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Recent Anthropogenic Plant Extinctions Differ in Biodiversity Hotspots and Coldspots

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SUMMARY

During the Anthropocene, humans are changing the Earth system in ways that will be detectable for millennia to come [1]. Biologically, these changes include habitat destruction, biotic homogenization, increased species invasions, and accelerated extinctions [2]. Contemporary extinction rates far surpass background rates [3], but they seem remarkably low in plants [4, 5]. However, biodiversity is not evenly distributed, and as a result, extinction rates may vary among regions. Some authors have contentiously argued that novel anthropic habitats and human-induced plant speciation can actually increase regional biodiversity [6, 7]. Here, we report on one of the most comprehensive datasets to date, including regional and global plant extinctions in both biodiversity hotspots (mostly from Mediterranean-type climate regions) and coldspots (mostly from Eurasian countries). Our data come from regions covering 15.3% of the Earth’s surface and span over 300 years. With this dataset, we explore the trends, causes, and temporal dynamics of recent plant extinctions. We found more, and faster accrual of, absolute numbers of extinction events in biodiversity hotspots compared to coldspots. Extinction rates were also substantially higher than historical background rates, but recent declines are evident. We found higher levels of taxonomic uniqueness being lost in biodiversity coldspots compared to hotspots. Causes of plant extinctions also showed distinct temporal patterns, with agriculture, invasions, and urbanization being significant drivers in

hotspots, while hydrological disturbance was an important driver in coldspots. Overall, plant extinctions over the last three centuries appear to be low, with a recent (post-1990) and steady extinction rate of 1.26 extinctions/year.

RESULTS AND DISCUSSION

Extinction Rates and Trends

To assess general trends and dynamics of processes underlying recent plant extinctions, we expanded upon the International Union for Conservation of Nature’s (IUCN) current list of 153 global vascular plant extinctions [8], using data from regional and country-specific Red Lists, Red Data Books, and expert surveys, covering floras from both biodiversity hot- and coldspots (Tables S1 and S2; Figure S1). Our data included floras from ten hotspots (California Floristic Province, Cape Floristic Region, Chilean Winter Rainfall and Valdivian Forests, Mediterranean Basin, Maputuland-Pondoland-Albany, New Zealand, Easter Island as part of Polynesia-Micronesia, Southwest Australian Floristic Region, Succulent Karoo, Sri Lanka as part of the Western Ghats, and Sri Lanka hotspot) and six coldspots (Chile—excluding areas that politically belong to the country but are declared biodiversity hotspots, England, Germany, Russia, Ukraine, and Uzbekistan). In total, these regions represent around 15.3% of the globe’s land surface (Figure S1). Both global (i.e., EX/EW) and regional (RE *sensu* IUCN) extinctions were included. The latter was only included when they led to the extinction of a particular species from a biodiversity hot- or coldspot region considered here. In three instances, extinction of the same species was documented in two coldspot regions: *Crassula aquatica* and *Najas flexilis* (England and Germany) and *Subularia aquatica* (Germany and Ukraine). Despite obvious shortcomings, we argue that regional extinctions still provide valuable data to make general inferences around plant

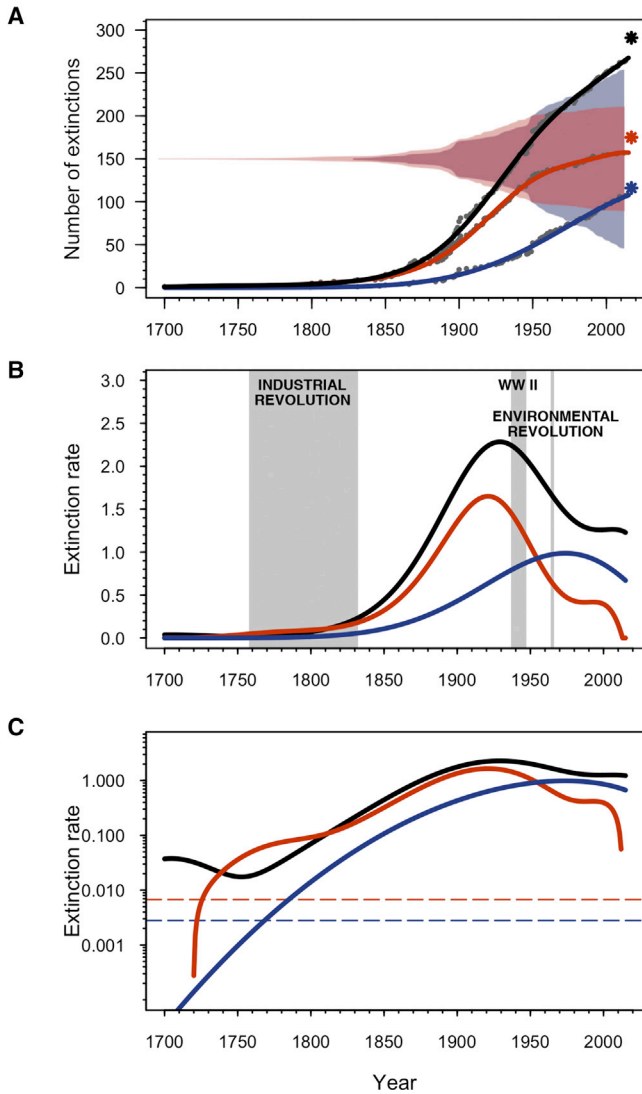


Figure 1. Plant Extinctions over the Last 300 Years for Biodiversity Hotspots (Red Lines, $n = 157$), Coldspots (Blue Lines; $n = 107$), and Hot- and Coldspots Combined (Black Lines; $n = 264$)

(A) Cumulative number of documented extinction events since 1700. Gray dots indicate recorded extinction events and curve-fitted polynomial GLM-Poisson regressions from our modeling approach (see [Supplemental Information](#) for details). The cumulative proportion of lost hotspot and coldspot plant diversity is indicated by red and blue shaded area graphs, respectively, in the background.

(B) Annual extinction rate (i.e., number of extinctions per year).

(C) Annual extinction rate presented in a logarithmic scale for comparison with the background extinction rates calculated for biodiversity hotspots (dashed red line: calculation based on number of all plant species in the corresponding hotspots) and coldspots (dashed blue line: calculation based on number of all plant species in the corresponding coldspots; see [Supplemental Information](#) for details). Please note that these graphs only include extinction events for which the date of extinction is known (for 27 extinctions, these data were unavailable). Asterisks in [Figure 1A](#) indicate the total number of extinctions when including these extinction events lacking dates (18 for hotspots and 9 for coldspots).

Please see also [Figure S1](#) and [Tables S1](#) and [S2](#).

extinctions and that the drivers underlying these extinctions are likely representative of those faced by plants across their distributional ranges.

While a recent study documented more than 500 globally extinct plant species [9], our dataset is remarkable in that for most of the 291 extinctions we identified, we were able to obtain information on: the number of years since extinction ($n = 264$), reason(s) for extinction (11 non-exclusive categories, together with a category for *multiple reasons* as well as *unknown reasons*; [Figures 2](#) and [3](#); [Tables S1](#) and [S3](#)), a measure of lost taxonomic uniqueness (i.e., proportion of genus lost per extinction event), and life-form (see [STAR Methods](#)). Our data show that extinction rates for both hotspots and coldspots accelerated since the Industrial Revolution ([Figure 1B](#)). The Industrial Revolution resulted in rapid increases in human population sizes and densities, in part due to higher longevity as afforded by better living conditions, especially in Eurasia and North America. This period also coincided with an increased need for raw materials for construction and manufacturing, leading to high levels of habitat destruction through infrastructure development, the introduction of exotic species [10], and the rapid expansion of forestry and agricultural areas [11, 12]. Cumulative extinctions (CumExt) accelerated for both hotspots (HS) and coldspots (CS) from 1750 to present ([Figure 1A](#)) (GLM: $\text{CumExt} \sim \text{Exp}[a + b \cdot \text{year} + c(\text{HS versus CS}) + d \cdot \text{year} \cdot c(\text{HS versus CS})]$; Efron's Pseudo $R^2 = 0.868$; $b = 0.0139 \pm 0.0002$, $Z = 61.2143$, $p < 0.0001$), but faster for hotspots ($c = 1.6743 \pm 0.1265$, $Z = 13.2391$, $p < 0.0001$) with the rising rate occurring later in coldspots than in hotspots ($d = 0.0031 \pm 0.0005$, $Z = 6.5932$, $p < 0.0001$). Indeed, we expected biodiversity hotspots to have disproportionately higher numbers and faster rates of plant extinction events compared to coldspots due to their high levels of endemism and diversity, usually confined to small and unique geographic areas [13]. Plant extinctions peaked half a century later in coldspots than in hotspots (1974 versus 1921) ([Figure 1B](#)), likely as a result of lower levels of endemism in these areas, which, in turn, are usually linked to wider geographic distributions and therefore generally less susceptibility to extinction [14]. As the 114 RE events predominantly occurred in coldspots (76.3%), removing these records led to a rather similar estimate of the extinction rate in hotspots (peaking at 1.47 E/Y in 1921) and a continuously rising, but much lower, extinction rate in coldspots (< 0.2 E/Y).

Current estimates of background extinction rates (BERs: typical rates of extinction during the planet's geological and biological history, prior to human influence) vary around 0.1 (between 0.05 to 0.15) extinctions per million species years (E/MSY) [3, 15, 16] and would, for the biodiversity hotspots included here, translate to 0.00701 E/Y ([Figure 1C](#); [Table S2](#); [STAR Methods](#)). For biodiversity hotspots, we estimated the extinction rate to be 0.036 E/Y in 1750, or 5.1 times that of the estimated hotspot BER, jumping to 0.321 E/Y or 45.8 times the BER in 1850. In 1921, the extinction rate for biodiversity hotspots reached its peak: 1.65 E/Y or 235.4 times the BER (i.e., 23.5 E/MSY) and declined in the 1970's from 0.540 to 0.437 E/Y or from 77.0 to 62.3 times the BER (extinction rates calculated as the derivative of the 7th order GLM fitted cumulative rate of extinction). These rates correspond well with another recent estimate for global plant extinctions [9] and

are still at least one order of magnitude lower than previous estimates of between 1,000 to 10,000 times the BER (e.g., [17]). For the biodiversity coldspots considered in this study, a BER of 0.1 would translate to 0.00279 E/Y, which is 2.4 times lower than that for hotspots (Figure 1C; Data S1; STAR Methods). In 1921, when the extinction rate peaked in hotspots, the extinction rate for coldspots was 0.636 E/Y or 228 times the BER (i.e., 22.8 E/MSY), and it reached its maximum in 1974 with an estimated rate of 0.987 E/Y or 353.8 times the BER (i.e., 35.4 E/MSY, Figure 1C). After 1974, extinction rates for biodiversity coldspots decelerated to around 0.670 E/Y or 240 times the BER (Figure 1).

We did not find the overall plant extinction rate to increase linearly over time, but rather to fluctuate, mainly due to the extinction dynamics in the biodiversity hotspots. The initial extinction peak in hotspots in 1921 was followed by a decline until around 1980. After 1980, hotspot extinction rates appear to remain constant (Figure 1). While it is difficult to explain these fluctuations, it is conceivable that a combination of global socio-economic trends and, to some extent, conservation-related policies may partially be responsible for the patterns. The first half of the 20th century coincides with a dramatic increase in human populations, higher land use, and disturbance of natural ecosystems, notably along coastal regions such as in the Mediterranean Basin. This likely led to regional and global extinctions of many plants. By the 1950s (our extinction peak in 1921 in hotspots), there was a marked decline of domesticated land use (cities, croplands, heavily managed grazing lands), accompanied by the migration of people from rural to urban areas [18]. The trend of declining domesticated land use largely reflects the modernization of agriculture, focused on more intensive production in the most favorable environments. Second, and more recent, the implementation of policies concerning environmental health, initially including the extensive application of environmental measures to reduce air and water pollution, and later the implementation of biodiversity conservation measures, may have led to further declines in plant extinctions. The establishment of protected areas occurred long before the adoption of most conservation policies and treaties, with marked expansions of protected areas globally since the 1970s [19]. These areas substantially restrict human perturbation within their boundaries and, if well planned and managed, are generally much more effective in preventing plant extinctions than individual conservation policies [20, 21]. Lastly, any predictions in ecology are only as good as the data at hand. Therefore, a lack of updated biodiversity assessments may have contributed to changes in plant extinction rates observed here and certainly to the supposed recent declines in extinction rates.

Causes of Extinction

Traditionally, habitat destruction and overexploitation have been put forward as main drivers of global extinctions across taxonomic groups, followed by the impacts of invasive species [22, 23]. We found the main drivers of plant extinctions in hotspots, based on raw count data, to be ranked as agriculture (26.9%), urbanization (23.4%), invasive species (13.7%), and grazing (12.6%), with 29.7% of all extinctions resulting from multiple causes (Figure 2; Table S1). Our results suggest that habitat

destruction and land-use changes, mainly induced by urbanization and agriculture, are the major causes of plant extinction, well ahead of biological invasions. Previous analyses based on IUCN data ranked drivers of plant extinction as: agriculture > biological resource use (overexploitation) > urbanization > invasive species [22]. Blackburn et al. [24] recently found that for the 153 plant extinctions listed by the IUCN, 25.5% resulted, in part or solely, because of the impacts of invasive species. Based on the *n*-order polynomial GLM-logistic regression, biological invasions are undeniably an important contributing cause of extinctions, with clear temporal trends for plant extinctions in hotspots, rising to contributing to 19.6% of extinctions in 1819 (first peak) but then declining to only contributing 3.02% by 1884, followed by a steady increase reaching a second peak of 14.6% in 1957 and then steady declines to contributing < 1% after 2008 (Figure S2 for annual extinction rate; see also Figure 3 for decadal extinction rate based on raw counts). Invasions are often passengers rather than drivers of biodiversity loss and may therefore simply be symptomatic of other extinction-causing disturbances [25]. They are, nevertheless, often the sole drivers of plant extinction [24], often from exotic animals that trample or consume plants [26]. In contrast to those in biodiversity hotspots, the main drivers of extinction in coldspots, based on raw counts (Table S1), can be ranked as: hydrological disturbance (18.1%), agriculture and habitat degradation (13% each), urbanization (7.8%), and grazing (6%), with 18.1% of all extinctions resulting from multiple drivers (Figure 2). Biological invasions only contributed to 0.9% of coldspot extinctions during this period (Figure 2). Based on the *n*-order polynomial GLM-logistic regression, hydrological disturbance (e.g., dam building) drove three waves of coldspot extinctions, with the first peak in 1831 (32.1%), second in 1909 (21.8%), and third in 1986 (19.2%), but declined to less than 1% after 2006 (Figure S2; see also Figure 3 for decadal extinction rate based on raw counts). Urbanization became an important driver of extinction in coldspots (mostly old-world regions) during pre-1840 and 1961–1989 (annual contribution > 10%); it was an important driver of extinction much earlier in hotspots (mostly new-world regions) during 1771–1806, 1885–1912, and post-1994 (annual contribution > 15%; Figure S2), reflecting the time lag in development between regions. One should bear in mind that drivers of extinction, as defined here, remain subjective black boxes, often lacking robust empirical support. These drivers may simply be symptomatic of broader, more complex, and multi-dimensional processes such as habitat destruction and high levels of disturbance. For example, hydrological disturbance, agriculture, and urbanization would all contribute to habitat loss and disturbance. Importantly, based on raw counts, we could not identify causes of extinction for 37.7% of hotspot and 51.7% of coldspot taxa included here. Despite these shortcomings, we argue that our attempt to disentangle the relative contribution of different extinction drivers do provide insights on temporal dynamics of different processes underlying these broader processes that ultimately lead to the same outcome.

Taxonomic Uniqueness and Life-Forms

Do biodiversity hotspots and coldspots differ in the amount of taxonomic uniqueness they lose to extinction? When answering this question, one needs to keep in mind that

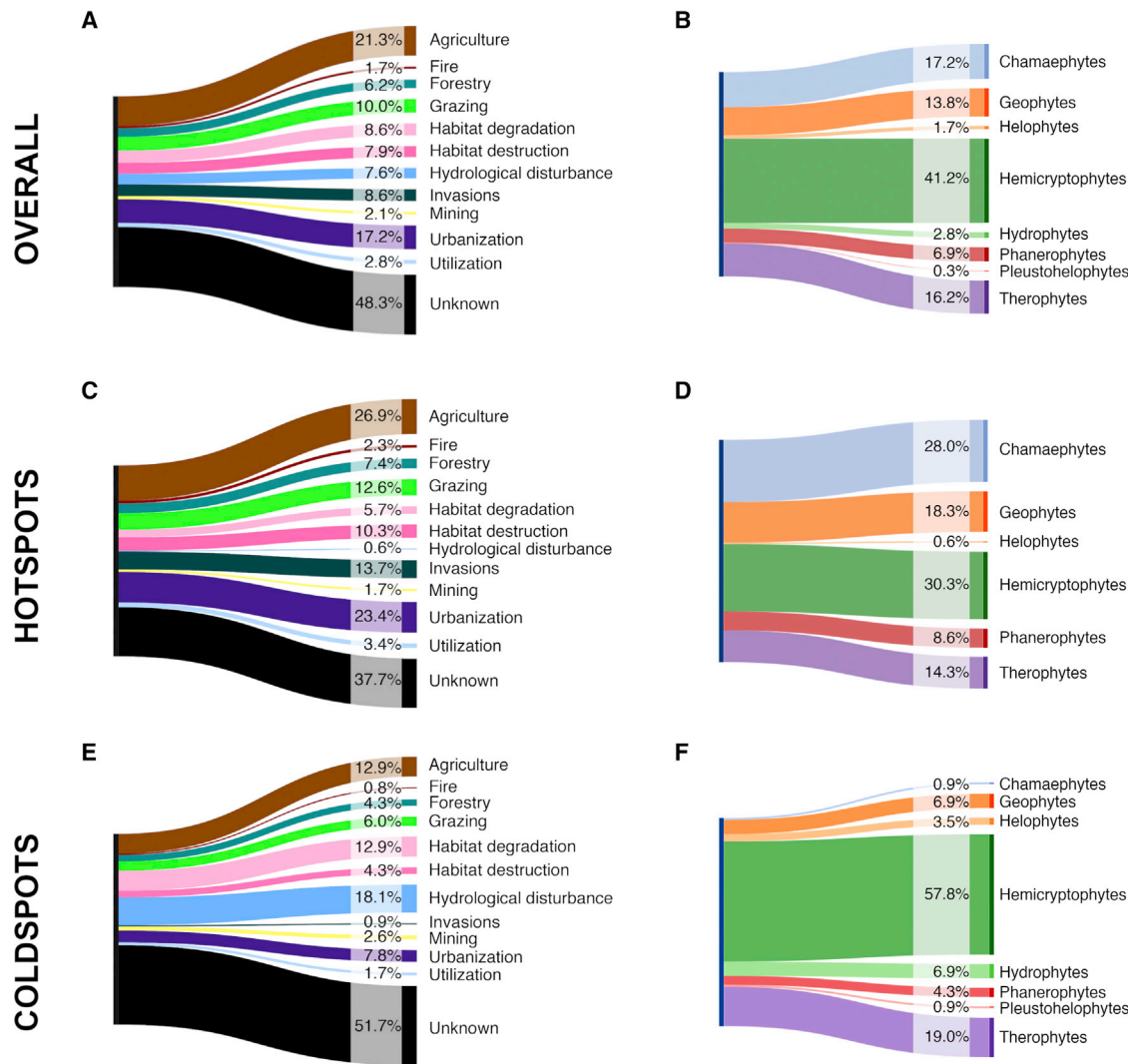


Figure 2. Primary Drivers of Anthropocene Plant Extinctions and Plant Life-Forms Affected by These Events for Overall, Biodiversity Hotspot, and Biodiversity Coldspot Floras

Graphs in the first column (A, C, and E) show the proportions of identified drivers in these floras. Please note that multiple drivers were found for 18.1% and 29.7% of the coldspot and hotspot extinctions, respectively (not shown here). The panels in the second column (B, D, and F) provide information on the proportional make-up of life-forms affected by extinctions events. Please see also [Figure S1](#) and [Tables S1, S2 and S3](#).

species numbers alone do not fully account for evolutionary diversity. Yet, the use of species-based metrics (e.g., richness) remains the primary approach in defining biodiversity hotspots. However, because evolutionary history is unequally distributed between taxa and areas [27], extinctions represent not only the loss of a species per se but also the loss of potentially unique phylogenetic diversity. A recent study found modern plant extinctions to be randomly distributed among evolutionary lineages [9]. We found higher losses of taxonomic uniqueness in coldspots compared to hotspots (Welch t test, $t = 3.35$, $df = 147.62$, $p = 0.001$; mean of 31.62% and 16.22% of all species within a genus lost due to extinction in cold- and hotspots respectively), which may reflect the generally lower number of species contained in the coldspot genera included here compared to those in hotspot genera (Kruskal-Wallis test, $\chi^2 = 18.28$, $df = 1$, $p < 0.001$; mean of 31.85 versus 56.10

number of species per genus in cold and hotspots, respectively). A null model based on random selections of hot- and coldspot taxa (1,000 permutations) confirmed that losses of taxonomic uniqueness were higher in the latter than in hotspots ($p < 0.05$). We found numerous instances of extinctions of monospecific genera in coldspots (e.g., *Podophorus bromoides* in Chile, *Trilepidea adamsii* in New Zealand, *Amphoricarpus elegans* in Russia, *Echinophora sibthorpiana*, *Subularia aquatica*, *Ludwigia palustris*, *Zingeria beibersteiniana* in Ukraine), or even families, such as the Scheuchzeriaceae following the extinction of *Scheuchzeria palustris* in England. As it is generally accepted that larger floras will harbor disproportionately more species per genus than smaller floras [28], the higher loss of taxonomic uniqueness in biodiversity coldspots may be unsurprising. However, when we considered the floras for some of the regions included here ($n_{\text{coldspot}} = 5$; $n_{\text{hotspot}} = 6$, [Table S2](#)), we

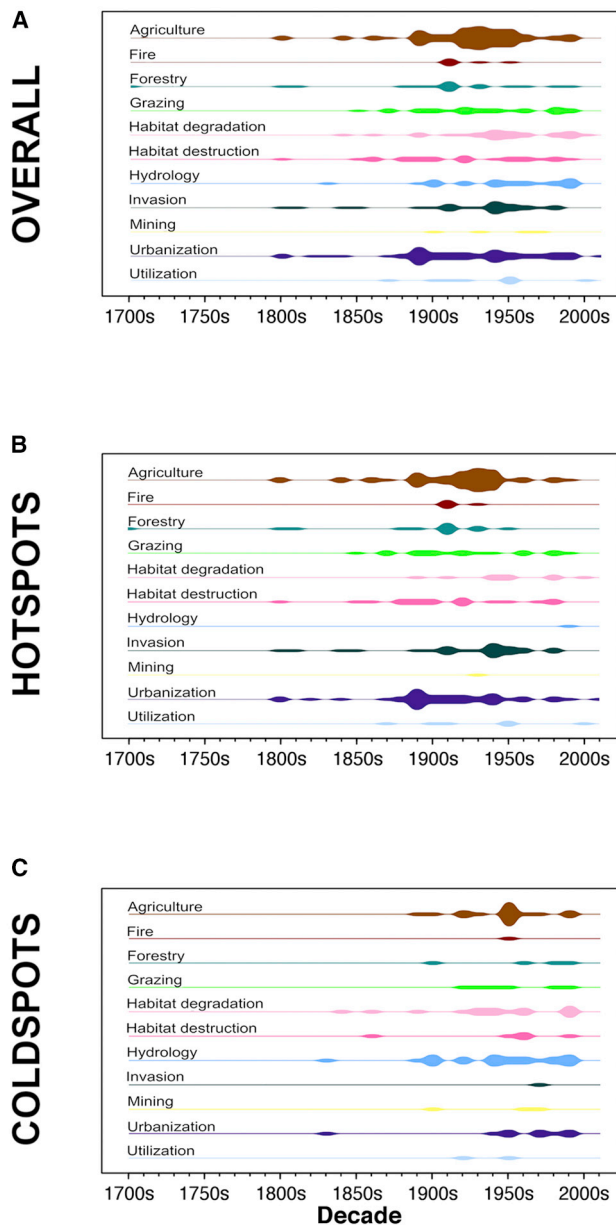


Figure 3. Primary Drivers of Plant Extinctions over the Last 300 Years Shown as Area Graphs to Visualize the Temporal Changes in the Relative Contribution of the 11 Identified Primary Extinction Causes Temporal dynamics for each extinction driver are shown for (A) overall, (B) biodiversity hotspot, and (C) biodiversity coldspot floras. To aid visualization, dates of extinction events are shown in decadal increments and extinctions for which no reason could be identified in the literature were excluded. Please note that multiple extinction causes were found for 18.1% and 29.7% of the coldspot and hotspot extinctions, respectively (not shown here). See also [Tables S1, S2 and S3](#); [Data S1](#); and [Figure S1](#); see also [Figure S2](#) for annual rates.

found no difference in the average number of species per genus between hot- and coldspots (Kruskal-Wallis test, $\chi^2 = 0.80$, $df = 1$, $p = 0.37$; mean of 4.9 versus 5.6 number of species per genus in cold and hotspots, respectively). Our data also suggest that overall, hemicryptophytes appear to be a particularly extinction-prone life-form (contributing to 57.8%

of coldspot extinctions, 30.3% of hotspot extinctions, and 41.2% of all extinctions [Figure 2]). Hemicryptophytes are over-represented in boreal and arctic habitats and, to some extent, at higher elevations. On the other hand, this life-form is generally less common at lower elevations in, for example, Mediterranean areas, where therophytes are more common [29]. Therefore, our findings suggest that hemicryptophytes in hotspots, especially Mediterranean-type climate regions (e.g., California Floristic Province, Cape Floristic Region, Mediterranean Basin), may be more prone to extinction than other life-forms. In coldspots, therophytes were the second most common extinct life-form (19.0%; Figure 2), while chamaephyte extinctions were the second most common life-form in hotspots (28.0%; Figure 2) as well as overall (17.2%; Figure 2). Chamaephytes also seem to be more than ten times more vulnerable to extinction in hotspots than in coldspots (Figure 2).

Back to Extinction Rates and Trends

Generally, the march toward extinction is slow for plants [4]. Some plants are among the longest-living organisms and many can persist in low densities due to, among other, adaptations for autonomous reproduction, long-lived seeds, and long dormancy periods. Plants also often persist locally, even under prolonged periods of unfavorable environmental conditions, e.g., in refugia [30]. Our future predictions of plant extinctions, like previous estimates, may reflect a skewed picture of reality.

Assuming the same steady extinction rate of 1.26 E/Y [standard deviation = 0.0095; = 13.3 E/MSY = 133 times the BER] in our data after 1990 (Figure 1), we predict, from 2014, that an additional 21 plant species will go extinct by 2030 in our study regions, 47 species by 2050, and 110 species by 2100. This is in stark contrast to the general idea that as much as "...half of all [plant] species.... may disappear within the remainder of this century" (ca. 58,784 times the BER [31]), which would translate into >49,000 extinctions in the regions included here over the next ca. 80 years, which seems unlikely, bar a cataclysmic event such as an asteroid strike!

Previous estimates of extinction rates are highly variable [3]. On the one hand, plants previously thought to be extinct are often rediscovered [9, 32], while on the other, critical and accurate data on plant extinctions are often non-existent. For example, none of the 17 globally extinct plant taxa in California were listed among endangered or extinct taxa in the IUCN's 2017 Red List [32], while for the same area, four globally extinct species were missing, and one erroneously listed as rediscovered, in the most recent global analysis of modern plant extinctions [9]. Notwithstanding the lack of comprehensive and accurate data, the disjunction between extinction and dramatic population declines also means that extinction is often a long game for plants, with many species able to persist under extremely low numbers [4, 33, 34]. The ability of plants to "hang in there" has been described as analogous to functional extinction [35] and therefore high extinction debt [33]. Importantly, as primary producers, the loss of plant species is also expected to cause co-extinctions of organisms that rely on them, i.e., consumers [36]. A recent analysis on plant-seed disperser and plant-pollinator interaction networks found that plant extinctions are more likely to trigger animal co-extinctions than vice versa [37]. It is therefore important to consider mutualistic

interactions when predicting extinction risk in the face of global change [38]. Extinction debt, in other words, those plant species hanging in there, makes the real number of future extinctions likely to surpass the 1.26 extinctions per year estimated here. Given the scarcity of available global data and the urgent need for updated plant inventories [39, 40], our analyses are likely biogeographically skewed. Factors like differential intensity of biodiversity research in the regions included here (e.g., Europe versus South America), the disproportionate representation of hot- and coldspots, the fact some species may have gone extinct before their discovery (especially in biodiversity hotspots), and the complex nature, and often unknown reasons for extinctions (37.7% in hotspots versus 51.7% in coldspots, Figures 2 and Table S1), may have all limited our inferences. For example, some of the hottest plant biodiversity hotspots, like Madagascar, were not included in our analysis because of a crucial lack of data related to species extinction.

It is likely that extinction drivers operate differently in different ecoregions of the world and even in the same area due to political and socio-economic factors and temporal dynamics underlying these. Despite this, our data suggest that the relative importance of existing plant extinction drivers may change over time or that novel drivers may emerge, especially under conditions of rapid global change [41]. In the near future, utilization > urbanization > hydrological disturbance and habitat destruction will remain the primary drivers of plant extinctions in hotspots, while the main drivers in coldspots are largely unknown but with certain impacts from habitat destruction.

Concluding Remarks

Along with previous estimates suggesting 20% of the world's plants to be threatened by extinction [23], the recently released IPBES report paints a depressing picture of global biodiversity. Yet, in our study, we found surprisingly few documented plant extinctions (i.e., 291 global or regional extinction events, but see [9]) and that these accrued at rates much lower than previously thought. Plants may represent a particularly challenging taxon to unambiguously claim extinction, given their often-inconspicuous presence in the environment and the difficulties associated with locating the last-living individuals or propagules.

Our glimpse into the causes and trends in plant extinctions over the last three centuries left us with more questions than answers. The only way to better understand the magnitude of, and processes driving, the extinction crisis faced by plants, and biodiversity in general, is to urgently initiate regional- (preferably based upon a biogeographical framework) or at least country-level biodiversity assessments and to update existing ones. This needs to be done using standardized methodologies documenting not only specific reasons for extinction but also key functional and life-history traits (e.g., breeding system, pollination ecology, seed crop sizes, seedbank persistence). Such assessments will be vital to more accurately infer the main drivers and trends of plant extinctions during the Anthropocene and to make informative forecasts about the future and preservation of Earth's flora.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- LEAD CONTACT AND MATERIALS AVAILABILITY
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND CODE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2019.07.063>.

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AUTHOR CONTRIBUTIONS

The ideas for this paper resulted from initial discussions between J.L.R., H.H., F.A.Y., J.-H.K., G.T., and M.L.C. J.L.R. and H.H. led the writing of the manuscript. M.R., H.H., J.-H.K., F.A.Y., M.L.C., G.T., A.A.K., J.M.I., and F.M. compiled data. C.H. and H.H. analyzed data and contributed to the interpretation of results. All authors discussed the results and contributed to the writing of the final manuscript.

DECLARATION OF INTERESTS

The authors have no competing interests to declare.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Dataset with compiled information on extinct plant species	This paper	Table S1
Model outputs for GLM-logistic regressions	This paper	Data S1
Software and Algorithms		
Mathematica 11.0	Wolfram Research, Inc.	https://www.wolfram.com/mathematica/
R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; v. 3.5.3	R Core Team (2019)	URL https://www.R-project.org/ .

LEAD CONTACT AND MATERIALS AVAILABILITY

This study did not generate new unique reagents and requests for other data resources should be directed to and will be fulfilled by the Lead Contact, Johannes Le Roux (jaco.leroux@mq.edu.au).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We identified biodiversity hotspots (HS) following Mittermeier et al. [42] and coldspots (CS) as regions falling outside these areas. CS included in this study were mostly confined to the borders of individual countries, since the geographic demarcation of these is less clear than for HS [43, 44]. We included all HS and CS for which we could gather or compile credible data on plant extinctions. Specifically, we compiled information on species extinctions using Red List, Red Data Books, IUCN data [8] and/or expert knowledge. For some HS, no specific Red Lists were available (i.e., Mediterranean Basin and California Floristic Province). For these we combined available Red Lists of the countries which fall within the hotspot region (e.g., Mediterranean Basin) for which local Red Lists were available and combined such published data with inputs from local experts. In addition to documented global extinctions, we also included regional extinctions (i.e., RE *sensu* IUCN) when they led to the extinction of a particular species from a biodiversity hot- or coldspot region considered here. Overall, we were able to compile a comprehensive dataset with detailed information of plant extinctions within ten biodiversity hotspots and six coldspots (Figure S1; Table S1).

METHOD DETAILS

We contacted experts on regional floras to verify all identified extinctions. To gather additional information for each extinction event, we searched various data sources including online databases, scientific peer-reviewed literature, government reports, books and herbaria (Table S2). Scientific names of plant species were standardized according to The Plant List (<http://www.theplantlist.org>) and we did not consider extinctions of subspecies in our analyses. For each extinct species we recorded, where possible: the date of extinction (some of the earliest records were only indicated as decade or century (e.g., 1700s, 1850s, etc.), driver (reason/cause) of extinction, number of species found in genus within the corresponding HS or CS (i.e., in the same genus as extinct species) and Raunkiaer life form [45]. Since different descriptions of extinction causes may refer to the same overall driver (e.g., urbanization and development), we grouped these into 13 distinct categories that captured all information (see Table S3 and Data S1). For taxa where dates of extinctions were given as century (e.g., 1700), we used the midpoint (e.g., 1750) in all statistical analyses.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were done in Mathematica 11.0 (Wolfram Research Inc.). First, we ran a Generalized Linear Model (GLM) with Poisson distribution for the accumulated number of extinctions, with the nominal variable of CS/HS and date of extinction, as well as their interaction as predictors.

We fitted an n-order polynomial GLM-Poisson regression for the accumulated number of extinction events over years (for total [n = 10, HS [n = 7] and CS [n = 3] separately); assuming that the logarithm of the expected value of the response variable can be modeled by the n-order polynomial function of the independent variable [year]; n = 1 for the standard GLM-Poisson regression). For all extinctions grouped together the following model was used, $\text{CumExt} \sim \text{Exp}[-0.07 + 0.04 \cdot t - 0.0006 \cdot t^2 + 3.88 \times 10^{-6} \cdot t^3 + 7.03 \times 10^{-9} \cdot t^4 - 1.31 \times 10^{-10} \cdot t^5 + 3.95 \times 10^{-13} \cdot t^6 - 3.81 \times 10^{-16} \cdot t^7]$, where t is year-1699. For hotspot extinctions, the model $\text{CumExt} \sim \text{Exp}[0.11 - 0.13 \cdot t + 0.005 \cdot t^2 - 0.00006 \cdot t^3 + 4.47 \times 10^{-7} \cdot t^4 - 1.69 \times 10^{-9} \cdot t^5 + 3.25 \times 10^{-12} \cdot t^6 - 2.5 \times 10^{-15} \cdot t^7]$ was used, and for coldspot the model

$\text{CumExt} \sim \text{Exp}[-7.82 + 0.08 \cdot t - 0.0001 \cdot t^2 + 5.13 \times 10^{-8} \cdot t^3]$. These model results are presented in [Figure 1A](#). All three fits were extremely well, with Efron's Pseudo $R^2 > 0.99$. Note, the use of higher orders (a large n) in the regression, compared to the above hypothesis testing using GLM-Poisson regression with $n = 1$, was to ensure the accuracy for estimating the annual extinction rate ([Figures 1B and 1C](#)) as the derivative (i.e., slope) of the fitted accumulation curves in [Figure 1A](#). Results from this analysis were compared to current estimates of background extinctions rates (BER [[3](#)]). To calculate the BER for the biodiversity hotspots and coldspots considered here, a general BER of 0.1 extinctions per million species per year (E/MSY [[15, 16](#)]) was used. If the number of species in the biodiversity hotspots or coldspots ([Table S2](#)) is S , the corresponding background extinction rate at 0.1 E/MSY was calculated using the following formula: $0.1 \times S / 1000000$. Further, we used a linear model to test the role of the number of species within a genus in explaining accumulated extinctions. The model did not fit well, with the number of species per genus not being a significant predictor ($p = 0.87$). We also ran separate n -order polynomial GLM-logistic regressions (with the Logit function) for total, HS and CS data for specific extinction drivers ($n = 5$ or less based on the number of positive points; detailed results for each of the extinction reasons are shown in [Data S1](#) and [Figure S2](#)). Note, we used separate runs of these logistic regressions, instead of a single multinomial logistic regression, as these specific reasons are not mutually exclusive.

To compare the loss of taxonomic uniqueness between biodiversity HS and CS, we first summarized the number of extinction events for each genus within corresponding HS and CS. This information was then used to calculate the proportion of species lost within each genus within corresponding HS and CS. A Welch t test was then applied to test if taxonomic uniqueness losses differ between HS and CS. We applied Kruskal-Wallis tests to test whether the number of species as well as the average number of species per genus differ between HS and CS. These analyses were performed using R statistical software (R Core Team 2019).

DATA AND CODE AVAILABILITY

The published article includes all datasets and code for statistical models generated or analyzed during this study.