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LETTER

Final countdown for biodiversity hotspots

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Abstract

Most of Earth's biodiversity is found in 36 biodiversity hotspots, yet less than 10% natural intact vegetation remains. We calculated models projecting the future state of most of these hotspots for the year 2050, based on future climatic and agroeconomic pressure. Our models project an increasing demand for agricultural land resulting in the conversion of >50% of remaining natural intact vegetation in about one third of all hotspots, and in 2–6 hotspots resulting from climatic pressure. This confirms that, in the short term, habitat loss is of greater concern than climate change for hotspots and their biodiversity. Hotspots are most severely threatened in tropical Africa and parts of Asia, where demographic pressure and the demand for agricultural land is highest. The speed and magnitude of pristine habitat loss is, according to our models, much greater than previously shown when combining both scenarios on future climatic and agroeconomic pressure.

KEYWORDS

agricultural area expansion, biodiversity loss, climate change, demographic pressure, habitat conversion, habitat deterioration, living standard, protected area, species loss

1 | INTRODUCTION

More than half of all endemic plant and terrestrial vertebrate species, and probably similar proportions of less well-known megadiverse groups such as invertebrates and fungi, are only found in 36 global biodiversity hotspots that collectively comprise just 2.5% of Earth's land surface (Myers et al., 2000; Noss et al., 2015; Stork & Habel, 2014). Most hotspots are located in tropical developing countries that house more than a third of the global human population (Veech, 2003). These countries face strong challenges, such as high demographic pressure, food shortage, poverty and corruption (Williams, 2011). These problems are expected to multiply in the future (Bradshaw & Brooks, 2014). Current estimates indicate that in most hotspots less than 10% of natural intact vegetation (NIV) remains (i.e., nondisturbed pristine ecosystems, see Sloan, Jenkins, Joppa, Gaveau, & Laurance, 2014). Since such NIV is essential for the survival of many species, its potential rapid conversion into agricultural land is assumed to have severe consequences for biodiversity (Bradshaw & Brooks, 2014; Venter et al., 2016a,b). In addition to the complete destruction of NIV, its deterioration through the exploitation of natural resources such as timber harvesting and the collection of wood for domestic use (such as cooking) is leading to what is known as “empty forests” (Wilkie et al., 2011).

Recent modeling of future land use change impacts on habitats and biodiversity found that by the year 2100, global NIV will be reduced by a further 26–58%, with estimated species extinction of 0.2%–16% based on species-area models (Jantz et al., 2015). While this study focused on the impact of land use change on ecosystem health and biodiversity, and other studies examined the influence of climate change (Midgley, Hannah, Millar, Rutherford, & Powrie, 2002, Thomas et al., 2004), we here combine both factors and run joint models for 33 hotspots for the year 2050. While the changes in climatic conditions are highly dependent on the global circulation system, agroeconomic pressure strongly depends on local and regional factors, such as demographic pressure, land-use practices, human development, and societal factors like political stability (Roe & Siegel, 2011). However, both factors may also influence each other, antagonistically (when climate change causes lower productivity due to dryer conditions, and thus reduces agricultural output and diminishes land-use pressure, or synergistically (when increasing precipitation allows future improved agricultural conditions for some regions) (see Challinor et al., 2014). We analyze which hotspots are likely to suffer the most in the near future under multiple, global and local factors. Furthermore, we test if the susceptibility of a hotspot depends on properties of the hotspot itself, such as limited geographical size, the climate zone, or the continent where the hotspot is located.

2 | MATERIAL AND METHODS

In all models conducted, we omitted the hotspots New Caledonia and Polynesia-Micronesia due to their limited size and data deficiencies. For the remaining 33 hotspots considered in our study, we compiled the following information: continent, climate zone, size, altitude, number of endemic plants, protected area, and remaining vegetation (Table 1).

2.1 | Assessing the impact of climate change on biodiversity hotspots

We define climate change as potential future shifts in precipitation and temperature. To quantify the magnitude of climate change, we calculated the currently realized climate space within each hotspot and compared it to projected future climate spaces (01/2045–12/2054) based on different scenarios of climate change. Climate data were obtained from the Coupled Model Intercomparison Project (CMIP5) and comprise four IPCC greenhouse gas emission scenarios (i.e., representative concentration pathways, RCPs 2.6, 4.5, 6.0, 8.5; IPCC 5th assessment report). The RCPs stretch from a “best-case” (2.6) to a “worst-case” (8.5) scenario (van Vuuren et al., 2011). We randomly chose 8,522 grid cells (0.5° × 0.5°) located within the hotspot areas, extracted 10 daily climate parameters for these cells from the comprehensive dataset, and conducted a principal components analysis in order to reduce the redundancy in the dataset. We then tested for each grid cell whether any value of the 14 PCs exceeded the baseline range; if that was the case, we assumed that climate changed significantly in this cell. The hotspot area “lost” to climate change is thus the ratio of the cells with a significantly changed climate to the total number of cells in a hotspot.

2.2 | Assessing the impact of agroeconomic change on biodiversity hotspots

The factor agroeconomic change depicts the external pressure exerted on hotspots by changes in the human population and income and thus changes in demand for agricultural goods. Climate change effects are also indirectly considered in this factor via changes in crop yields. Future changes in national food demand are assumed to be proportional to changes in the human population, for which projections were taken from Shared Socioeconomic Pathway (SSP) scenarios: RCP 2.6 (SSP1), RCP 4.5 (SSP1), RCP 6.0 (SSP2), and RCP 8.5 (SSP3) (Riahi et al., 2017). We further assume that the demand also depends on income; a higher income leads to higher demand, but with decreasing marginal effects of income (Engel curve). Future changes in agricultural productivity were estimated with the climate-data driven EPIC model (Williams, 1995). The overall change in crop productivity was computed for each spatial unit as the weighted sum over all major crop management systems, (weight = estimated current agricultural land share of each system). The change in agricultural productivity is thus only driven by climate changes, not adaptation of agricultural management. Lastly, we calculated the area needed to compensate for changes in demand for agricultural commodities as well as agricultural productivity, thus yielding the change in pristine hotspot area due to agroeconomic change.

TABLE 1 Characteristics of global biodiversity hotspots. Given are name of hotspot, running number (ID corresponds with Table and Fig. provided in the article), continent, climate zone, size (km^2), Altitude (m), number of endemic plant species, protected area (km^2, and %), and an estimate of current remaining vegetation RV for each hotspot using a combination of automated and visual satellite-image analyses of land-cover classes and conditions as well as the mapping of major landscape disturbances from Sloan et al. (2014). Hotspots are listed in alphabetic order

Hotspot	ID	Continent	Climate zone	Size	Altitude	Endemic plants	Protected area		RV
				km^2	(m)		km^2	%	%[1]
Atlantic Forest	1	South America	Subtropics	1,440,960	2,000	8,000	128,746	8.93	3.5
California Floristic Province	2	North America	Temperate	471,100	4,400	2,124	66,675	14.15	34.8
Cape Floristic Region	3	Africa	Temperate	112,450	1,000	6,210	53,679	47.74	32.9
Caribbean Islands	4	South America	Tropics	260,671	3,100	6,550	46,967	18.02	5.8
Caucasus	5	Asia	Temperate	983,006	5,000	1,600	79,397	8.08	8.2
Cerrado	6	South America	Tropics	2,180,700	500	4,400	246,089	11.28	19.8
Chilean Winter Rainfall-Valdivian Forests	7	South America	Temperate	641,913	3,000	1,957	130,866	20.39	34.2
Coastal Forests of Eastern Africa	8	Africa	Tropics	308,220	700	1,750	63,267	20.53	3.8
East Melanesian Islands	9	Asia	Tropics	101,227	2,700	3,000	1,215	1.20	10.7
Eastern Afromontane	10	Africa	Subtropics	1,043,190	1,700	2,356	170,099	16.31	9.0
Forests of Eastern Australia	11	Oceania	Subtropics	330,154	1,600	2,144	75,955	23.01	34.8
Guinean Forests of West Africa	12	Africa	Tropics	626,398	2,000	1,800	84,213	13.44	10.6
Himalaya	13	Asia	Temperate	980,399	6,000	3,160	137,471	14.02	17.6
Horn of Africa	14	Africa	Subtropics	1,712,970	2,200	2,750	144,116	8.41	23.8
Indo-Burma	15	Asia	Tropics	2,655,060	1,200	7,000	248,534	9.36	8.7
Irano-Anatolian	16	Asia	Temperate	1,384,930	4,200	2,500	62,100	4.48	3.6
Japan	17	Asia	Subtropics	597,278	3,800	1,950	124,195	20.79	8.2
Madagascar and the Indian Ocean Islands	18	Africa	Tropics	674,509	2,900	11,600	70,744	10.49	4.4
Madrean Pine-Oak Woodlands	19	North America	Temperate	551,819	2,000	3,975	84,423	15.30	18.1
Maputaland-Pondoland-Albany	20	Africa	Subtropics	360,369	1,800	1,900	37,755	10.48	6.4
Mediterranean Basin	21	Europe	Subtropics	3,319,280	4,500	11,700	642,237	19.35	4.4
Mesoamerica	22	North America	Subtropics	1,236,450	4,200	2,941	218,988	17.71	14.1
Mountains of Central Asia	23	Asia	Temperate	1,538,860	6,100	1,500	129,609	8.42	5.8
Mountains of Southwest China	24	Asia	Temperate	346,608	5,500	3,500	35,758	10.32	21.3
New Caledonia	25	Oceania	Tropics	21,779	600	2,432	942	4.33	17.5
New Zealand	26	Oceania	Temperate	488,327	3,700	1,865	162,995	33.38	30.2
Philippines	27	Oceania	Tropics	310,103	3,000	6,091	46,282	14.92	8.0
Polynesia-Micronesia	28	Oceania	Tropics	51,969	600	3,074	5,211	10.03	5.2
Southwest Australia	29	Oceania	Subtropics	492,455	600	2,948	83,694	17.00	30.6
Succulent Karoo	30	Africa	Temperate	138,266	1,500	2,439	41,972	30.36	6.5
Sundaland	31	Oceania	Tropics	1,500,310	4,100	15,000	130,946	8.73	22.8
Tropical Andes	32	South America	Tropics	1,656,940	5,000	15,000	360,903	21.78	33.3
Tumbes-Chocó-Magdalena	33	South America	Subtropics	276,395	1,000	2,750	32,240	11.66	29.8
Wallacea	34	Oceania	Tropics	339,828	3,800	1,500	32,298	9.50	13.8
Western Ghats and Sri Lanka	35	Asia	Tropics	198,824	2,700	3,049	38,810	19.52	6.3

2.3 | Combined climatic and agroeconomic change

The combined pressure from climate change and agroeconomic change is given as the projected total change in pristine area from 2010 to 2050, calculated as the sum of the change in agricultural area in the hotspot and the area of remaining pristine vegetation, of which the ratio of area with significantly different climate in 2050 is subtracted. Figure 1 displays a summary of our modeling approach. A detailed description of the methods is provided in Appendix S1.

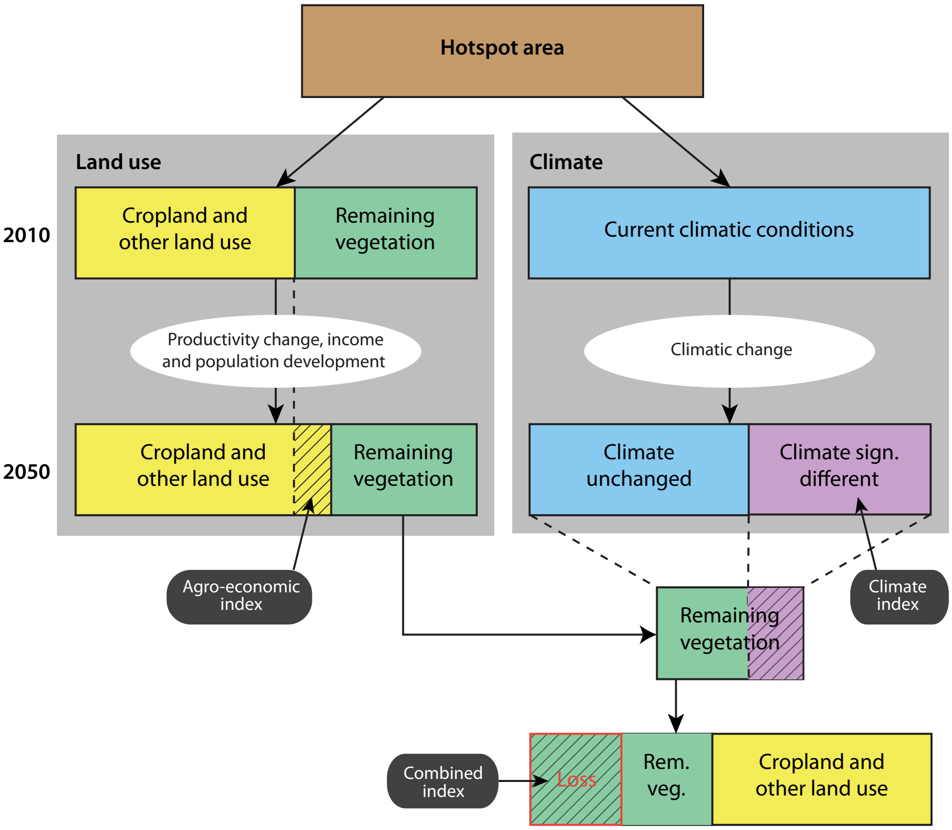

FIGURE 1 Graphical illustration of the derivation of agroeconomic, climate and combined pressure indices. The agroeconomic index depicts the loss of current pristine area (in percentages) to agroeconomic pressure, which is dependent on changes in agricultural production levels, population, and income development. The climate index depicts the share of hotspot area where climate will be significantly different in 2050 in comparison to today, given as loss of total area. The same share is then applied to the area of remaining vegetation calculated in step 1 (agroeconomic pressure), which yields the final area of remaining vegetation, of which the total loss of pristine area can be calculated (combined index)

2.4 | Estimating endemic plant species loss based on area loss

We calculated total endemic species loss following the method described in Jantz et al. (2015). A species-area relationship is used to estimate potential extinction rates based on area loss. The number of species in a smaller area A is calculated based on the species numbers in a larger area A_0:

$$S(A) = \left(A/A_0\right)^z S_0 \tag{1}$$

with $S(A)$ as the number of species in subarea A within the larger area A_0, z as the slope of the power function relating species numbers to area (Rosenzweig, 1995) and S_0 as the total number of species in A_0. Values for A and A_0 were taken from Table 1, values for S_0 from Mittermeier et al. (2005) and values for z from Jantz et al. (2015). This is a simplistic model for predicting species loss, but without data for individual species, more sophisticated modeling (e.g., Fordham et al., 2016) is not possible.

2.5 | Effects of hotspot characteristics on the susceptibility to change

The susceptibility of all hotspots to climate change, agroeconomic change and combined changes were analyzed with all characteristics of hotspots listed in Table 1 used as explanatory variables. Linear models were fitted for all three drivers of change separately. Explanatory variables were included in the order continent, size, remaining vegetation, climate zone, endemic plant species and altitudinal in full models, which were simplified stepwise removing terms of least significance first base of F-ration tests. Models were fitted using base function in R, version 3.3.0.

3 | RESULTS

Climate will change significantly on 25–33% of hotspot area on average, depending on RCP scenario (Table 2, and Table S2 and Figure S2.1 in Appendix S2). A total of 2–6 hotspots are projected to experience a significant change in climate for more than 50% of their area, and 2–3 for less than

TABLE 2 Results from modeling the percentage loss of pristine hotspot area ("Remaining vegetation") under climate pressure (temperature, precipitation, "Clim"), and the need of land according agroeconomic pressure (yield, population, income, "Agr"), and combined pressure ("Com"), for a range over all RCP/SSP scenarios. For climate pressure we assume that if climate changes significantly from baseline conditions in the remaining pristine area of the hotspot, the area is "lost" for biodiversity conservation. Values higher than 100% (as e.g., in hotspot "Eastern Afromontane") indicate that even more area than is available would be needed to satisfy future demand for commodities. Hotspots New Caledonia and Polynesia-Micronesia were not considered as their geographic area is too restricted and thus do not allow the running of stable models. The endemic plant species loss was calculated based on the species-area relationship described in Jantz et al. (2015) and is based on scenario RCP4.5/SSP1

		Range over all scenarios (%)			Endemic plant sp. loss	
Hotspot	**ID**	**Clim**	**Agr**	**Comb**	**(%)**	**(#)**
Atlantic Forest	1	22–33	94–221	96–221	28–83	2,201–6,637
California Floristic Province	2	28–47	5–6	32–50	5–25	109–535
Cape Floristic Region	3	45–61	0–1	45–61	7–33	439–2,063
Caribbean Islands	4	27–51	77–189	83–189	100	6,550
Caucasus	5	18–23	15–37	30–51	4–20	65–327
Cerrado	6	17–24	6–16	25–34	3–16	136–699
Chilean Winter Rainfall-Valdivian Forests	7	21–31	0–1	22–31	4–18	71–361
Coastal Forests of Eastern Africa	8	30–55	131–241	131–241	100	1,750
East Melanesian Islands	9	41–53	7–12	47–59	7–35	224–1,043
Eastern Afromontane	10	15–33	152–261	152–261	100	2,356
Forests of Eastern Australia	11	29–46	6–11	35–49	–	–
Guinean Forests of West Africa	12	25–33	213–366	213–366	100	1,800
Himalaya	13	24–28	65–145	74–145	18–67	583–2,131
Horn of Africa	14	17–42	6–12	22–49	3–15	78–402
Indo-Burma	15	7–10	68–129	71–129	12–49	815–3,457
Irano-Anatolian	16	15–24	106–199	106–199	100	2,500
Japan	17	27–35	−7– +5	26–34	4–20	79–398
Madagascar and the Indian Ocean Islands	18	19–33	100–175	100–175	100	11,600
Madrean Pine-Oak Woodlands	19	21–32	18–46	38–63	5–27	217–1,057
Maputaland-Pondoland-Albany	20	42–53	15–27	51–66	7–32	131–617
Mediterranean Basin	21	5–12	97–128	98–128	100	11,700
Mesoamerica	22	12–26	43–107	50–107	11–47	317–1,369
Mountains of Central Asia	23	14–27	20–50	33–63	4–22	65–326
Mountains of Southwest China	24	32–52	0–3	33–52	7–33	248–1,163
New Caledonia	25	–	–	–	–	–
New Zealand	26	23–29	0–1	23–29	3–17	63–320
Philippines	27	20–45	266–535	266–535	100	6,091
Polynesia-Micronesia	28	–	–	–	–	–
Southwest Australia	29	39–49	15–31	56–65	10–44	294–1,293
Succulent Karoo	30	46–87	0–1	46–87	10–46	256–1,113
Sundaland	31	11–19	16–27	26–39	4–20	589–2,965
Tropical Andes	32	7–9	4–9	10–17	1–7	207–1,106
Tumbes-Chocó-Magdalena	33	41–52	17–35	52–63	7–33	195–913
Wallacea	34	31–57	20–35	48–72	10–45	153–671
Western Ghats and Sri Lanka	35	51–74	189–597	189–597	100	3,049

TABLE 3 Summary of linear models of variation in the two drivers of change and the combined index of change and possible explanatory characteristics of the 33 biodiversity hotspots analyzed. Data in brackets were not significant and have been removed from the minimum adequate model given in bold in the order indicated by the superscripts. Trends are displayed in Appendix S3

	Hotspot characteristics					
Driver of change	**Continent**	**Size***	**Remaining vegetation**	**Climate zone**	**Endemic plant species***	**Altitudinal range**
Climate change*	**$F_{5,21} = 8.38$; $p < 0.001$**	**$F_{1,21} = 52.8$; $p < .001$**	($F_{1,20} = 2.52$; $p = .128$)^4	($F_{2,17} = 0.55$; $p = .585$)^2	($F_{1,19} = 1.87$; $p = .187$)^3	($F_{1,16} = 0.21$; $p = .649$)^1
Agroeconomic change*	($F_{5,16} = 0.26$; $p = .931$)^2	($F_{1,25} = 3.33$; $p = .080$)^5	**$F_{1,26} = 14.9$; $p < .001$**	($F_{2,23} = 1.50$; $p = .334$)^4	($F_{1,22} = 0.01$; $p = .925$)^3	($F_{1,21} < 0.01$; $p = .997$)^1
Combined change*°	($F_{5,18} = 0.78$; $p = .576$)^3	($F_{1,23} = 1.17$; $p = .290$)^5	**$F_{1,26} = 8.60$; $p = .007$**	($F_{2,24} = 0.42$; $p = .661$)^4	($F_{1,17} = 0.13$; $p = .719$)^2	($F_{1,16} = 0.07$; $p = .800$)^1

*ln transformed.

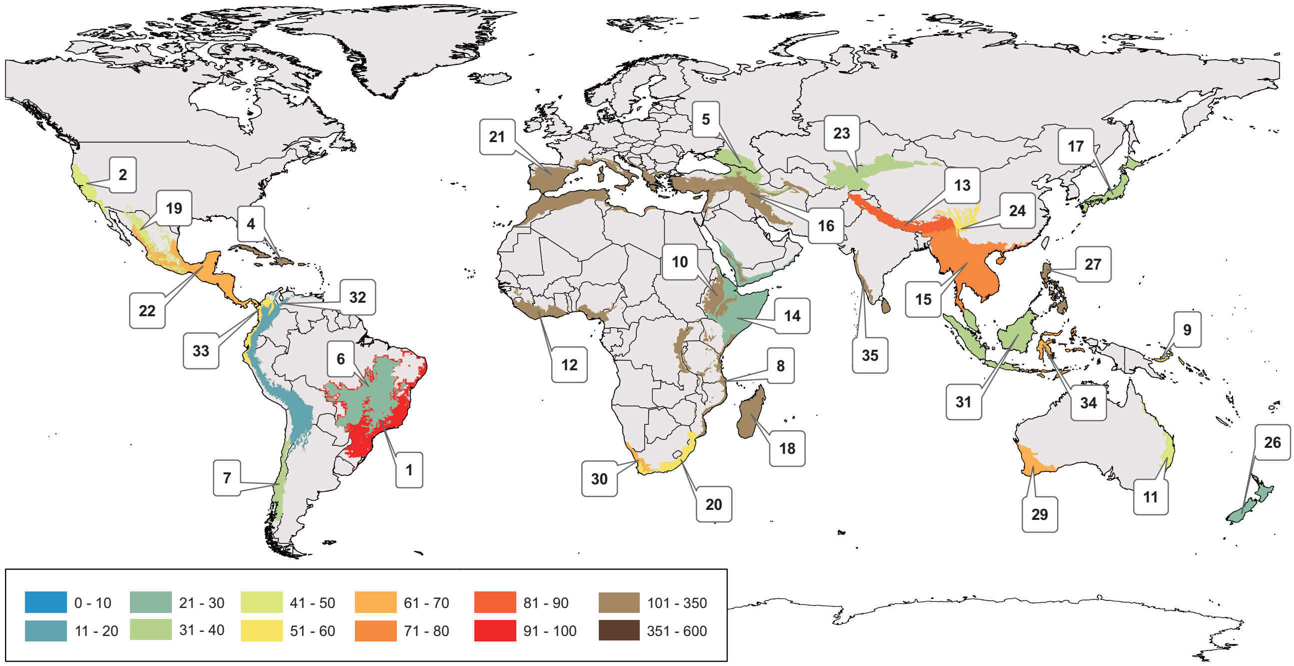

FIGURE 2 Projected combined effects of agroeconomic and climate change on biodiversity hotspots computed for the year 2050. Red colors indicate strong changes of climate and agroeconomic pressure, blue colors indicate no or little changes, that is, reduction in agroeconomic pressure. Changes are according to the RCP 4.5/SSP 1 scenario, data and maps of the other scenarios can be found in Appendix S2

10%. The main explanatory variable for changes in climate is the continent on which a hotspot is located and the size of the hotspot, with hotspots on the African continent and small hotspots suffering the highest change in climate space (Table 3, Figure S2.2 in Appendix S2). The pressure from agroeconomic changes is more severe: 9–13 hotspots are projected to lose all accessible NIV to agriculture, depending on RCP/SSP scenario. For these hotspots, the modeling indicates that to satisfy local and global food and energy demand, more agricultural area than is actually available as remaining NIV would be needed. Another 1–4 hotspots will lose 50–99% of NIV by the year 2050 (Table 2, Figure 2). The main driver of agroeconomic change is a change on the demand side, that is population growth and income increase, whereas changes on the supply side, that is climate-induced changes to crop productivity, are of secondary importance (Table 2, Table S2 in Appendix S2). The main explanatory variable for agroeconomic pressure is the currently remaining vegetation, where hotspots with an already low remaining pristine area are more likely to suffer further degradation (Table 3, Figure S2.2 in Appendix S2).

According to our model projections, hotspots on the African and Asian continent are expected to suffer particularly under future increased habitat transformation (Figure 2). In many, but not all cases, the combined climate and agroeconomic pressure is similar to agroeconomic pressure alone, indicating that climate change in these hotspots is slight. Seven to eight hotspots appear to be little affected by agroeconomic pressure and will only lose 5% or less of its remaining NIV. Only 1–2 hotspots (Western Ghats and

Sri Lanka in all four scenarios, plus Caribbean Islands in scenario RCP4.5/SSP1 and Coastal Forests of Eastern Africa in scenario RCP8.5/SSP3) are expected to suffer under both, increasing agroeconomic pressure (>100% of losses of NIV due to increasing demand for agricultural area) and strong climate change (>50% loss of area under original climatic conditions). Of great concern is the fact that losses of NIV through agroeconomic pressure are projected to be especially high in hotspots which already have a low percentage of NIV remaining (Table 1, Table 2). The hotspots projected to lose all or large parts of the remaining NIV by 2050 include many with the highest diversity of endemic species, for example, the Philippines, Caribbean Islands, Mediterranean Basin, Madagascar and Indian Ocean Islands, and Atlantic Forest.

Based on the calculated area loss, we estimate that in at least 9 hotspots all endemic species will be committed to extinction, and overall 36.5–52.1% (depending on the *z*-value) of endemic plants will be committed to extinction across all 33 assessed hotspots.

4 | DISCUSSION

Our results show that agroeconomic pressure will continue to be the main driver of NIV loss in hotspot areas. Contained in this driver are supply and demand side changes for food crops, with the demand side affected by demographic and income changes. Demographic pressure is extraordinarily high in most hotspot regions (Williams, 2013), leading to an increasing demand for food crops and the expansion of agricultural area. Furthermore, a higher wealth in societies is generally accompanied by a higher caloric intake per capita, particularly in developing and newly industrialized countries (Davidson & Andrews 2013). To produce the additional calories, agriculture needs to be intensified and cropland expanded (D´Amour et al., 2017), even more so if the higher demand is mainly for meat (Green et al., 2005). The exploitation of landscapes may also have an impact on the pressure onto pristine ecosystems: Soil quality is low in most tropical regions, so that rapid soil nutrient depletion after land conversion creates further need for new, fertile land (Habel et al., 2015).

Macroeconomic processes such as increasing global demand for meat, cash-crops and bioenergy plants may also cause large-scale transformation and cultivation of remaining NIV, as projected for hotspots in Brazil, West Africa, and parts of Asia, particularly the Sundaland hotspot (Koh, 2007). The growth of the palm oil industry in Malaysia and Indonesia adds little food benefits to the local community, but has resulted in large-scale loss of natural habitats (Koh & Ghazoul 2010). Increasing demand for meat in industrialized countries frequently results in the production of soybeans to feed EU-based livestock but also in outsourcing of meat-production to developing countries (Green et al., 2005), where it may seriously impact NIV, including in hotspots. Thus, habitat transformation for agriculture has been identified repeatedly as the most important driver of biodiversity loss worldwide (Maxwell, Fuller, Brooks, & Watson, 2017).

We recognize that some habitats and species may persist even in largely anthropogenic landscapes. Some hotspots are too steep, too difficult to access and/or have soils with low fertility and are unlikely be cleared for agriculture. Thus, there is no homogenous pressure across hotspots as assumed by our models and some endemic species may be less endangered than estimated. Furthermore, an average of 13% of hotspot area has some form of protected status, designating an area where species may survive. However, as previous studies have shown, most remaining pristine habitats are small and isolated and not able to hold viable populations over long periods. Environmental and demographic stochasticity and reduced genetic variability may lower individual fitness and species persistence (Melbourne & Hastings 2008). On the positive side, there is emerging evidence that in some tropical hotspots of rural depopulation (e.g., Philippines, Andes, Caribbean), habitats regrow and biodiversity recovers (Posa, Diesmos, Sodhi, & Brooks, 2008), but this has not been examined systematically yet.

The loss we estimate should be interpreted as an upper boundary, as we do not consider potential adaptation, neither on the sides of human beings, nor on biota. There may evolve various improvements in respect of agricultural production, food processing, and environmentally friendly intensification. Species may also adapt to persist in anthropogenic landscapes, that is, novel ecosystems, even after NIV has become modified (Pereira, Ziv, & Miranda, 2014; Newbold et al., 2015). We recognize that our projections for some places, such as the Mediterranean Basin, where the area of pristine vegetation cover is currently increasing, do not provide a realistic picture. In these regions, the negative trend of land-conversion is slowing down or is reversed either because of more sophisticated land management regimes or because the countries housing these hotspots import large quantities of food.

Our results indicate that the impacts of climate change are surprisingly small given the dire predictions from many other researchers. The time period to 2050 is relatively short compared to other projections, and climate changes will be less advanced than in projections to 2100 (e.g., Maxwell et al., 2017). However, climate change will and is having severe direct and indirect effects on pristine habitats and biodiversity, of which some aspects may not be well addressed in our models. Direct effects are particularly relevant for geographically restricted hotspots, as most endemic species will not be able to respond to climate change by colonizing new suitable areas and thus vanish entirely. Even in more accessible areas, many endemic species are adapted to and dependent on specific interactions with other taxa, resources, niches and environmental conditions, and do not possess high levels of phenotypic plasticity (Huey et al., 2012).

In addition to these direct effects, climate change may affect biodiversity indirectly through its impact on crop yields. According to our model, improved climate conditions may in some hotspots lead to a slight increase in yields, potentially encouraging farmers to clear more area to reap the benefits of higher returns for the same investment. Dryer and hotter climatic conditions, on the other hand, may reduce agricultural yields in specific regions and reduce the local pressure while shifting the burden of producing food to other, more productive areas (Schneider et al., 2011).

The major driver of biodiversity loss is the rapid destruction of pristine habitats across the globe, particularly the African and Asian continent (see also Maxwell et al., 2017; Tilman et al., 2017). Thus, there is a pressing need to anticipate and prevent further losses of the remaining NIV in hotspots. The situation is much more acute than previously expected and not evenly distributed, with some hotspots like the Philippines, Caribbean Islands, Madagascar and Indian Ocean Islands and the Atlantic Forest requiring further urgent conservation action, as they contain a large number of endemic species and are projected to face high pressure in future. In addition, only a small proportion of the land surface in these hotspots is under protection. Factors driving this demand for land are acting at various spatial scales, from local, regional, country-wide to global, mainly driven by increasing demographic pressure and life standards. As previous studies have suggested (Maxwell et al., 2017; Tilman et al., 2017), new national and international measures are needed to seek ways in which the demand for land can be reduced and current agricultural practices improved. While much effort has been invested in new policies to mitigate climate change, our study shows that threats from land conversion are much more urgent. The world's governments have committed to reduce the demand for land and for improved agricultural practices through the Sustainable Development Goals (SDGs) but this needs to be done in an integrated way that delivers across all SDGs including those on food security and climate change, as well as on biodiversity.

AUTHOR CONTRIBUTIONS

JCH, LR, UAS, and NES developed the idea of this study; LR, UAS, ES, NT, and RSD calculated agroecological models; and JOE and DR performed climate models. All contributed with writing and the interpretation of data.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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