



Linking worldwide past and present conifer vulnerability

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ABSTRACT

Inventories of species recently extinct or threatened with extinction may be found in global databases. However, despite the large number of published fossil based-studies, specific databases on the vulnerability of species in the past are not available. We compiled a worldwide database of published fossil records of plant range losses over the last 30 ka across all continents. Widespread range losses of plant taxa across all latitudes were identified, with the majority representing gymnosperms. Focusing on conifers, a group of plants with well understood distribution and conservation status, we found that past range losses often overlapped areas where species are endangered at present, suggesting that such areas have been prone to biodiversity loss through time. During phases of past rapid climate change, even areas that currently have low levels of endangered species were affected by plant range losses, in some cases with disappearance of taxa from entire continents, islands or major geographic regions. Integration of modern and palaeoecological data enhance our understanding of the complex processes underlying the modes, rates, and extent of threats to plants under changing climate and increasing human pressure, which is vital information for effective conservation actions.

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1. Introduction

In the last decades, the scientific community has put much effort into constructing comprehensive open-source databases documenting both the distribution and vulnerability to extinction of species at a global scale, for example GBIF *Global Biodiversity Information Facility* (www.gbif.org) and the IUCN *Red List of Threatened Species* (www.iucnredlist.org). However, despite the large number of published fossil-based studies, many of which are stored in regional or global databases such as the *Neotoma Paleocology Database* (www.neotomadb.org; Williams et al., 2018), specific databases on the vulnerability of species in the past are not available. This lack induced us to assemble a worldwide compilation of published fossil records focusing on plant range losses over the last 30 ka across all continents. Then, we utilised data of both modern

and past distributions of plants threatened with extinction or subject to range contraction to assess whether there is overlap between the location of plant species currently endangered and evidence for past range losses. Such analysis has to our knowledge never been undertaken in plants, or, indeed, for other organisms with sufficient fossil records, and has great potential for better understanding spatio-temporal processes of biodiversity loss and improving models of threatened species vulnerability to extinction under future environmental change.

The rationale for comparing these data is that both modern endangered species and plant populations regionally lost in the past are characterized by having very reduced or very fragmented ranges, with little or no prospect of shifts in population trajectories leading to recovery. Thus, even if fossil and modern data are substantially different in the methods of collection, sources of error and taxonomic detail (see Methods), they may be compared on a geographical basis as indicators of vulnerability of plant populations/species. Both current databases of endangered species and palaeo-vegetation reconstructions from fossil data are universally considered as highly informative and valuable. Modern data are

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taxonomically accurate and allow detecting taxa that went extinct even in recent times (Humphreys et al., 2019; Knapp et al., 2020). On the other hand, fossil data record long-term trends that cannot be captured at the time scale of human observation and may encompass major climate changes at a millennial time scale.

Here, firstly we review global records of fossil pollen, stomata, plant macro-remains and ancient DNA (aDNA) over the last 30 ka for evidence of last occurrences of plant taxa at regional, continental or worldwide scales. These records represent either species extinction or loss of populations of extant taxa. Secondly, we use the distance of the last occurrences to nearest modern population, or closest relative, as an estimate of the minimum range loss in distance that has not since been recovered. Thirdly, we compare the records of past range losses for conifers with the distribution of modern endangered species at different timescales to evaluate where and when a correspondence may be found, including in relation to past climate changes. Lastly, we propose a new protocol integrating different databases to map plant vulnerability through time at different geographical scales.

2. Methods

Last occurrences of plant taxa in pollen and macrofossil records (Supplementary Table 1) were searched in the following ways. Firstly, they were systematically searched for online in published scientific literature (both research articles and reviews) documenting past range-losses of plants using Google Scholar, using combinations of the terms 'extinct', 'disappear' (and synonyms), 'tree', 'plant', 'fossil', 'Holocene' and 'glacial'. Each online source found was also interrogated for further records both available online and not available online. In order to ensure wide global geographic coverage of plant range losses, separate searches were made for each continent (excluding Antarctica) and in a range of languages including English, Chinese, Japanese, Italian, French, German, Portuguese, and Spanish.

Secondly, we searched for last occurrences by examining worldwide fossil records of the last 30 ka on the online Neotoma Paleocology Database (www.neotomadb.org), Canadian Pollen Database (www.lpc.uottawa.ca/data/cpd), Czech Quaternary Palynological Database (<https://botany.natur.cuni.cz/palycz/index.php>), European Pollen Database (www.europeanpollendatabase.net), Latin American Pollen Database (<http://www.latinamericapollendb.com>), and datasets published in PANGAEA® - Data Publisher for Earth & Environmental Science (www.pangaea.de). Searches were made in the years 2017–2019. We limited our search to the last 30 ka as older records are sparse.

In order to increase certainty of each inferred regional range loss, records were restricted to those more than 25 km from the nearest modern population for macrofossils and stomata, or 100 km for those based solely on pollen. Keeping these limits is important to reduce false positives. Where pollen and macrofossil (including stomata) data supported an individual plant last occurrence, macrofossil data was given precedence.

This estimate of both global and regional range losses may be an underestimate due to limitations of the plant fossil record. This is mainly because many fossil studies based on pollen and plant parts can have relatively low taxonomic resolution, particularly pollen which suffers from the fact that most identifiable pollen types are produced by multiple extant species and any pollen produced by any extinct relatives of living species cannot be identified. In some cases, the rare and fragmentary nature of macrofossils may also not be sufficient to determine whether the fossil represents a living or extinct species. A number of Pleistocene fossils in Japan and North America, for example, present morphological differences from extant species (Minaki et al., 1988; Miller et al., 2014) that could

represent variety, sub-species or species status. A classic case is a spineless Asteraceae pollen taxon, widespread across eastern Australia in the glacial periods until around 11 ka BP, but its nearest living relative is unknown (Macphail and Martin, 1991). However, while range losses are likely to be common, species extinctions over the 30-ka period we examine are likely to be rare given the time frame. Before our paper, there was only one well documented extinction as described by Jackson and Weng (1999). Considering that the background rate of plant and animal extinctions - those before human impacts - appear to be about one extinction per ten million species per year (Pimm and Joppa, 2015), it is possible to argue that the majority of fossils can be assigned to extant taxa.

For each fossil or aDNA record, the taxonomic classification given in the publication was adopted 'as is'. In most cases it was sufficiently detailed to allow comparison with modern distribution of extant populations. For example, 91 out of 125 records of conifers were identified at the species level. In addition, many conifer records identified at the genus level do not present any taxonomic ambiguity, as those genera include only one species living in the study area. For example, in NW Europe *Picea* and *Abies* are represented only by *P. abies* and *A. alba*, respectively.

The fossil record may have overlooked large areas of vegetation simply because fossils from these regions have not been studied. This is particularly problematic for tropical and arid regions (when packrat species are absent), where evidence for Quaternary plant last occurrences may be missing due to the poor taxonomic resolution of pollen for many taxa (Bush and Mosblech, 2012), and the lack of fossilisation of other taxa (Bohte and Kershaw, 1999). However, from most regions of the Earth a large number of pollen records are available that allow detailed reconstructions of past plant distributions, especially over the last 30 ka.

The ages of the plant last occurrences may have different sources of uncertainty. For example, macrofossil records generally predate the disappearance event, as it is unlikely that they represent the last surviving individual, while pollen records may post-date the regional loss event, as pollen may be transported from a long distance, depending on its dispersal ability. On the other hand, many pollen diagrams provide near-continuous records of past plant population dynamics that is not equalled by any other palaeoecological technique. The date of the last fossil evidence was considered the maximum age for range loss. Ages are always expressed as calibrated years (cal BP). When calibrated ages were not available in the original publications, radiocarbon dates were calibrated using the Radiocarbon Calibration Program Calib rev7.1 based on the Intcal13 calibration dataset (Reimer et al., 2013). In order to overcome chronological uncertainties and represent the results in a simple way, data were grouped in time intervals of 1 ka (Fig. 1).

Records were excluded where the chronology was uncertain and where there was disagreement in the literature as to whether the fossil record represents the last local occurrence of a past population or long-distance pollen dispersal (e.g. *Cedrus atlantica* in southern Europe) (Postigo-Mijarra et al., 2010; Magri, 2012). For six fossil taxa (*Larix* sp. in Russia, *Picea glauca*, *Picea* sp. in USA, *Picea abies*, *Betula* sp. in Russia and *Yucca brevifolia*) a large number of records were identified, so in these cases a maximum of five records were chosen representing those with the greatest distance from the modern range. Where multiple macrofossils of the same taxa from one site were reported, the youngest was chosen.

Potential range losses within the modern range of species were excluded as these could represent either continual occurrence or re-occupation of sites. Range losses that in the original publications were wholly attributed to human activities including via direct habitat destruction (Sun et al., 2011), or otherwise of uncertain cause, were excluded from the analysis as were fossil records of

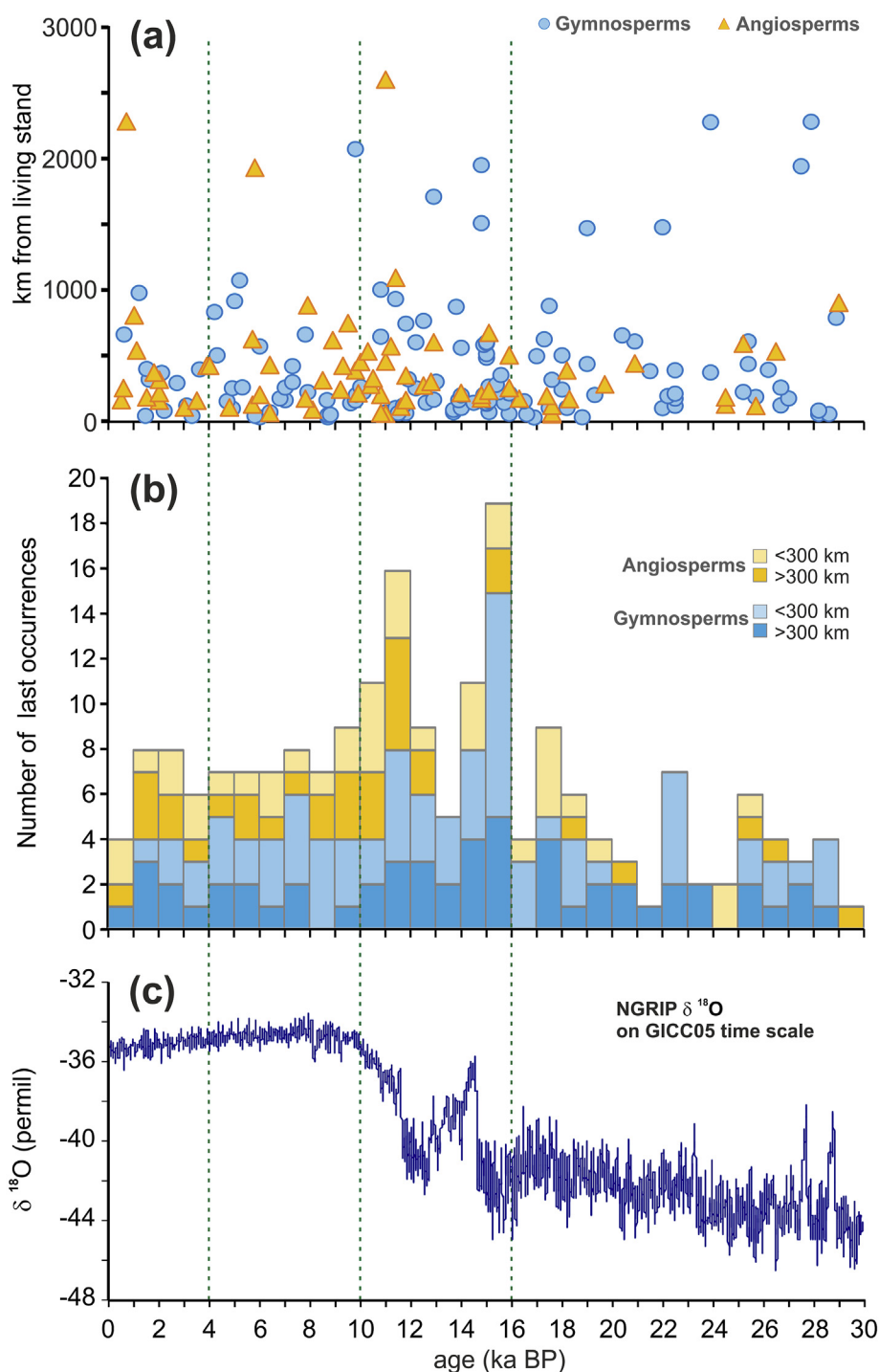


Fig. 1. Last occurrences of plant populations in relation to climate change over the last 30 ka. (a) The distance to nearest living stand (km) versus time (ka) for the last occurrences identified in this study. Two records are not shown due to their great distance from nearest living stand being *Carya* sp. and a Taxodiaceae species from Anatolia 6400 and 7400 km from nearest living stand of a relative, respectively, that disappeared ca. 2000 years ago. (b) Number of worldwide records of last occurrences (indicating loss of plant ranges) over the last 30 ka (1-ka time-slices). Different colours are used for gymnosperms and angiosperms, and for last occurrences closer or further than 300 km from nearest extant population of the same genus/species. The peaks in plant last occurrences correspond to phases of considerable climate change in the late glacial and early Holocene. Vertical dashed lines separate time intervals corresponding to Fig. 2. (c) NGRIP $\delta^{18}\text{O}$ values on GICC05 time scale (Vinther et al., 2006; Rasmussen et al., 2006; Andersen et al., 2006).

aquatic plants which may form ephemeral populations more readily than most terrestrial plants (Väliranta et al., 2015) as were parasitic plants and mangroves.

For each regional last occurrence, the distance (km) from the nearest modern occurrence was recorded (Figs. 1a and 3). The distance to nearest modern occurrence was evaluated using

distribution records from a range of sources (Supplementary Table 2) in Quantum GIS 3.8.3 'Zanzibar' (<http://qgis.osgeo.org>). Past and modern distributions were compared at the same taxonomic level. Thus, any fossil record identified at the genus level was compared with the modern distributions of that genus. The distance to nearest modern population is used here as an estimate of

the minimum range loss in distance that has not since been recovered.

3. Results

We found a total of 198 records of last occurrences including 56 genera across six continents (Figs. 1–2 and Supplementary Tables 1–2). A total of 88 of these records (44.54%) were based on pollen, 105 (53%) were based on macrofossils, 4 on stomata (2%), and 1 was based on ancient DNA (Supplementary Table 1). The date of the last fossil evidence was considered the maximum age for range loss.

Last occurrences were observed all around the world (Fig. 2), mostly in regions now dominated by temperate broadleaf forests (41.9%) followed by deserts/xeric shrublands (19.2%), montane grasslands and shrublands (3.6%), Mediterranean vegetation (10.6%), tropical and subtropical broadleaf forests (12.6), and taiga-tundra (12.1%).

Most records are of tree taxa (Supplementary Table 1). All of these taxa were assigned by the original authors to extant genera/species, many of which are still widespread. The majority of range losses were of gymnosperms with 126 records in 5 families (mostly conifers of the Cupressaceae, Pinaceae and Podocarpaceae). Notably, in Africa where there are few conifers, angiosperms clearly dominate the range loss record. Major range contractions included loss of plant genera from continents (e.g. *Dacrycarpus*, *Dacrydium*, *Gunnera*, *Phyllocladus*, and *Xanthomyrtus* from mainland Australia) and from major geographic regions (e.g. *Carya* from Anatolia, *Tsuga* from Mexico, *Podocarpus* from large areas of western Africa and the Amazon, *Larix* from the western Himalayas, and *Picea* from West Europe). Species were also lost from many islands, including several tree taxa from Kyushu, Honshu and Hokkaido (Japan), *Abies* and *Picea* from Britain, *Buxus* from various Mediterranean islands, *Carpinus* from the Canary Islands, *Phyllocladus* from Sumatra and Cycadaceae and *Artemisia* from Mauritius. Peaks of last occurrences are found in the time intervals 16–14 ka and 12–10 ka, two time periods characterized by abrupt climate changes (Fig. 1a–c), while plant range losses were more or less constant in frequency during the last 10 ka, paralleling the more stable record of climate change.

The mean distance of the regional extinction events from nearest living populations or closest known relative was 482 km, with 44.4% representing range losses of over 300 km and 13.1% over 800 km (Fig. 3). Both macrofossil and pollen-based records were similar in terms of distance to the nearest living stand or closest relative apart from a higher number of macrofossils at <300 km and more pollen-based records in the over 800 km class. Stomata records were <150 km from the closest living populations.

4. Discussion

4.1. Patterns of range loss

Our data show that no relation exists between the age of last occurrences and the distance of last occurrences from modern populations, as a range of different distances are found at any time of the analysed period of 30 ka (Fig. 1a). Thus, our data indicate that range losses are not time dependent. In contrast, they appear to be space dependent: the number of records of last occurrences, grouped by classes of 100 km distance from nearest extant populations, decrease with distance from living stands (Fig. 3). However, this decrease is not linear but follows a power law (correspondence with a negative power function ($R^2 > 0.93$)), which is a common pattern of many biological systems (Newman and Palmer, 2003; Taylor, 2019).

Most range losses were over small geographic scales (Figs. 1a and 3) which may suggest that species might be able to re-occupy their former range when the climate becomes suitable and if human activity does not prevent it. However, in many cases plant populations failed to re-occupy habitats even close to areas from which they were lost thousands of years ago. For example, the conifer *Larix kaempferi* disappeared from the Kansai region of Japan around 22 ka BP less than 100 km from its nearest modern population despite the presence of suitable habitat (Minaki and Matsuba, 1985).

Significantly, range-edge populations appear to be most vulnerable to loss: most records occurred at the edge of species' ranges (186 cases), far outnumbering those that occurred in the centre (12 cases). These range-edge populations are often of significant conservation value, sometimes comprising distinct subspecies (Hampe and Arroyo, 2002; Martín et al., 2008) and/or harbouring unique genetic stock (Hampe and Petit, 2005) so that loss of such populations may result in a reduction of species' climatic niches as divergent adaptive genotypes are lost.

A stark finding was the higher number of gymnosperm range losses, particularly conifers in Asia and North America, consistent with the high proportion of conifers currently facing extinction (Forest et al., 2018). However, this finding may be related to the slower decomposition of gymnosperm wood and leaves than angiosperms (Weedon et al., 2009). It may be argued that some losses of gymnosperms such as *Podocarpus* from parts of Africa and the Amazon may be part of the range contraction and expansion of these cool climate taxa with the climate oscillations of the Quaternary glacial/interglacial cycle. However, for some conifer extinctions, the range loss is inscribed in much longer processes (Crisp and Cook, 2011). For example, *Picea*, abundant in both the Iberian Peninsula and central-southern Italy during the Early Pleistocene, decreased during the Middle Pleistocene and eventually disappeared from these regions at the end of the last glacial period (Magri et al., 2017; Di Rita et al., 2020). Similarly, the extinction of multiple genera of Podocarpaceae from mainland Australia including *Dacrydium*, *Dacrycarpus* and *Phyllocladus* reflects continuing fragmentation and eventual loss of fire-intolerant mesic species that began in the Neogene (Hill, 2004). It seems reasonable to hypothesise that the range losses framed in long-term trends of disappearance of species have very little chance of recovering.

4.2. Mapping past and present conifer vulnerability

Considering that an inventory of modern endangered angiosperm species is far from being complete (Mounce et al., 2018; Humphreys et al., 2019), partly due to the high number of angiosperm species (estimated at 295,383 (Christenhusz and Byng, 2016)) and deficiency of data for many species concerning their geographic ranges and conservation status (Corlett, 2016; Bachman et al., 2018), we limited the comparison of fossil and modern data to conifers. Conifers are an ideal group for such an analysis given their almost global distribution, dominance of major biomes and the easily manageable number of species estimated at 629 (Christenhusz and Byng, 2016). In addition, their distribution and conservation status are well understood (<http://threatenedconifers.rbge.org.uk>; Debreczy et al., 2011; Farjon and Filer, 2013).

The comparison of past lost ranges and modern threatened conifers shows that areas with populations that disappeared in the past often include endangered species at present (Fig. 2). Thus, in a sense, fossil data would anticipate the modern threats of biodiversity loss. However, in some cases conifer populations of the past were lost in areas where there is no conservation concern at

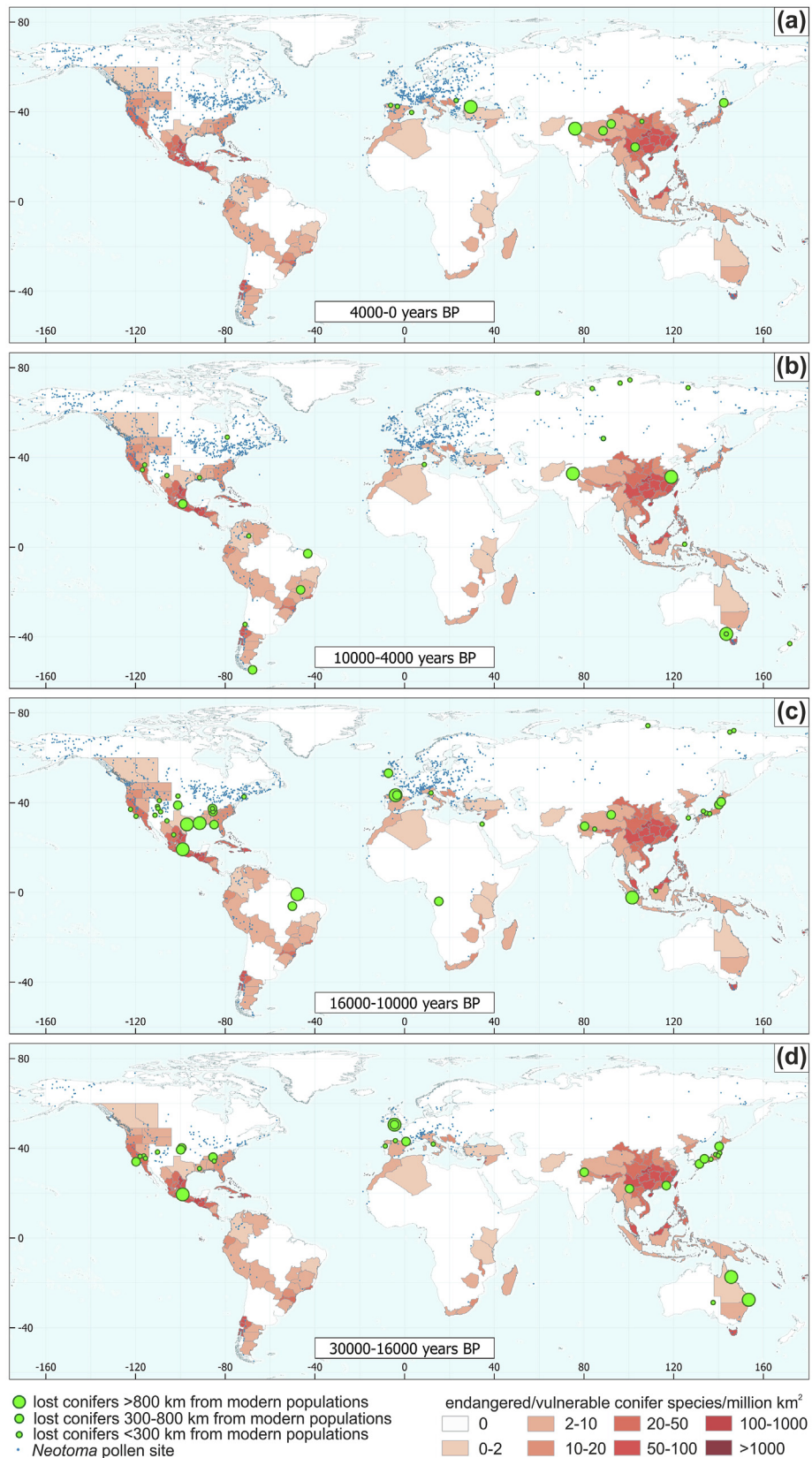


Fig. 2. Comparison of the worldwide distribution of modern endangered conifers and the records of lost ranges over the last 30 ka. The number of critically endangered, endangered and vulnerable conifers based on the IUCN Red List of threatened species (www.iucnredlist.org, last accessed August 08, 2020) is represented for each administrative region, after normalization for the surface area of each region. Green dots represent records of last occurrences of conifers, indicating lost ranges, in different time windows: (a) 0–4 ka BP, (b) 4–10 ka BP, (c) 10–16 ka BP, (d) 16–30 ka BP. The size of the green dots is proportional to the distance from the nearest extant population of the same species/genus. Small blue dots represent the pollen records available in the Neotoma fossil database for each time window (Williams et al., 2018). The map was generated using QGIS version 3.8.3 ‘Zanzibar’ (<http://qgis.osgeo.org>).

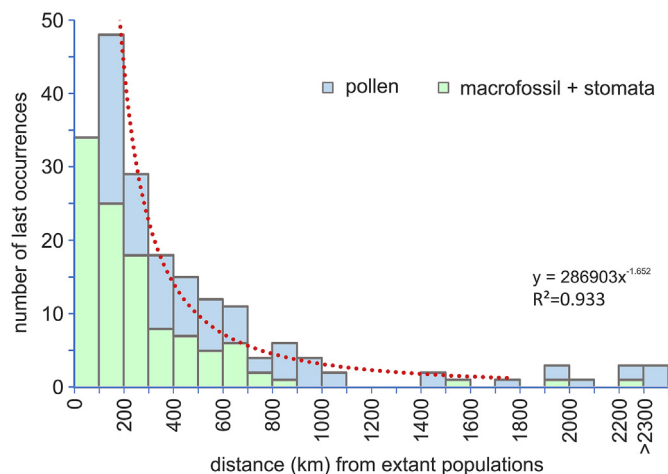


Fig. 3. Number of worldwide records of last occurrences over the last 30,000 years grouped by their distance from extant populations (100 km classes). The dashed line represents the best fitted negative power function. Pollen data are considered only for distances >100 km.

present. This may indicate either that vulnerable conifer populations have already become extinct, or that lost conifers were threatened by environmental, climatic, biological, or anthropogenic pressures different from the present ones.

Between 30 ka and 16 ka BP (Fig. 2d), losses of conifers are recorded in China, Japan and North America in areas currently including many endangered species. In Japan, one of the species that underwent range contraction is currently critically endangered (*Picea koyamae*), one is endangered (*Picea maximowiczii*) and one is near threatened (*Picea alcoquiana*). In contrast, there is no correspondence between the past and present vulnerability in Western Europe, where *Picea abies*, currently common in central, eastern and northern Europe, completely lost its western populations before the onset of the postglacial (Magri et al., 2017). In Australia, the genus *Dacrydium* disappeared around 19 ka and did not recover (Moss et al., 2013). In these regions, long-term drying and/or increasing seasonality trends may have been the primary cause for the loss of species.

Between 16 ka and 10 ka BP, a large number of permanent range losses coincides with significant climate oscillations (Fig. 1b-c). In many cases, these range losses occurred in areas currently including endangered conifer species (Fig. 2c). For example, in Mexico, *Tsuga* disappeared from areas located 2000 km south of its modern distribution (Lozano-Garcia et al., 1993). In Texas and Louisiana, the last occurrence of *Picea glauca* is documented by pollen and macrofossil records at >1500 km distance from the present populations (Holloway and Bryant, 1984). Near the equator, *Phyllocladus* disappeared from the island of Sumatra around 11 ka (Flenley and Butler, 2001). The question arises whether these taxa will ever be able to re-occupy their lost territories, a process made more unlikely given current habitat fragmentation due to anthropogenic activity. In contrast, in the Western United States several lost populations are recorded at a modest distance from the modern ones (<300 km) suggesting potential for recovery via dispersal. In addition to Western European sites, some lost ranges of conifers, mostly of the genus *Podocarpus* at equatorial latitudes in the Brazilian Amazon and the Congo, are located outside modern endangered areas (Fig. 2c). The Brazilian populations of *Podocarpus* lost during the late glacial and early Holocene climatic transition (Behling, 1996) were located up to 1000 km distance from the modern ones.

Between 10 ka and 4 ka BP (Fig. 2b), several conifer taxa

disappeared along a stretch of thousands of kilometres at the tundra-boreal forest/taiga interface in Eurasia and North America, as a result of declining summer insolation and cooling arctic waters (Kremenetski et al., 1998; MacDonald et al., 2000). In this case, climate change was a main driver of plant population contractions at the margin of their geographical range, where they underwent progressive fragmentation and disappearance, although within distances <300 km from modern ranges. This early Holocene reduction of conifer populations at a time of rapid climate change has no modern analogue in the distribution of endangered species, however, it provides a clear example of the risks of biodiversity loss at the edge of species ranges controlled by global climate changes.

In the last 4000 years, despite the ever-increasing human impact on the natural environment, a relatively low number of losses are recorded (Figs. 1b and 2a). They converge along a longitudinal belt stretching from the Western Mediterranean to Japan around 35°N, within which many conifers are threatened at present (Fig. 2a). Human impact may be held responsible for at least part of this loss, for example in the Mediterranean area. However, in Central-Northern Europe a massive human impact on vegetation, documented in a very high number of fossil sites (see the number of Neotoma sites in Fig. 2a), has not provoked any range loss in conifers, which are not endangered even at present in the region. Most importantly, late Holocene fossil-based losses are completely missing in regions where conifer species are not currently endangered.

4.3. Linking past and present plant vulnerability

Our database of past plant losses is the first step of a new strategy for the assessment of biodiversity loss based on the joint use of spatio-temporal information of plant vulnerability from fossil and modern data, presented in Fig. 4 in the form of a flow chart. On the fossil side, palynological, palaeobotanical and aDNA data form the database of past lost ranges of plant taxa, which also takes into account the current species distribution. On the modern side, ecological, biogeographical and genetic data form the database of currently endangered taxa. Past lost ranges and geographical distributions of modern endangered taxa, mapped together at different time windows, show the spatio-temporal pattern of range loss and highlight the geographical areas where plant taxa have been especially vulnerable to extinction through time.

Different maps can be produced for different taxonomic or ecological groups and for different geographical areas. Downscaling to specific regions may prove especially effective to inform actions aimed at appreciating and managing the biodiversity on the territory. For example, a pollen record of last occurrence of *Podocarpus* in the island of Borneo (Anshari et al., 2001) (not included in our database as it is located <100 km from the nearest living stand) may warn of which environmental conditions can lead to a lethal risk for the three endangered and two vulnerable *Podocarpus* species currently living in the island (<https://www.iucnredlist.org>; <http://threatenedconifers.rbge.org.uk>). Thus, relating modern threatened species to past lost ranges of populations at a regional/local scale is indispensable to trace back the current vulnerability of threatened species and to evaluate the rate of range loss through time.

Improvements in the quality of chronological and taxonomical detail of fossil records, of the biogeographical accuracy of modern data, and routine inclusion of genetic analyses of modern and past plant populations will provide valuable data for statistical analyses at different geographical scales and will make this tool more effective for conservation planning (environmental impact assessments, specific conservation and management actions, and resource allocation) and useful for scientific research.

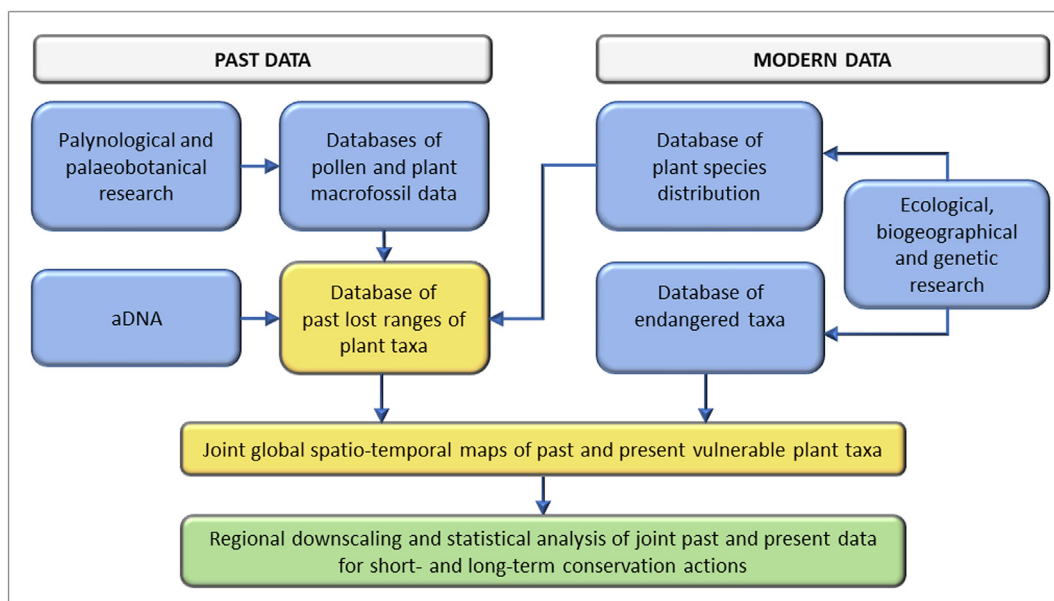


Fig. 4. Flow chart of the proposed protocol for the assessment of spatio-temporal trends in biodiversity loss. Blue boxes include data already available, yellow boxes represent the advancement of this paper (Fig. 1 and 2), the green box is the implementation of the protocol for effective conservation actions.

5. Conclusions

Our analysis gives unique insights into the geographical contractions of plant populations over the last 30 ka, of which many led to range losses. For the first time we provide a worldwide estimate of the geographic location and extent of late Quaternary range losses of plants. In particular, the records for conifers capture not only the well understood contraction of taiga species in the northern hemisphere related to the mid-Holocene lowering of solar radiation, but also provide less expected results including the confirmation of multitudes of last occurrences at mid- and low-latitudes sometimes representing major range losses.

Linking knowledge from both modern and millennial-scale perspectives reveals new and pertinent information on the modes, location, timing and extent of past-range losses of plant species that holds great promise to enhance the effectiveness of conservation planning. Such an approach is possible at both global and regional scales by taking advantage of the massive amounts of data available from open-source databases and the scientific literature, as well as the knowledge of palynologists, palaeobotanists, ecologists, biogeographers and molecular ecologists that are collecting data from all over the world.

While the attention of the palaeoecological community has mostly focussed on the rates of spread of plant populations in the postglacial as a measure of their ability to survive predicted global warming, this study reveals that during the last 30 ka many plant species were also undergoing more or less severe range contractions that have not been since recovered. This global analysis of range loss of plant species raises several unexpected questions, including the contrasting fate of gymnosperm versus angiosperm species, the high rate of range losses at middle-low latitudes, which are generally considered to be effective refuge areas for plant species, and the failure of several species to re-occupy their lost nearby ranges over time spans of thousands of years.

Author statement

All authors have made substantial contributions to the

submission: J.R.P.W. and D.M. devised the study and contributed equally to this article. J.R.P.W., D.M., F.D.R., K.S. and J.N. undertook the literature and databases search. J.R.P.W., D.M. and I.P. undertook all data analyses and all authors contributed to the interpretation of results., D.M., I.P. and J.R.P.W. led the writing of the manuscript with significant contributions from K.S., F.D.R., and J.N.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2020.106640>.

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