilderness*	Hannah et al. (1995)[k] *Undisturbed Areas*	Bryant et al. (1997) *Frontier Forests*	Sanderson et al. (2002) *Wild Areas*	Hoekstra et al. (2005) *Undisturbed Habitat*	Schmitt et al. (2009) *Relatively Natural Forest Cover*	Potapov et al. (2008) *Intact Forest Landscapes*	Present Study *Natural Intact Vegetation*
1. Atlantic Forest of Brazil	1,236,664	2♦	---	7.5♦	8	0.63	20♦	1.6	0.42	39.6	19.9	0.2[j]	3.5
2. California Floristic Province	294,463	---	76	24.7[e]	25	4.4	19	0	19.4	80.5	52.6	3[j]	34.8
3. Cape Floristic Region	78,731	---	66♦	24.3	20	0	17.1♦♦	0	23.5	85.4	19.1	0[j]	32.9
4. Caribbean Islands	230,073	---	---	11.3	10	0.12	12	0	2	49.8	19.6	0.6	5.8
5. Caucasus	533,852	---	---	10	27	0	---	0	1.2	52.7	16.7	4.1[j]	8.2
6. Cerrado	2,036,548	---	---	20	21.3	11	---	0.1	20.4	48.2	18	1.2	19.8
7. Chilean Winter Rainfall and Valdivian Forests	398,035	---	33[f]♦	30	30	16.3	---	15.8	25.4	87.5	33.7	15.3[j]	34.2
8. Coastal Forests of Eastern Africa	291,905	---	19♦	6.7[a]♦	10	1.3	---	0	9.1	87.8	64.4	0.2	3.8
9. East Melanesia Islands	99,630	---	---	---	30	0	---	20.6	1.5	91.6	72.3	25.3	10.7
10. Eastern Afromontane	1,020,095	---	---	6.7[a]♦	10.5	6.3	---	3.2	2.8	55.8	28.9	5.2	9.0
11. Forests of Eastern Australia	255,328	---	---	---	---	0	---	4.1	24.9	94.4	---	4.4	34.8
12. Guinean Forests of West Africa	621,706	---	2♦	10	15	7.4	6	1.5	0.6	40	37.5	3.2	10.6
13. Himalaya	743,371	15[b]	---	See Indo-Burma[b]♦	25[b]	4.7	See Indo-Burma[b] ♦	2.9	20.6	69.4	28.4	7.5[j]	17.6
14. Horn of Africa	1,663,112	---	---	---	5	14	34.4♦♦	0	19.3	92.5	0.12	0[j]	23.8
15. Indo-Burma	2,378,318			4.9[b]	5[b]	2.1	7[b]	3.8	3.6	37.5	31.2	3.2	8.7
16. Irano-Anatolian	901,790		---	---	15	0	---	0	1.3	71.4	0.22	0[j]	3.6
17. Japan	374,328	---	---	---	20	0	---	0	0.2	69.1	65.2	0.7	8.2
18. Madagascar & Indian Ocean	601,830	16♦	---	9.9	10	1.2	15	0	10.1	77.4	21.4	2.9[j]	4.4
19. Madrean Pine-Oak Woodland	462,300	---	---	---[c]	20	0.1	---	7.5	8.2	87.8	60.8	1.1	18.1
20. Maputaland-Pondoland-Albany	273,018	---	---	---	24.6	0	---	0	12.4	85.9	45.4	0	6.4
21. Mediterranean Basin	2,089,974	---	---	4.7	4.7	<0.1	5	0	2.9	60.3	12.7	0[j]	4.4
22. Mesoamerica	1,132,551	---	---	20[c]	20	3.8	50.8	11.2	3.6	53.8	52.4	4.2	14.1
23. Mountains of Central Asia	865,299	---	---	---	20	6.6	42.8♦♦	0	10.6	82.8	1.3	0[j]	5.8
24. Mountains of Southwest China	263,034	---	---	8	8	10.6	---	10.2	14.8	93.8	47.5	10.8	21.3
25. New Caledonia	19,015	10	---	28	5 [27][d]	0	0	0	74 0.4	96.5	31.5	0	17.5
26. New Zealand	270,803	---	---	22	22	13.2	27	7.7	28.6	70.1	28.1	16.1	30.2
27. Philippines	297,846	3	---	3	7	0	3	0	0.6	31.6	27.9	1.7	8.0
28. Polynesia-Micronesia	47,361	---	---	21.8	21	0	---	0	6.6	91	12.7	1.5	5.2
29. Southwest Australia	357,516	---	49♦	10.8	30	6.2	50.4♦♦	0	35.4	60.1	20.4	3.3[j]	30.6
30. Succulent Karoo	102,922	---	---	26.8	29	16.7	---	0	47.4	99.8	0.1	0[j]	6.5
31. Sundaland	1,504,430	33♦	---	7.8	6.7	4.8	20.3	20	24.8	54.8	50.1	11.4	22.8
32. Tropical Andes	1,546,119	35♦	---	25	25	5.9	7.9♦♦	10.8	21.5	82.9	27.5	10.2[j]	33.3
33. Tumbes-Chocó-Magdalena	275,203	64[h]		24.2	24	3.1	35.6	18.7	6.8	57.6	28	8.6	29.8
34. Wallacea	339,258	---	---	15	15	6.1	9.3	14.8	13.5	69.8	57.5	12.7	13.8
35. Western Ghats and Sri Lanka	190,037	---	12[i]	6.8	23	0	0	7.7	0.12	62.7	51	0	6.3
TOTAL less East Australia	**23,541,137**	---	---	---	**3,379,246 (14.3)**	**1,144,859 (4.8)**	---	**1,052,542 (4.4)**	**2,632,422 (11.1)**	**14,747,185 (62.6)**	**6,375,100 (27)**	**911,208 (3.8)**	**3,456,954 (14.6)**
TOTAL	**23,796,465**	---	---	---	---	**1,144,859 (4.8)**	---	**1,063,115 (4.5)**	**2,695,891 (11.32)**	**14,988,250 (63)**	---	**922,466 (3.9)**	**3,545,975 (14.9)**

Notes: See Table A1 for absolute aerial estimates and detailed interpretative notes a-k. Greyed cells indicate that the study in question delimited the hotspot in question inconsistently with Mittermeier et al. (2004). While absolute aerial estimates in greyed cells are not directly comparable with those of non-greyed cells, their percentage estimates may still be loosely comparable, except where denoted with a ♦ symbol. Delimitations for greyed cells were typically more confined than the current delimitations. Slight adjustments to published Expert Estimates and Independent Estimates have been made to enhance comparability, where indicated. Figures for the Independent Estimates were derived by using the original spatial data, excepting the published estimates of Hannah et al. (1995), Schmitt et al. (2009) and Wright (2010). ♦ As above. ♦♦ Estimate considered inexact (Table A1).

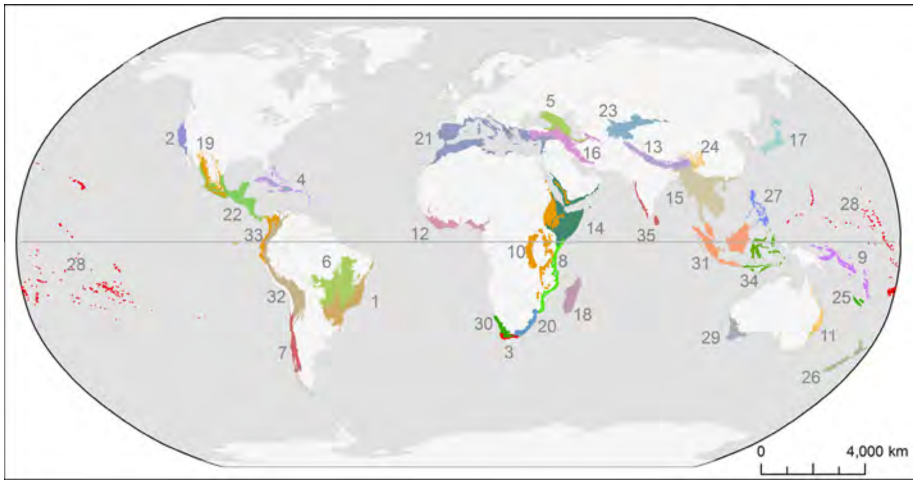

Fig. 1. The biodiversity hotspots. *Notes:* See Table 1 for hotspot names.

2.2. Independent estimates of natural areas

A second set of global natural-area estimates – here termed *Independent Estimates* – variously delineate natural unperturbed areas by combining satellite imagery, vegetation maps, and maps of human disturbances. These estimates may in turn be subdivided according to whether they observe the absence of human disturbance as a proxy for the presence of natural areas or rather observe natural vegetation more directly. Of the seven estimates discussed below, one was realised for the hotspots specifically (Schmitt et al., 2009), one was presented at the hotspot level (Hannah, 2001; Hannah et al., 1995), and the remainder were realised globally. The latter were not designed for the hotspots specifically, nor have they been explicitly brought to bear on matters of remaining natural area in the hotspots. Nonetheless they do present relevant empirical approaches for consideration, if not insight into the extent of natural areas within the hotspots, in light of the fact that the hotspots span nearly one-fifth of the Earth's land surface.

Among those analyses observing natural vegetation directly, Hoekstra et al. (2005) estimate intact habitat as areas exclusive of "cultivated and managed areas [as well as] artificial surfaces and associated areas" according to the 1-km Global Land Cover 2000 (GLC2000) satellite dataset (ECJRC, 2003). Schmitt et al. (2009) go further to define "relatively natural forest cover" by removing 'non-natural' areas from the satellite-derived 2000 Global Forest Map (UNEP-WCMC, 2000), namely agro-ecosystems and similar covers according to the GLC2000 dataset (ECJRC, 2003) as well as areas with <10% tree cover according to the MODIS Vegetation Continuous Field satellite dataset (Hansen et al., 2006). More precisely still, Potapov et al. (2008) delineated 'intact forest landscapes' within the 'zone of current forest extent' as contiguous natural ecosystems at least 1 km removed from settlements, roads and other infrastructure, agriculture, and burned areas, as visually observed in Landsat satellite imagery for forest patches >500 km^2.

While direct, these estimates do not necessarily approximate the total area and distribution of NIV in the hotspots. Their focus on forested biomes discounts the non-forest and open-forest vegetation formations such as savannahs or montane shrublands prominent in many hotspots, and even overlook some desert hotspots entirely (also true of Bryant et al. (1997), discussed below). Further, the GLC2000 data used by Hoekstra et al. (2005) and Schmitt et al. (2009) to distinguish natural from non-natural cover are prone to significant errors in this respect. Even after accounting for those GLC2000 land-cover classes clearly indicative of perturbation, there remain numerous generic classes such as 'Mosaic Tree Cover/Other Natural Vegetation' that often incorporate appreciably disturbed land covers, agricultural-forest gradations, and even agro-pastoral covers, as confirmed in the course of the present study. Without additional scrutiny, the GLC2000 dataset and thus Hoekstra et al. and Schmitt et al. overestimate what is reasonably termed natural forest (e.g., Kalacska et al., 2008; Fig. A1).

Among those analyses focusing on an absence of human disturbance as a proxy for unperturbed natural areas, McCloskey and Spalding (1989) delineated 'wilderness areas' as 6 km removed from all roads, tracks, and human structures (e.g., towns, gas wells) according to global navigational charts. Hannah et al. (1995, 1994) similarly mapped 'undisturbed areas' as having a record of primary vegetation and <10 people km^2 with reference to population and infrastructure maps as well as compiled land-cover maps, agricultural maps, and remote-sensing analyses. Bryant et al. (1997) delineated 'frontier forests' as large, natural, relatively undisturbed forests by identifying candidate areas with reference to McCloskey and Spalding (1989) and The World Forest Map (1996), and then revising these on the basis of expert opinion. Finally, Sanderson et al. (2002) made use of global GIS datasets of population density, settlements, major roads and rivers, broad land-cover classes, and coastlines to delimit 'wild areas' by deriving an additive index reflecting these features, normalizing the index to a 1–100% scale by biome and biogeographic realm, and then delimiting 'wild areas' as the ten largest areas having index values of <10% by biome and realm.

These estimates are too indirect and coarse to account for the fragmented remnant vegetation patches that, in the hotspots, often occur in close proximity to human disturbances and may comprise an appreciable proportion of total remanent vegetation (Ribeiro et al., 2009). They do not capture unperturbed vegetation *per se*, but rather conservatively map those larger and remote expanses distant from the disturbance proxies of interest (minimum mappable areas range from >500 km^2 to >4000 km^2, with scales around 1:1,000,000), as only such areas can be taken as 'natural' with any degree of confidence. Sanderson et al. (2002) is illustrative of the point. Their index implicitly reflects *'urbanality'*, that is, concentrations of roads, population, electric lights, and managed land covers. While high levels of urbanality would correspond with high levels of disturbance, less 'urban' environments are not necessarily proportionally less disturbed or more natural. Indeed, even a single road and sparse rural population can decimate an otherwise intact area (Laurance et al., 2009). An 'absence of evidence' of human disturbance is taken as 'evidence of absence', so that only the very lowest disturbance values may be taken as indicative of 'natural areas', and only then at broad scales. These 'natural areas' are by definition the most remote, extensive, and spatially-confined, and their delineation thus neglects vast swaths of the hotspots' intervened and 'cluttered' landscapes.

3. Methods

In consideration of such issues, we estimated NIV area in the hotspots via a combination of automated and visual satellite-image analyses of land-cover classes and conditions as well as the mapping of major landscape disturbances. The methodology may be summarised by two stages. In the first we assessed the vegetation condition, spatial pattern, and local ecological appropriateness of each land-cover class of the global GlobCover 2009 satellite-image classification (Bontemps et al., 2011) for each ecoregion of Olson et al. (2001) (Fig. A2) using moderate- and high-resolution satellite imagery, and defined preliminary 'naturally occurring' areas on that basis. In the second, we removed disturbed areas according to various disturbance maps. NIV is defined broadly as mature vegetation in its natural state having minimal signs of human perturbation. The following details our approach (see also Text A1 in online appendix).

3.1. Stage One: preliminary classification

The moderate-resolution GlobCover global land-cover classification defining 22 classes (Table 2; Bontemps et al., 2011) was combined with the ecoregions dataset of Olson et al. (2001) to yield 6863 unique combinations of land-cover class by ecoregion within the hotspots. Each class-by-ecoregion combination was assessed individually in order to account for the biogeographic heterogeneity within the hotspots. For each class-by-ecoregion combination a preliminary classification of 'naturally occurring' or 'other' was made via consideration of three criteria – namely, local ecological appropriateness, integral spatial pattern, and vegetation condition with few signs of human perturbation – with each criteria yielding a nominal likelihood that the combination is naturally occurring.

Table 2
Land-cover classes of the GlobCover 2009 dataset.

Post-flooding or irrigated croplands (or aquatic)
Rainfed croplands
Mosaic cropland (50–70%)/vegetation (grassland/shrubland/forest) (20–50%)
Mosaic vegetation (grassland/shrubland/forest) (50–70%)/cropland (20–50%)
Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5 m)
Closed (>40%) broadleaved deciduous forest (>5 m)
Open (15–40%) broadleaved deciduous forest/woodland (>5 m)
Closed (>40%) needleleaved evergreen forest (>5 m)
Open (15–40%) needleleaved deciduous or evergreen forest (>5 m)
Closed to open (>15%) mixed broadleaved and needleleaved forest (>5 m)
Mosaic forest or shrubland (50–70%)/grassland (20–50%)
Mosaic grassland (50–70%)/forest or shrubland (20–50%)
Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5 m)
Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
Sparse (<15%) vegetation
Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) – fresh or brackish water
Closed (>40%) broadleaved forest or shrubland permanently flooded – Saline or brackish water
Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil – fresh, brackish or saline water
Artificial surfaces and associated areas (Urban areas >50%)
Bare areas
Water bodies
Permanent snow and ice

The biophysical characteristics of the GlobCover land-cover classes (Table 2; Bontemps et al. (2011)) were considered relative to ecoregion descriptions and characteristics in order to flag classes that were locally 'ecologically appropriate', that is, likely (or unlikely) to be naturally occurring in a mature state a given ecoregion. For example, the class "closed to open (>15%) shrubland (broadleaved or needleleaved, evergreen or deciduous, <5 m)" was considered unlikely to be naturally occurring in the 'Araucaria Moist Forests' ecoregion of the Atlantic Forest hotspot, considering that this ecoregion is naturally dominated by tall, closed-canopy moist tropical forests exclusive of shrublands. However, this class was considered likely to be naturally occurring within the 'Atlantic Coast *Restingas*' ecoregion of the same hotspot, as this ecoregion is characterised by mixed coastal shrubs, grasses, and low tree cover on poor soils.

The spatial pattern of each class-by-ecoregion combination was visually assessed at the 300-m spatial resolution of the GlobCover classification using both a GIS (Fig. 2) and high-resolution imagery in Google Earth (Fig. 3). This analysis similarly identified class-by-ecoregion combinations that were likely or unlikely to be naturally occurring by considering the following three aspects of spatial pattern: (i) Spatial associations, principally in the form of consistent adjacency or coincidence with clearly disturbed land covers (e.g., croplands) or ancillary disturbance on settlements, roads and fires, described below. Such associations frequently identified moderately-disturbed covers separating highly-disturbed covers from intact covers (Fig. 2a–c); (ii) Patch contiguity, shape, texture, and size, as for example observed as smooth or abrupt vegetation patch edges, gradual or sudden land-cover transition gradients, and acute patch fragmentation and isolation (Fig. 2d–f). Such aspects of pattern often helped identify unmanaged but still disturbed remnant patches in larger managed landscapes, e.g., disturbed forest/grassland mosaic patches in pastoral landscapes within a larger humid tropical forest settings;, and (iii) Biogeographic context suggestive of particular land-cover distributions and gradients, e.g., elevational gradients from closed forest to montane steppe in mountainous terrain, or precipitation gradients from coastal forests to inland grasslands in semi-arid regions. Such distributions and gradients helped to more confidently flag non-forest land covers as locally appropriate and thus likely to be naturally occurring (Fig. 2d and f). Finally, the vegetation condition and disturbances of each class-by-ecoregion combination were visually inspected using high-resolution imagery in Google Earth (Fig. 3). This imagery showed the condition and context of vegetation cover in minute detail and served to confirm the general status of a given class-by-ecoregion combination, e.g., whether a given area of 'Closed to Open Herbaceous Vegetation' was largely intact remote grasslands or rather fenced and grazed pasture, or whether 'Mosaic Forest or Shrubland / Grassland' was indicative of unnatural forest perturbation or rather natural variation in the forest canopy or structure. Inspection of this imagery also facilitated the detection and appropriate treatment of misclassified or otherwise incompletely classified nominal land covers, e.g., in certain Mediterranean ecoregions, the 'Mosaic Grassland/Forest or Shrubland' class was observed to incorporate disperse low-intensity agriculture alongside extensive grazing (grasslands) and shrubs, and was therefore treated as such when determining whether a relevant combination constituted 'naturally occurring' vegetation. Instances of outright misclassification were rare, whereas instances of incomplete classification such as described above were rare but relatively more common, reflecting the marked diversity and heterogeneity of land covers within and between the hotspots. In this way, the inspection of high-resolution imagery verified not only that a given land-cover class in a given locale was natural and intact, but also that its actual land-cover composition was as described by the GlobCover global land-cover classification and treated accordingly if otherwise.

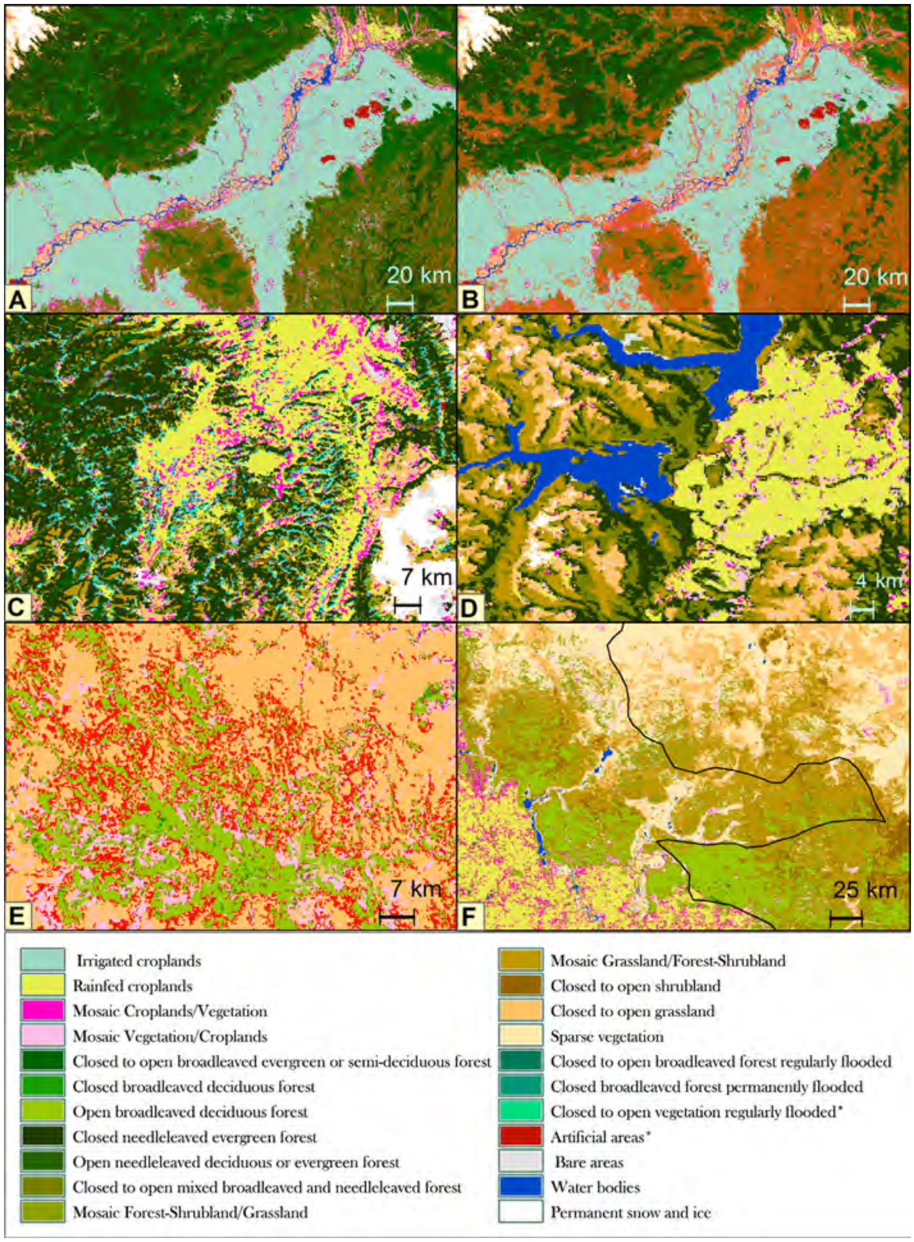

Fig. 2. Land-cover association, contiguity, and biogeographic context for visual analysis. *Colour may not correspond to the class in question in a given panel. See interpretive notes. *Interpretive Notes:* Panels A and B: Irrigated cultivated river valley in southwest Himalayas hotspot. The coincidence of 'closed to open shrubland' in Panel A with fire hotspots in Panel B (orange dots), as well as a proximity to agriculture, suggests local perturbation. Panel C: In the Mts of Central China, 'closed to open mixed broadleaved and needleleaved forest' (highlighted in aqua) tracks the agriculture-forest interface in narrow bands, including in cultivated river valleys, separating agriculture from more substantial expanses of closed forest, thus suggesting that it is naturally occurring. Panel D: In mountainous southern New Zealand, the contiguity of vegetation classes indicates the integrity of vegetation cover, as well an elevational gradient along which shrubland and bare lands occur naturally. Panel E: In contrast, in southwest Maputaland-Pondaland-Albany, sharp and 'spattered' fragments of 'mosaic forest-shrubland/grassland' (highlighted in red) suggest an intervened state, as does a consistent adjacency with (pastoral) grasslands. Panel F: In the northern reaches of the South West Australia hotspot is a gradient from open forest to shrub-grassland mosaics to open grasslands and bare areas, tracking a declining precipitation gradient with distance from the coast. Non-forest classes in this context are more confidently interpreted as naturally-occurring vegetation despite their proximity to (well-fenced) agro-pastoral activities.

Where the assessments of these three criteria agreed in their determination of 'naturally occurring' or 'other', a class-by-ecoregion combination was classified accordingly. In rare cases of disagreement or an indeterminacy of a given criterion, the assessments were revisited and revised for consensus, typically settling on determinations made on the basis of the high-resolution imagery in Google Earth.

Visual analyses in the production of this preliminary 'naturally occurring' classification were favoured over potential automated quantitative 'thresholding' or change-detection analysis or similar that might have been adapted (e.g., Hansen and DeFries, 2004). The great diversity and contextuality of land covers, landscapes, disturbances, biogeographies, and ecosystems in the hotspots preclude the use of quantitative classifiers to this end, which in any case have no explicit bearing on the status of 'unchanged' lands (Hansen et al., 2013). In this respect, visual analysis provides a far more nuanced tool with which to discriminate 'naturalness' in satellite imagery, and has been increasingly adopted for this purpose (King, 2002; Margono et al., 2012; Miettinen and Liew, 2010; Potapov et al., 2008; Zhuravleva et al., 2013). In the present

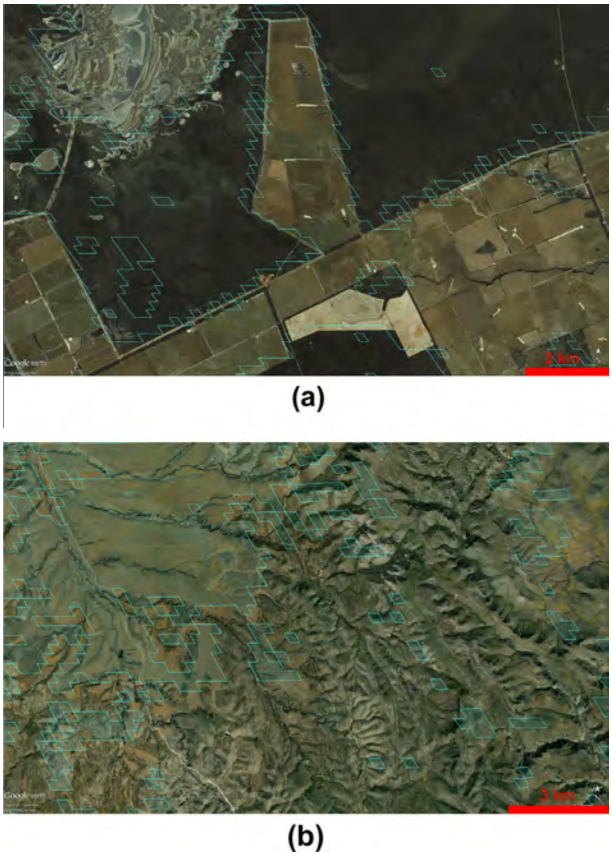

Fig. 3. Visual inspection of class-by-ecoregion combinations using google earth: (a) Land-Cover Class 'Open (15–40%) broadleaved deciduous forest/woodland (>5 m)' in Ecoregion 'Esperance Mallee', South West Australian Hotspot (latitude 33°16′09.60″S, longitude 121°00′21.76″E), (b) Land-Cover Class 'Closed to open (>15%) shrubland (broadleaved or needleleaved, evergreen or deciduous, <5 m)' in Ecoregion 'Sierra Madre Occidental Pine-Oak Forests' in Madrean Pine-Oak Forests Hotspot (latitude 29°44′22.03″N, longitude 107°17′25.08″W).

study visual analysis was particularly useful for open-forest mosaic and shrubland/grassland mosaic environments wherein intact and disturbed covers may have similar structures and nominal land-cover classes and where land-cover classification accuracy may be relatively low.

3.2. Stage Two: human disturbances

This preliminary classification of naturally-occurring areas was subjected to a series of disturbance 'filters' to remove major disturbed areas from its extent (Text A1), similar to Potapov et al. (2008), Sanderson et al. (2002), and Hannah et al. (1995). The disturbance filters removed the following areas:

(i) Burned sites, observed daily or near-daily at ∼900 m pixel resolution over 1995–2012 using MODIS FIRMS (Davies et al., 2009; NASA and University of Maryland, 2012) and ATSR World Fire Atlas (Arino and Rosaz, 1999; ESA DUE, 2012) satellite data (Fig. A3), exempting arid or fire/adapted hotspots (excluded hotspots are No. 2, 3, 5, 6, 11, 14, 16, 21, 26, 29, and 30 in Table 1). Burned sites capture the direct spatial and temporal relationships between active agricultural disturbance and fires (Eva and Lambin, 2000), both of which have increased exponentially in the tropics and subtropics over the 20th Century (Mouillot and Field, 2005; Pechony and Shindell, 2010) to the point where the vast majority of the tropics and subtropics host highly unnatural anthropogenic fire regimes (Crutzen and Goldammer, 1993; Hoekstra et al., 2010; Saarnak, 2001; Shlisky et al., 2007);

(ii) Major roadways according to the gROADS v1 (CIESIN, 2013) and VMap0 (NIMA, 2000) global road datasets, valid as of 2010 or earlier depending on country. Roads were rendered as 900-m swaths (i.e., 300 m on either side of a road pixel) in keeping with observations of the proximate ecological effects of roads (Forman, 2000; Forman and Deblinger, 2000). Roads not only facilitate habitat conversion (Southworth et al., 2011) but deleteriously divide and isolate habitats and their fauna locally (Forman and Alexander, 1998; Laurance et al., 2009; Trombulak and Frissell, 2000)

(iii) Settlements, including small villages and disperse communities, observed as electric night lights at 500-m pixel resolution via 2010 DMPS-OLS satellite data (NOAA, 2010). Settlements are indicative of local human impacts, such as hunting (Abernethy et al., 2013), fuel-wood collection (Leach and Mearns, 1988), or simply the local displacement of ecological functions. Settlements were not 'buffered' spatially, but immediately adjacent vegetation illuminated by electric lights was excluded, typically at distances ranging from <∼1–2 km for smaller towns to ∼5–10 km for major bright cities; and

(iv) Small fragments and patch edges, defined respectively as fragments <100 ha and pixels immediately adjacent to non-natural areas. These parameters are in keeping with observations of species extirpation and the loss of ecological function in small fragments (Gibson et al., 2013; Laurance et al., 2002; Turner, 1996) as well as a review citing 273 m as the mean distance to which 'edge effects' penetrate tropical forests patches (Broadbent et al., 2008).

The parameters for these various disturbance filters are conservative for their spatial resolution and in comparison to similar parameters in studies distinguishing 'intact' from 'perturbed' areas (Bucki et al., 2012; Laporte et al., 2007; Margono et al., 2012; Potapov et al., 2008; Sanderson et al., 2002; Zhuravleva et al., 2013). A sensitivity analysis of parameters for the settlement-extent and fragment-size filters – for which a wider range of more and less conservative parameters were possible – found NIV to vary only by <1.8% by hotspot area relative to current estimates and recommend the present parameter values as the most precise and reasonable (Text A2). Following this filtering process, the remaining 'naturally occurring' area constituted the final NIV estimate.

Our approach combines fine-scale, direct observation of vegetation condition and ecological appropriateness with local contextual information of human activities and disturbances. As such it adopts the strengths of previous estimates while avoiding their problematic aspects concerning generality, certainty, scale, transparency, and the range of ecotypes surveyed. Assessments of the NIV delineation in the Atlantic Forest and Sundaland hotspots confirm that the delineation is largely confined to natural, intact, unperturbed vegetation (Text A1). In Sundaland, the NIV delineation excludes 95% of the timber and tree-crop plantation area established over 1980–2010 and 64–83% of the length of selective-logging roads established over 1972–2010 as manually digitised using time-series Landsat satellite imagery having a 30-m spatial resolution (Gaveau et al., 2009, in press). In the highly fragmented and disturbed Atlantic Forest hotspot, the NIV delineation conservatively encompassed 'total forest cover' (including sucessional forest cover) manually digitised using Landsat imagery for 2004/2005 (SOSMA/INPE, 2008), excluding some 41% due to the disturbance filters and approximating at least 79–88% of the total potential NIV area.

4. Results

4.1. Natural intact vegetation in the hotspots

While not directly comparable, previous estimates of natural area in the hotspots are nonetheless significantly variable, tending towards high or low extremes partially reflecting methodological approach (Fig. A1, Table 1). Previous inventories spanning all hotspots range from 992,466 km^2 to just greater than 6,375,100 km^2, or higher if considering Hoekstra et al. (2005) (Table A1). According to our estimates, the hotspots retain 3,545,975 km^2 of NIV or 14.9% of their original extent (Table 1, Fig. 4, Fig. A1).

Our estimates most resemble those of Mittermeier et al. (2004), at 3,379,246 (excluding East Australia) and give credence to the global hotspot conservation prioritisation informed by the Expert Estimates. However, our estimates also reveal a systematic difference with these prior estimates. Hotspots which Mittermeier et al. (2004) estimated to retain relatively larger percentage areas of primary vegetation are adjusted downward most severely by the present analysis (Fig. 5). Hence there is a significant inverse correlation between these previous estimates and their discrepancies with the present estimates (correlation for hotspots registering downward adjustments: $r = -0.44$, $p < 0.05$, $n = 22$; correlation for all hotspots: $r = -0.37$, $p < 0.05$, $n = 34$). Therefore, those hotspots previously deemed to be least threatened are now those wherein habitat loss appears to have advanced most aggressively. Conservation prioritisation among the hotspots may require adjustment to reflect these trends.

The hotspots are generally more perturbed than previously observed. Of the 20 hotspots with ⩾20% natural area according to Mittermeier et al. (2004), only 7 are now estimated to have ⩾20%, again with many of these suffering significant downward adjustments (Table 1, Fig. 5). There are now 17 hotspots with ⩽10% natural intact vegetation, compared to 10 in Mittermeier et al. (2004) (Table 1, Fig. 5). While the number of hotspots with ⩽5% natural vegetation is comparable, at 5 and 4, respectively, 10 hotspots cross this threshold once NIV patches <1000 ha are excluded from consideration (Text A2), highlighting their highly fragmented status. Indeed, we observe an inverse relationship between mean NIV patch size and the percentage of hotspot area in NIV indicating that that mean patch size drops precipitously below 1000 ha once NIV area falls below 10% (Fig. 6). The apparent trend towards lower levels of NIV with attendant fragmentation bodes poorly for global biodiversity considering that biodiversity declines exponentially with incremental losses of habitat and that each hotspot is uniquely biodiverse (Rybicki and Hanski, 2013; Storch et al., 2012).

Contrasting these dire hotspots are 10–12 hotspots for which the area of natural intact vegetation is greater than previously estimated (Fig. 5). These tend to be mountainous, Mediterranean-type and/or non-tropical hotspots for which non-forest and open-forest land covers contribute relatively large proportions of natural area.

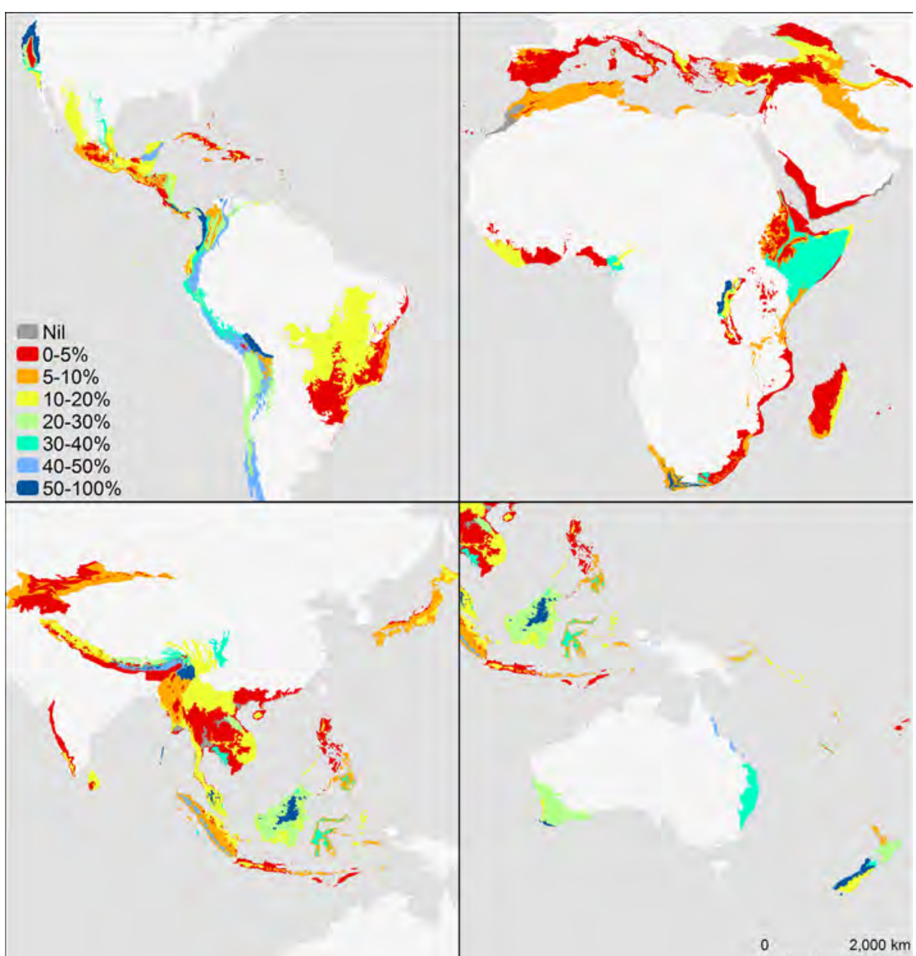

Fig. 4. Percent natural intact area in the hotspots, by ecoregion. *Note:* Ecoregion boundaries not apparent where adjacent ecoregions have the same colour. A global view is given as Fig. A4.

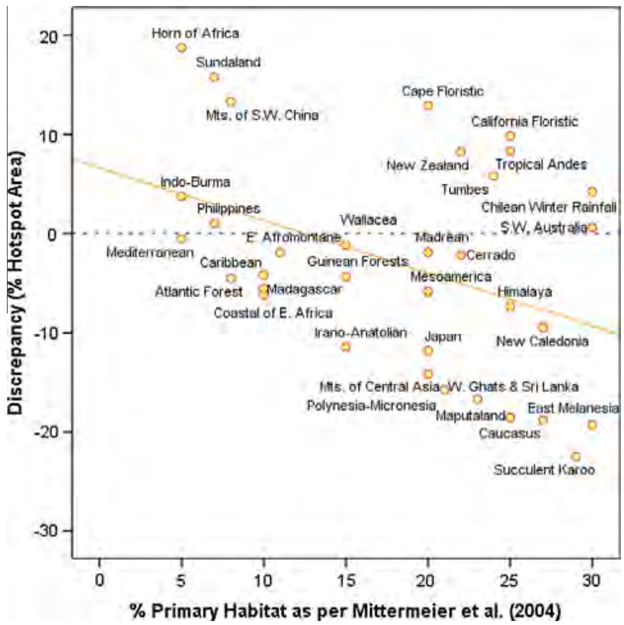

Fig. 5. Present estimates of natural intact vegetation versus estimates of Mittermeier et al. (2004), as percentage of hotspot area. *Notes: Y*-axes indicates the discrepancy between the present NIV estimate and that of Mittermeier et al. (2004), defined as the present estimate less that of Mittermeier et al. (2004), expressed in terms of percent hotspot area. The orange line is a regression line-of-best-fit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

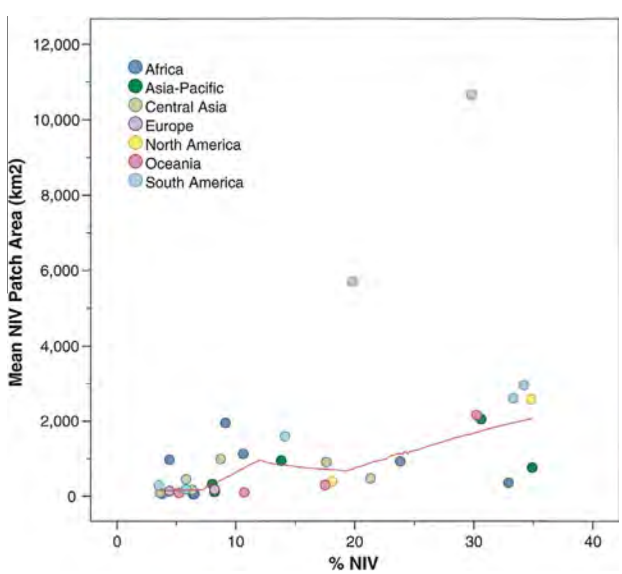

Fig. 6. NIV Area versus Mean NIV patch size by hotspot. *Notes:* Sundaland is an extreme outlier on the *y* axis due to large contiguous forest in highland central Borneo, and so is excluded to enhance the visibility of the other data. Line-of-best fit is defined by iteratively-weighted lest-squares biweight loess function robust to outliers (Jacoby, 2000). Mean patch sizes are conservatively high, given the moderate-resolution imagery and filtering process defining NIV, but trends are unaffected. Hotspot grouping by world regions are as follows, where hotspot numbers are as per Table 1: Africa: 3, 8, 10, 12, 14, 18, 20, 30; Asia–Pacific: 11, 17, 27, 29, 31, 34; Central Asia: 13, 15, 16, 23, 24, 35; Europe: 5, 21; North America: 2, 19; Oceania: 9, 25, 26, 28; South America: 1, 4, 6, 7, 22, 32, 33.

In the vast majority of these cases, present estimates are also greater than those of Sanderson et al. (2002) and Potapov et al. (2008). These positive increments therefore likely reflect the more precise accounting of such land covers by the present analysis as well as a finer accounting of non-forest and open-forest fragments in proximity to disturbances. For three such hotspots (Sundaland, Mts of SW China, Horn of Africa) the increment is particularly notable, both for its magnitude and for the fact that these hotspots were previously estimated to be highly disturbed. The other hotspots experiencing positive increments were relatively less disturbed, however, such that their increments represent a more limited but still important boost to overall biodiversity retention. Indeed, there are now seven hotspots having just over the 30% NIV threshold criterion defining a hotspot.

4.2. The distribution of natural areas

Within the hotspots the spatial distribution of NIV across biomes (Olson et al., 2001) and the Global 200 Ecoregions (Olson and Dinerstein, 1998, 2002) provides further insight into the precarious global status of NIV (Table 3). The Global 200 Ecoregions are "the set of ecoregions with the greatest biological distinctiveness based on ... species richness, endemism, taxonomic uniqueness ..., unusual ecological or evolutionary phenomena ..., and global rarity of [major habitat type]" (Olson and Dinerstein, 1998: 509). These are, in a sense, the priority areas within the priority areas. Analysis of the distribution of NIV across these two biogeographical classifications yields mixed results. One the one hand, the percentage area of NIV within the Global 200 Ecoregions is modest but slightly more than for the hotspots generally, at 18.3% versus 14.9% respectively (Tables 3 and 1). On the other hand, the biome-level inventory reveals a marked scarcity of NIV in particular biomes.

Six of the 12 biomes represented across the hotspots are of a critical status, hosting <10% NIV by area (Table 3). These are dominated by dry forests and woodlands, grasslands, and savannas, all of which have strong historical affinities with agro-pastoral activity (Baldi et al., 2013; Jones, 1989; Miles et al., 2006) (Text A3). The paucity of NIV within these biomes implies that their flora and fauna are highly and disproportionately perturbed and therefore that species survival in the hotspots may now be increasingly confined to the subset of relatively intact biomes. This paucity is also manifest in various individual hotspots, most of which are relatively perturbed. Of the 25 hotspots with at least two biomes and ⩽95% of their total area in their predominant biome (Table A2), nine hotspots register appreciably high 'coefficients of concentration' (Joseph, 1982) of NIV across their biomes, at 25–43%

Table 3
Natural intact vegetation for the global 200 Ecoregions and by Biome, for areas within the hotspots.

	Region	Area (km^2)	% NIV
	Global 200 Ecoregions	15,003,805	18.3
Biomes	Flooded Grassland and Savanna	31,782	3.8
	Temperate Grassland, Savanna and Shrub	918,262	3.9
	Desert and Xeric Shrubland	1,028,587	3.8
	Tropical/Subtropical Dry Broadleaf Forest	1,589,574	6.5
	Mangrove	181,851	8.8
	Mediterranean Forest, Woodland, Scrub	2,757,057	9.9
	Tropical/Subtropical Coniferous Forest	710,834	14.1
	Tropical/Subtropical Moist Broadleaf Forest	8,768,717	14.9
	Montane Grassland and Shrubland	1,848,056	17.6
	Temperate Broadleaf and Mixed Forest	1,946,196	18.6
	Tropical/Subtropical Grassland, Savanna, Shrub	3,191,784	24.1
	Temperate Coniferous Forest	678,548	27.2

Notes: Global 200 Ecoregions are according to Olson and Dinerstein (1998, 2002). Some 65 Global 200 Ecoregions were selected for analysis where contained by or concordant to the hotspots, or very nearly so. These Global 200 Ecoregions encompass 178 ecoregions of Olson et al. (2001) (Table A3). Biomes are according to Olson et al. (2001) and mapped by ecoregion. The total area of the biomes is slightly less than the total area of the hotspots in Table 1 because the 'lakes' and 'rock and ice' biomes are excluded.

(Table A2). Of these nine hotspots, seven are relatively disturbed, having <15% NIV by area. Collectively these observations signal that although the most biologically distinctive ecoregions appear no more perturbed than the hotspots generally, many hotspots have lost major biogeographical components of their overall biodiversity, as indeed have the hotspots generally.

5. Discussion

The biodiversity hotspots are a key foundation of global conservation prioritisation, action, and funding, and aerial estimates of their remnant vegetation are an important metric used to prioritise among the hotspots. Despite this and the intimate relationship between biodiversity retention and the extent of remaining habitat (Brook et al., 2006; Brooks et al., 2002; He and Legendre, 1996), prior estimates of remaining natural intact vegetation in the hotspots were generally wanting. We have presented updated estimates, and find the state of the hotspots to be more critical than previously described, particularly for those hotspots considered to be relatively intact. Our estimates derive from straightforward observations of publicly-available data and may therefore serve as a replicable first-order benchmark to periodically track the status of the hotspots. In this way, conservation priorities may be updated accordingly, and remedial action taken relatively quickly (Martin et al., 2012).

The present estimates underscore the tough choices facing global biodiversity conservation. Increased funding is needed to arrest the decline of the hotspots, but shortfalls are daunting (Balmford et al., 2003; McCarthy et al., 2012; Waldron et al., 2013). Twenty-nine of the 50 countries with the most underfunded biodiversity conservation programs are concentrated in the hotspots. These countries require an additional $620 million per year merely to approximate globally comparable funding levels, and much more to meet their conservation targets (Waldron et al., 2013). These countries span only a fraction of the hotspots' total extent, yet alone their shortfalls are significant if considering that biodiversity conservation funding in developing countries derives almost entirely from $2 billion per annum of international 'biodiversity aid' and NGO support (Waldron et al., 2013). For comparison, the funding for the effective management of important bird areas globally (BirdLife International, 2014) – a proxy for the hotspots with about half their global extent – is over $7 billion, and only half met, while funding requirements for additional protection are orders of magnitude greater (McCarthy et al., 2012).

Against this reality, the hotspots are generally not faring well (Canale et al., 2012). Conservation success stories exist (Kierulff et al., 2012), but they are situated in the context of an ever-steeper uphill battle. The prospect of funding 'triage' among hotspots arises (Bottrill et al., 2008), however unthinkable. Yet this prospect would ultimately present particularly difficult choices in these endemic-rich regions. The most disturbed hotspots, being presumably the first choice for triage, will also host the greatest number of endemics closer to extinction. Thus, the most disturbed hotspots are those wherein any conservation expenditure may well have the greatest conservation utility (extinction prevention) but also the greatest financial inefficiencies and logistical challenges. By most standards this utility prevails over the inefficiencies, once multiplied by the hundreds of vulnerable, endangered, and critically endangered endemic species within a given hotspot. We therefore renew calls for increased and targeted funding, but recognise that it will require judicious allocation as well as debate over the values underling notions of conservation 'optimisation'.

The present estimates also highlight the uncertainties of global biodiversity retention in the hotspots. The *primary* habitat of the hotspots has long been discussed as essential to biodiversity retention. In reference to the Expert Estimates, Myers et al. (2000) for example describe the vast endemic biodiversity of the hotspots as being "confined to [remaining primary habitat] comprising only 1.4% of the land surface of the Earth". This is not entirely the case, however. Recent analyses emphasize the species richness of successional and logged tropical forests (Dent and Wright, 2009; Dunn, 2004; Putz et al., 2012), although fewer such studies exist for drier or non-forest biomes. Similarly, predictions of the number of extinct or threatened birds, plants, reptiles, and amphibians in the hotspots based on Myers et al.'s (2000) 'primary habitat' figures appreciably overestimate the actual numbers, seemingly because secondary vegetation was overlooked, among other factors (Brooks et al., 2002). Secondary vegetation is increasingly ascendant in many regions (Aide et al., 2013; Asner et al., 2009; Gaveau et al., 2013, in press), complementing degraded primary cover. Indeed, there are between 3.1 and 7.5 parts secondary/degraded vegetation for every part NIV estimated here if the estimates of Schmitt et al. (2009) and Hoekstra et al. (2005) (Table 1) may be respectively taken as conservatively and liberally inclusive of secondary/degraded vegetation. While neither secondary nor degraded cover may substitute for the biodiversity of intact primary cover (Gibson et al., 2011), the proportion of species actually requiring primary mature habitats or tolerating disturbed habitats remains less certain (Wright, 2010), as does therefore their fate in 'mixed landscapes'. Having established the decline of NIV and that secondary and degraded formations may retain appreciable species richness, for a time at least, the potential non-linearities of species tolerances to increasingly secondary and degraded biogeographic regions in the hotspots should receive greater attention. Such uncertainties should however in no way detract from the Precautionary Principal advocating aggressive and urgent NIV conservation in the hotspots.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.05.027.

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