Accepted for publication in *Trends in Plant Science* published by Cell Press: https://doi.org/10.1016/j.tplants.2023.04.014

Anthropogenic Land-Use Legacies Underpin Climate Change-Related Risks to Forest Ecosystems

Albert Vilà-Cabrera[1,2,3,‡,*], Julen Astigarraga[3,‡], Alistair S. Jump[2], Miguel A. Zavala[3], Francisco Seijo[4], Dominik Sperlich[5] and Paloma Ruiz-Benito[3,6,‡]

[1]CREAF, Bellaterra, Catalonia, Spain
[2]Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Scotland, UK
[3]Universidad de Alcalá, Grupo de Ecología y Restauración Forestal, Departamento de Ciencias de la Vida, 28805 Alcalá de Henares (Madrid), Spain
[4]Instituto de Empresa, School of Global and Public Affairs
[5]Department of Forestry Economics and Forest Planning, Faculty of Environment and Natural Resources, University of Freiburg, Germany
[6]Universidad de Alcalá, Grupo de Investigación en Teledetección Ambiental, Departamento de Geología, Geografía y Medio Ambiente, 28801 Alcalá de Henares (Madrid), Spain

‡These authors led the manuscript

*Correspondence: albert.vilac@uah.es (A. Vilà-Cabrera)

Abstract

Forest ecosystems with long-lasting human imprints can emerge worldwide as outcome of land-use cessation. However, the interaction of these anthropogenic legacies with climate change impacts on forests is not well understood. Here, we set out how anthropogenic land-use legacies that persist in forest properties following alterations in forest distribution, structure, and composition can interact with climate change stressors. We propose a risk-based framework to identify anthropogenic legacies of land-uses in forest ecosystems and quantify the impact of their interaction with climate-related stress on forest responses. Considering anthropogenic land-use legacies alongside environmental drivers of forest ecosystem dynamics will improve our predictive capacity of climate-related risks to forests and our ability to promote ecosystem resilience to climate change.

Anthropogenic land-use legacies can exacerbate the impacts of climate change on forest ecosystems

Humans have exploited forest ecosystems for millennia [1–3]. Given the magnitude of land-cover changes, forest management practices and plantation establishment over the last few centuries, recent humanity's footprint today shapes more than 70% of the world's forests [4]. While high-intensity **anthropogenic land-uses** (*see glossary*) prevail in tropical and boreal regions [5,6], **land-use cessation** also spreads unevenly worldwide since the post-1950's **great acceleration** [7], from large areas and longer time periods in the Global North to scattered less-extensive patches and shorter time periods in the Global South [8]. As a consequence, forest ecosystems with long-lasting human impacts (Fig. 1) can emerge across multiple biomes [9,10]. Although broadly recognised to influence forest dynamics [11], there is still a lack of understanding on how these human imprints may exacerbate the vulnerability of forest ecosystems to climate change [12–14]. However, such understanding is essential to better predict **impacts of climate change on forests** and define mitigation and adaptation priorities.

The response of forest ecosystems to climate change strongly depends on historical factors [15]. Anthropogenic land-uses can affect the stability of forest dynamics to climate by altering forest main patterns in forest distribution [16], structure [12], and composition [17] (Fig. 1). These alterations may result in persistent impacts of land-uses on **forest properties** at different levels (genetic, population, community, and ecosystem). Despite their relevance, the effects of anthropogenic land-uses are rarely considered alongside environmental drivers, often hindering our ability to predict climate change impacts on forests [18]. Given that climate change stressors and other anthropogenic perturbations interact and today strongly impact biological communities [19], quantifying the long-lasting influence of anthropogenic land-uses is essential to better predict forest ecosystem responses to climate change [12,18]. This understanding might thus support the anticipation of climate-related disturbance impacts on forests, such as the occurrence of large-scale forest die-off events, mega-fires and forest degradation [12,20–22]. Consequently, a research agenda focused on identifying hotspots of increased vulnerability in areas dominated by **human-modified forests** is of critical importance if we are to develop and adopt mitigation and adaptation strategies to improve forest **resilience to climate change** [10,23,24]. A risk-based framework using the concept of **anthropogenic land-use legacy** could provide such an approach.

Disturbance legacies are ecological properties that persist in biological communities following disturbance, shaping the response capacity of ecosystems to subsequent disturbance [25,26]. Disturbance legacies may become detrimental and increase ecosystem vulnerability to environmental stressors, particularly when legacies result from anthropogenic disturbance. For example, historical management can facilitate tree biomass development such that forest stands might become structurally mismatched to water availability. During periods of increased drought stress, this process can lead to episodes of forest dieback [12]. Therefore, the effective study of anthropogenic land-use legacies depends on a deep knowledge of the history, ecological dynamics, and environmental factors that will ultimately determine forest ecosystem responses to climate change [11]. However, the lack of guidelines to quantify how anthropogenic land-use legacies increase climate change-related risks to forests makes it difficult to anticipate the outcomes of this interaction.

Here, we set out how anthropogenic land-use legacies that persist in forest properties following the alteration in forest distribution, structure, and composition can heighten the impact of climatic stressors on forest ecosystems. Based on existing literature, we first summarise hypotheses on how anthropogenic land-use legacies in forest ecosystems can interact with climate-related stress and lead to detrimental impacts on forests. We then introduce a risk-based framework to first identify anthropogenic land-use legacies and then quantify their impacts on forests and their interaction with climate change. Finally, we apply the framework in an example to show that detrimental anthropogenic land-use legacies contribute to large-scale risk of tree mortality at the driest distribution edge of Scots pine (*Pinus sylvestris* L.). We focus on detrimental anthropogenic land-use legacies given the urgency of reducing climate change-related risks to forests. However, the proposed framework is flexible and general enough to not only anticipate detrimental impacts of anthropogenic land-use legacies on forests in any given context, but also accommodate and assess potential beneficial legacy effects. Therefore, we provide scientists, managers, and policymakers with an approach to identify risk and promote ecosystem resilience to climate change in regions dominated by human-modified forests.

Processes underlying detrimental effects of anthropogenic land-use legacies in forest ecosystems

To identify processes leading to legacy effects of anthropogenic land-uses that can exacerbate climate change impacts on forests, we surveyed scientific studies that reported detrimental effects of land-uses on current forest ecosystem responses to climate change. Across studies, we identified processes driven by anthropogenic land-uses that, following the cessation of the land-use, shape the current forest distribution, structure, and composition, leading to persistent legacies in forest properties. Hypotheses on detrimental effects of anthropogenic land-use legacies are framed considering the outcomes of their interaction with climatic stressors (Table 1).

Forest distribution: Tree species re-expansion towards increased climatic stress

Although the emergence of **secondary forests** contributes to the recovery of ecosystem functionality to some extent [10,27], ongoing re-expansion of tree species distributions is occurring under a changing climate relative to past conditions. If anthropogenic land-uses (i.e., deforestation) are clustered in areas where species are climatically stressed, subsequent secondary forest regrowth may occur at the limit of species climatic tolerances. An increased climatic stress relative to species climatic niches can thus constrain forest recovery and heighten the impact of climatic stressors on forests (Table 1) [16,28–32]. Similar responses may occur when management practices lead to partial tree canopy loss. Following the cessation of management practices, species can have re-established at the limit of their climatic tolerances [31,33] (Table 1). Shifts in canopy cover can also exacerbate the climatic stress experienced by understory trees [34] (Table 1). Anthropogenic land-use legacies may emerge through the establishment of tree plantations, which can result in a broadening of tree species distributions where planting has occurred beyond the species' natural range. Planted tree populations growing at the limit or outside of the range of species climatic tolerances may be particularly vulnerable to increased environmental stress (Table 1) [24,35–38].

Forest structure: Exacerbated conspecific negative density-dependence and increased disturbance impact

Altered forest structure is characteristic of human-modified forests. Such changes can derive from the establishment of high-density, structurally homogeneous tree plantations, forest management practices, or the regrowth of secondary forests. Structural alterations may persist over time once land-use cessation has occurred (Fig. 1). Alteration of tree size distribution may result in exacerbated **conspecific negative density-dependence** and, therefore, increased impacts of climate change on forests (e.g., higher tree mortality under drought stress) (Table 1) [12,32,36,37,39,40]. Similar forest structural shifts may increase the impact of climate-related wildfires on forest ecosystems (Table 1) [20,21,24,41].

Forest composition: Shifts in functional traits, genetics, and interspecific interactions mediate reduced population and community resilience

Human-induced alterations in forest composition may lead to persistent anthropogenic land-use legacies in population- and community-level functional traits, genetic composition, and interspecific interactions, in such a way that forest resilience to climate change can be compromised. Following the cessation of forest management practices (e.g., clearcutting, thinning, pruning, pollarding), their imprint may persist over time, becoming a source of intraspecific functional variation (Fig. 1). These human-modified forests may hold trees with functional traits that display reduced resilience to cope with climate change stressors (Table 1) [12,39,41–47]. Such phenotypic constraints may also arise in forests growing on altered soils by former agriculture and pasture (e.g., altered soil fertility) (Table 1) [48,49]. Anthropogenic land use-derived shifts in forest composition may generate forest populations with altered genetic composition [50,51] that may decrease their ability to cope with environmental stressors (Table 1) [24,52–60]. Land use-driven species replacements may result in human-modified forests holding novel communities that display altered ability to respond to climate change due to altered functional trait composition (Table 1) [33,39,61]. Loss of forest resilience to climatic stressors may also occur if anthropogenic land-use legacies affect interspecific interactions such as mutualisms (Table 1) [48,62–64]. Species replacements may also lead to increased performance of antagonists under changing climatic conditions, including tree heterospecific competitors, invasive species, herbivores, and pathogens (Table 1) [42,54,65–73].

Limitations in the current state of knowledge of anthropogenic land-use legacies in forest ecosystems

Current studies suggest that anthropogenic land-use legacies can increase the vulnerability of forest ecosystems to climate change, but anthropogenic land-use legacies are rarely considered in experimental designs in research (see Table 1). This knowledge limitation is probably triggered by the scarcity of reliable data on anthropogenic land-uses, making it difficult to identify and predict detrimental legacy effects. Furthermore, as the effects of anthropogenic land-use legacies and climatic stressors interact, the detrimental outcomes may vary between different ecological and geographic contexts (Table 1), making comparisons among systems (e.g., regions, species, legacy types, etc.) difficult. However, risk-based approaches can support the predictive understanding of interaction outcomes between global change stressors across contexts [74]. To advance towards forest adaptation strategies and support forest resilience to climate change, we need to better understand where and to what extent anthropogenic land-use legacies increase climate change-related risks to forests.

A risk-based framework using the concept of anthropogenic land-use legacy

To overcome the limitations in knowledge of potential detrimental effects of anthropogenic land-use legacies due to the lack of experimental designs, data, and contexts, we incorporate three major knowledge needs to build up a risk-based framework (Fig. 2, Key Figure). First, we point out the need to characterise forest properties considering human land-use impact and to identify high-impact anthropogenic land-use legacies (Fig. 2A). For instance, current data on forest distribution, structure, and composition can be used as proxies of land use-driven alteration of forest properties together with available information on anthropogenic land-uses (Box 1). Second, we recommend that alterations of anthropogenic land-use legacies are explicitly incorporated the into empirical study designs, so that they are considered alongside environmental drivers of contemporary forest dynamics. Therefore, hypotheses on detrimental anthropogenic land-use legacies (Table 1) can be tested in the context of a particular study system (Fig. 2B; Box 1). Finally, the potential outcomes of interactions between anthropogenic land-use legacies and climatic stressors can be better quantified and understood using the risk components and the main forest patterns that can be altered (i.e., distribution, structure, and composition), as this can improve our ability to identify and anticipate detrimental ecological effects on current forest properties (Fig. 2B-C; Box 1).

To define the risk components summarised in *Fig. 2* (*Key Figure*) we adapt the IPCC framework [19] to forest ecosystems. When forest anthropogenic land-use legacies are linked to the components of risk (exposure, sensitivity, and adaptive capacity), responses of forest ecosystems to climatic stressors can be framed and understood through the interaction between anthropogenic land use-driven changes in distribution, forest structure, and composition.

A reduction in forest distribution followed by re-expansion of species ranges after land-use cessation may result in increased climate-related exposure (Fig. 2C). For example, secondary forests in the Brazilian Amazon are distributed more toward drier and more seasonal climatic conditions than the biome average because past deforestation was concentrated in these areas. Species re-expansions under dry climatic conditions are constraining the potential contribution of secondary forests to carbon sequestration [28]. The alteration in forest structure may result in increased sensitivity to climatic stressors (Fig. 2C). When management practices are ceased, their legacies can endure, for example in the form of increased competition in overcrowded even-aged stands, which may exacerbate processes of conspecific negative density-dependence and thus impacts of climatic stressors on forests [12,41,43].

Alteration in forest distribution and structure can result in anthropogenic land-use legacies that increase risk through exposure and sensitivity (Fig. 2C), such as in the case of tree plantations. For example, in the Carpathians where pine plantations have been established outside their natural distributions, pine species perform worse than the native conifers in response to drought stress [35]. Decreased performance of plantations may reduce the delivery of ecosystem services, especially in drier areas worldwide [38]. Anthropogenic land-use legacies derived from shifts in forest distribution and structure can also result in increased megafire risk, as reported in Australian forests where past logging generated extensive areas characterised by densely stocked forests that today influence fire dynamics [21].

Increased climate change-related risk to forests may occur by the reduction of adaptive capacity through alterations in forest composition. At the population level, the cessation of anthropogenic land-uses may result in the emergence of anthropogenic land-use legacies toward more vulnerable tree phenotypes, such as in form of high abundance of slow-growing weak trees [42] or increased canopy dominance of younger trees which have root traits less able to cope with climatic stressors [47]. Legacy-driven population-level functional shifts may also lead to increased structural and physiological constraints that exacerbate hydraulic failure and fire impact [39,44–46]. For example, past high-intensity management practices might underly increased drought-induced mortality of larger canopy trees in temperate forests [46]. Anthropogenic land-use legacies in the population genetic properties can also lead to decreased adaptive capacity to climate change. For example, widespread tree planting within a species' native range may result in forest dieback if seed material is translocated among lineages with differing climatic niches [58]. In addition, gene flow from planted non-local genotypes into native populations can result in landscape-level genetic homogenisation [55]. Although still highly uncertain, shifts in forest genetic properties have the potential of inducing long-term effects on the adaptive capacity of forest ecosystems [52,59,60].

Anthropogenic land-use legacies affecting interspecific composition in functional traits may increase risks to forests driven by shifts in their adaptive capacity. For instance, shifts towards reduced bark thickness and wood density compromises trait-mediated capacity of forests to withstand fire and drought in tropical and temperate regions [39,61]. Anthropogenic land-use legacies that affect interspecific interactions can also influence the adaptive capacity of forests to climatic stressors. For example, secondary forests may hold distinct and simpler ectomycorrhizal communities because of increased nitrogen and phosphorous availability due to former arable and pasture activities. This alteration may reduce the capacity of trees to cope with drought stress [48,63,64]. High occurrence of tree stumps or increased stand density and structural homogeneity may alter interspecific interactions and favour, for instance, the spread of pathogen and insect outbreaks [65,70,73] that in interaction with climate-related stress may exacerbate negative impacts on forests [42,72].

The proposed risk-based framework can improve our predictive understanding of forest dynamics and climate-related risks to forests, thus supporting adaptation strategies to foster long-term forest resilience to climate change in regions dominated by human-modified forests. As witnessed in Scots pine (*Pinus sylvestris* L.) in the Iberian Peninsula, anthropogenic land-use legacies derived from altered forest distribution, structure, and composition contribute to large-scale patterns of climate-driven tree mortality risk (Box 1).

Concluding remarks

Increased climate change-related risk to forest ecosystems can be intense and extensive in areas dominated by human-modified forests, particularly if anthropogenic land-use legacies interact with climatic stressors in such a way that their detrimental ecological effects act synergistically. We recommend that future research explicitly incorporates the impact of anthropogenic land-use legacies into experimental designs and investigates how forest exposure, sensitivity, and adaptive capacity to climatic stressors are modified by anthropogenic land-use legacies (Fig. 2, Key Figure). Such an approach can be of key importance to identify forest areas at high risk from climate change, and understand and anticipate climate change impacts on forest dynamics, biodiversity and ecosystem functioning, providing an opportunity to reduce risks to forests and improve forest resilience [10,23,24,75] (Box 1) (see **Outstanding Questions**). To apply the proposed framework and better predict the impacts of climate change on forests, we propose using current forest properties as proxies of anthropogenic land-use legacies using available data such as forest inventories and forest historical information (Box 1), and emerging high-resolution data as remote sensing technologies continue to develop [76]. In addition, understanding how anthropogenic land-use legacies shape forest genetics, functional traits, and interspecific interactions deserves urgent attention as these forest properties ultimately underpin responses of forest ecosystems to changing climatic conditions.

Importantly, although our approach here focusses on anthropogenic land-use legacies that are predominantly detrimental, the proposed framework allows the incorporation of (sometimes counteracting) beneficial legacy effects. For example, younger canopy-dominant trees can show larger growth reductions during drought, but this response can be counteracted by a quick recovery from impact [47]. As the proportion of younger trees increases across many forested regions (as a legacy of anthropogenic land-uses), the application of the framework has the potential to support adaptive management to reduce short-term risk of forest loss and enhance long-term C stocks [47]. Improved forest resilience can also be attained by considering the benefits of sustainable management practices and local knowledge in the framework application, such as traditional fire use and forest management [52,77]. Finally, while this framework centres on an ecological approach, emerging anthropogenic land-use legacies are inextricably dependent on previous socio-economic contexts [8,78]. Therefore, a key step towards mitigation and adaptation goals will involve the collaboration of natural and social scientists with local stakeholders and policymakers in decision-making processes from local to global scales. This cooperation will be pivotal for the success of the post-2020 UN Biodiversity Framework and the UN Decade on Ecosystem Restoration.

Acknowledgements

We acknowledge the insight comments and suggestions of three anonymous reviewers to improve the manuscript. A.V-C was supported by a Juan de la Cierva-Incorporación fellowship [IJC2018-038508-I] from the Ministry of Science and Innovation (Spain) and the 50th Anniversary Fellowship program of the University of Stirling (Scotland, UK). J.A was supported by a FPI fellowship of the Department of Education of the Basque Government. P.R-B was supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010). D.S acknowledges funding of the Federal Ministry of Food and Agriculture (BMEL) based on a decision of the Parliament of the Federal Republic of Germany. We also acknowledge support from the grants VERDAT (Organismo Autónomo de Parques Nacionales, Ref. 2794/2021) from the Ministry for Ecological Transition and Demographic Challenge (Spain), and LARGE (PID2021-123675OB-C41) from the Ministry of Science and Innovation (Spain).

References

1 Ellis, E.C. and Ramankutty, N. (2008) Putting people in the map: Anthropogenic biomes of the world. *Front. Ecol. Environ.* 6, 439–447

2 Mottl, O. *et al.* (2021) Global acceleration in rates of vegetation change over the past 18,000 years. *Science (80-.).* 372, 860–864

3 Grantham, H.S. *et al.* (2020) Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. *Nat. Commun.* 11, 5978

4 FAO (2020) *Global Forest Resources Assessment 2020 - Key Findings*,

5 Taubert, F. *et al.* (2018) Global patterns of tropical forest fragmentation. *Nature* 554, 519–522

6 Gauthier, S. *et al.* (2015) Boreal forest health and global change. *Science (80-.).* 349, 819–822

7 Steffen, W. *et al.* (2015) The trajectory of the Anthropocene: The Great Acceleration. *Anthr. Rev.* 2, 81–98

8 Winkler, K. *et al.* (2021) Global land use changes are four times greater than previously estimated. *Nat. Commun.* 12, 2501

9 Meyfroidt, P. and Lambin, E.F. (2011) Global Forest Transition: Prospects for an End to Deforestation. *Annu. Rev. Environ. Resour.* 36, 343–371

10 García, C. *et al.* (2020) Managing forest regeneration and expansion at a time of unprecedented global change. *J. Appl. Ecol.* 57, 2310–2315

11 Foster, D. *et al.* (2003) The importance of land-use legacies to ecology and conservation. *Bioscience* 53, 77–88

12 Jump, A.S. *et al.* (2017) Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob. Chang. Biol.* 23, 3742–3757

13 Bürgi, M. *et al.* (2017) Legacy Effects of Human Land Use: Ecosystems as Time-Lagged Systems. *Ecosystems* 20, 94–103

14 Verheyen, K. (2022) Land-use legacies predispose the response of trees to drought in restored forests. *Glob. Chang. Biol.* 28, 1204–1211

15 McDowell, N.G. *et al.* (2020) Pervasive shifts in forest dynamics in a changing world. *Science (80-.).* 368, eaaz9463

16 Goring, S.J. and Williams, J.W. (2017) Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States. *Ecol. Lett.* 20, 461–470

17 Filgueiras, B.K.C. *et al.* (2021) Winner–Loser Species Replacements in Human-Modified Landscapes. *Trends Ecol. Evol.* 36, 545–555

18 Vilà-Cabrera, A. *et al.* (2019) Refining predictions of population decline at species' rear edges. *Glob. Chang. Biol.* 25, 1549–1560

19 *IPCC, 2022: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change,*

20 Hermoso, V. *et al.* (2021) Tree planting: A double-edged sword to fight climate change in an era of megafires. *Glob. Chang. Biol.* 27, 3001–3003

21 Lindenmayer, D.B. *et al.* (2022) Logging elevated the probability of high-

severity fire in the 2019–20 Australian forest fires. *Nat. Ecol. Evol.* 6, 533–535

22 Silva Junior, C.H.L. *et al.* (2020) Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Sci. Adv.* 6,

23 Henne, P.D. *et al.* (2015) Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Front. Ecol. Environ.* 13, 356–362

24 Gómez-González, S. *et al.* (2022) Moving towards the ecological intensification of tree plantations. *Trends Plant Sci.* 27, 637–645

25 Johnstone, J.F. *et al.* (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14, 369–378

26 Schurman, J.S. *et al.* (2018) Large-scale disturbance legacies and the climate sensitivity of primary Picea abies forests. *Glob. Chang. Biol.* 24, 2169–2181

27 Poorter, L. *et al.* (2021) Multidimensional tropical forest recovery. *Science (80-.).* 374, 1370–1376

28 Smith, C.C. *et al.* (2020) Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon. *Glob. Chang. Biol.* 26, 7006–7020

29 Zhang, X. *et al.* (2019) Ecological contingency in species shifts: Downslope shifts of woody species under warming climate and land-use change. *Environ. Res. Lett.* 14,

30 Vilà-Cabrera, A. *et al.* (2017) “New Forests” from the Twentieth Century are a Relevant Contribution for C Storage in the Iberian Peninsula. *Ecosystems* 20, 130–143

31 Wason, J.W. and Dovciak, M. (2017) Tree demography suggests multiple directions and drivers for species range shifts in mountains of Northeastern United States. *Glob. Chang. Biol.* 23, 3335–3347

32 Elias, F. *et al.* (2020) Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes. *Ecology* 101, e02954

33 Vayreda, J. *et al.* (2016) Anthropogenic-driven rapid shifts in tree distribution lead to increased dominance of broadleaf species. *Glob. Chang. Biol.* 22, 3984–3995

34 Zellweger, F. *et al.* (2020) Forest microclimate dynamics drive plant responses to warming. *Science (80-.).* 368, 772–775

35 Hereş, A.-M. *et al.* (2021) Legacies of past forest management determine current responses to severe drought events of conifer species in the Romanian Carpathians. *Sci. Total Environ.* 751, 141851

36 Ruiz-Benito, P. *et al.* (2012) Large-scale assessment of regeneration and diversity in Mediterranean planted pine forests along ecological gradients. *Divers. Distrib.* 18, 1092–1106

37 Sánchez-Salguero, R. *et al.* (2013) Contrasting vulnerability and resilience to drought-induced decline of densely planted vs. natural rear-edge Pinus nigra forests. *For. Ecol. Manage.* 310, 956–967

38 Hua, F. *et al.* (2022) The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science (80-.).* 4649, 1–28

39 Berenguer, E. *et al.* (2021) Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proc. Natl. Acad. Sci.* 118, e2019377118

40 Camarero, J.J. *et al.* (2021) Differences in temperature sensitivity and drought recovery between natural stands and plantations of conifers are species-specific. *Sci. Total Environ.* 796, 148930

41 Dieleman, C.M. *et al.* (2020) Wildfire combustion and carbon stocks in the southern Canadian boreal forest: Implications for a warming world. *Glob. Chang. Biol.* 26, 6062–6079

42 Sangüesa-Barreda, G. *et al.* (2015) Past logging, drought and pathogens interact and contribute to forest dieback. *Agric. For. Meteorol.* 208, 85–94

43 Marqués, L. *et al.* (2018) Last-century forest productivity in a managed dry-edge Scots pine population: The two sides of climate warming: The. *Ecol. Appl.* 28, 95–105

44 Stojanović, M. *et al.* (2017) Forecasting tree growth in coppiced and high forests in the Czech Republic. The legacy of management drives the coming Quercus petraea climate responses. *For. Ecol. Manage.* 405, 56–68

45 Maes, S.L. *et al.* (2019) Environmental drivers interactively affect individual tree growth across temperate European forests. *Glob. Chang. Biol.* 25, 201–217

46 Meyer, P. *et al.* (2022) Management alters drought-induced mortality patterns in European beech (Fagus sylvatica L.) forests. *Plant Biol.* DOI: 10.1111/plb.13396

47 Au, T.F. *et al.* (2022) Younger trees in the upper canopy are more sensitive but also more resilient to drought. *Nat. Clim. Chang.* 12, 1168–1174

48 Mausolf, K. *et al.* (2018) Legacy effects of land-use modulate tree growth

responses to climate extremes. *Oecologia* 187, 825–837

49 Alfaro-Sánchez, R. *et al.* (2019) Land use legacies drive higher growth, lower wood density and enhanced climatic sensitivity in recently established forests. *Agric. For. Meteorol.* 276–277,

50 Ledig, F.T. (1992) Human Impacts on Genetic Diversity in Forest Ecosystems. *Oikos* 63, 87

51 Jump, A.S. *et al.* (2009) Environmental change and the option value of genetic diversity. *Trends Plant Sci.* 14, 51–58

52 Sjölund, M.J. and Jump, A.S. (2015) Coppice management of forests impacts spatial genetic structure but not genetic diversity in European beech (Fagus sylvatica L.). *For. Ecol. Manage.* 336, 65–71

53 Boyden, S. *et al.* (2008) Competition among eucalyptus trees depends on genetic variation and resource supply. *Ecology* 89, 2850–2859

54 Lindgren, D. (2016) The role of tree breeding in reforestation. *Reforesta* DOI: 10.21750/REFOR.1.11.11

55 Steinitz, O. *et al.* (2012) Effects of forest plantations on the genetic composition of conspecific native Aleppo pine populations. *Mol. Ecol.* 21, 300–313

56 Lind, B.M. *et al.* (2019) Effect of fire and thinning on fine-scale genetic structure and gene flow in fire-suppressed populations of sugar pine (Pinus lambertiana Dougl.). *For. Ecol. Manage.* 447, 115–129

57 Rajora, O.P. *et al.* (2000) Microsatellite DNA analysis of genetic effects of harvesting in old-growth eastern white pine (Pinus strobus) in Ontario, Canada. *Mol. Ecol.* 9, 339–348

58 Jia, Y. *et al.* (2020) Evolutionary legacy of a forest plantation tree species (Pinus armandii): Implications for widespread afforestation. *Evol. Appl.* 13, 2646–2662

59 Unger, G.M. *et al.* (2016) Assessing early fitness consequences of exotic gene flow in the wild: a field study with Iberian pine relicts. *Evol. Appl.* 9, 367–380

60 Jordan, R. *et al.* (2019) How well do revegetation plantings capture genetic diversity? *Biol. Lett.* 15, 20190460

61 Strahan, R.T. *et al.* (2016) Shifts in community-level traits and functional diversity in a mixed conifer forest: a legacy of land-use change. *J. Appl. Ecol.* 53, 1755–1765

62 Silva, C.A. da *et al.* (2020) Fine root-arbuscular mycorrhizal fungi interaction in Tropical Montane Forests: Effects of cover modifications and season. *For. Ecol.*

Manage. 476, 118478

63 Guerrieri, R. *et al.* (2021) Land-use legacies influence tree water-use efficiency and nitrogen availability in recently established European forests. *Funct. Ecol.* DOI: 10.1111/1365-2435.13787

64 Correia, M. *et al.* (2021) Land-use history alters the diversity, community composition and interaction networks of ectomycorrhizal fungi in beech forests. *J. Ecol.* 109, 2856–2870

65 Netherer, S. *et al.* (2019) Acute Drought Is an Important Driver of Bark Beetle Infestation in Austrian Norway Spruce Stands. *Front. For. Glob. Chang.* 2,

66 Umaña, M.N. *et al.* (2019) Dry conditions and disturbance promote liana seedling survival and abundance. *Ecology* 100,

67 Robert, L.-E. *et al.* (2018) Landscape host abundance and configuration regulate periodic outbreak behavior in spruce budworm Choristoneura fumiferana. *Ecography (Cop.).* 41, 1556–1571

68 Giuggiola, A. *et al.* (2018) Competition for water in a xeric forest ecosystem – Effects of understory removal on soil micro-climate, growth and physiology of dominant Scots pine trees. *For. Ecol. Manage.* 409, 241–249

69 Sangüesa-Barreda, G. *et al.* (2015) Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: Connecting climatic and biotic drivers of forest dieback. *For. Ecol. Manage.* 357, 126–137

70 Slaughter, G.W. and Rizzo, D.M. (1999) Past forest management promoted root disease in Yosemite Valley. *Calif. Agric.* 53, 17–24

71 Meentemeyer, R.K. *et al.* (2008) Influence of land-cover change on the spread of an invasive forest pathogen. *Ecol. Appl.* 18, 159–171

72 Burgess, T.I. *et al.* (2022) Anthropogenic Disturbances and the Emergence of Native Diseases: a Threat to Forest Health. *Curr. For. Reports* 8, 111–123

73 Nakajima, H. (2019) Region-wide mass mortality of Japanese oak due to ambrosia beetle infestation: Mortality factors and change in oak abundance. *For. Ecol. Manage.* 449, 117468

74 Schulte to Bühne, H. *et al.* (2021) Improving Predictions of Climate Change–Land Use Change Interactions. *Trends Ecol. Evol.* 36, 29–38

75 Perring, M.P. *et al.* (2016) Global environmental change effects on ecosystems: the importance of land-use legacies. *Glob. Chang. Biol.* 22, 1361–1371

76 Lines, E.R. *et al.* (2022) The shape of trees: reimagining forest ecology in three

dimensions with remote sensing. *J. Ecol.* DOI: 10.1111/1365-2745.13944

77 Seijo, F. *et al.* (2018) Traditional fire use impact in the aboveground carbon stock of the chestnut forests of Central Spain and its implications for prescribed burning. *Sci. Total Environ.* 625, 1405–1414

78 Infante-Amate, J. *et al.* (2022) From woodfuel to industrial wood: A socio-metabolic reading of the forest transition in Spain (1860–2010). *Ecol. Econ.* 201, 107548

79 Villar-Salvador, P. (2016) Restoration of Spanish pine plantations: A main challenge for the 21st century. *Reforesta* DOI: 10.21750/REFOR.1.04.4

80 Vilà-Cabrera, A. *et al.* (2011) Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. *Ecol. Appl.* 21, 1162–1172

81 Vadell, E. *et al.* (2016) Large-scale reforestation and afforestation policy in Spain: A historical review of its underlying ecological, socioeconomic and political dynamics. *Land use policy* 55, 37–48

82 Neumann, M. *et al.* (2017) Climate variability drives recent tree mortality in Europe. *Glob. Chang. Biol.* 23, 4788–4797

83 Ruiz-Benito, P. *et al.* (2017) Functional diversity underlies demographic responses to environmental variation in European forests. *Glob. Ecol. Biogeogr.* 26, 128–141

Box 1. Anthropogenic land-use legacies contribute to large-scale tree mortality risk in Iberian Scots pine forests

Scots pine (*Pinus sylvestris* L.) is a widespread species that reaches its driest range edge in the Iberian Peninsula. In this region, the distribution, structure, and composition of Scots pine forests have been historically altered by management practices and tree planting for wood extraction and erosion control. The cessation of these land-uses occurred at fast rates over the 20th century [79]. Previous studies have shown how stand-level structural characteristics influence current forest demography under drought stress [36,80], but the prevalence of anthropogenic land-use legacies exacerbating drought-related Scots pine mortality has not been explicitly assessed. We used large-scale datasets on historical anthropogenic land-use and forest inventory to apply the proposed risk-based framework (Fig. 2, Key Figure) in Scots pine-dominated forests. We first characterised forest inventory plots according to their natural or planted origin (i.e., stand origin, see Supplementary Information). We considered stand origin as an indicator of anthropogenic land-use legacies derived from alterations in the species' distribution and stand composition. We then identified two main forest structural typologies across natural- and planted-origin stands, one associated with high tree height diversity and sapling abundance ('C1'; Fig. S1-S2), and the other one associated with high tree density, basal area, height, height-to-diameter ratio, and height homogeneity ('C2'; Fig. S1-S2). Tree diameter distribution was similar between both structural typologies (Fig. S2). Within forest structural typologies, planted-origin stands (C1-planted and C2-planted) displayed higher tree density, lower tree size, higher structural homogeneity, and greater tree growth, but lower abundance of saplings than forests with natural origin (C1-natural, C2-natural) (Fig. S3-S4), in accordance with previous studies [79,81]. We considered these structural characteristics in plantations as indicator of anthropogenic land-use legacies derived from alterations in forest structure and stand age reduction. We hypothesised that anthropogenic land-use legacies in plantations, emerged following the cessation of high-intensity land-uses (Fig. 2A, main text), would exacerbate drought-related tree mortality risk (Fig. 2B-C, main text, Table 1). Tree mortality was overall higher in planted- than in natural-origin stands, suggesting that persisting anthropogenic land-use legacies following alterations in forest distribution, structure, and composition can increase overall mortality risk to forests (Fig. I, Fig. 2B-C). This pattern remained consistent within each forest structural typology (Fig. I). Under a climate change scenario that assumed 20% reduction in water availability and 20% increase in drought severity, mortality risk increased in C1 forest structural typology, being this increase 44% higher in plantations (Fig. I; SI). The higher mortality in plantations in C1 structural typology is consistent with increased climate change-related overall risk to forests. Increased exposure may derive from the altered species distribution towards the expansion of the species range, which may result in a greater chance to encounter drought stress out of the species' climatic tolerance [36]. Higher sensitivity may derive from the altered forest structure towards structurally homogeneous, denser, and younger stands, exacerbating conspecific negative density-dependence in response to drought stress [37]. Decreased adaptive capacity may derive from the alteration in composition towards increased abundance of younger trees which have functional traits with lower capacity to deal with drought stress [47]. On the contrary, climate change-type drought did not result in increased tree mortality in C2 forest structural typology (Fig. I), suggesting that other drivers than drought stress, such as long-term effects of altered stand genetic properties [60] or warmer temperatures in combination with tree antagonist organisms (e.g., pathogens)[72], might explain the larger mortality trends observed in plantations in this structural typology. This study case demonstrates that anthropogenic land-use legacies persisting in plantations can elevate the risk of climate change-related stressors to forests. At the same time, it also highlights that the proposed framework is a useful approach to identify hotspot forest types at critical risk and its potential drivers, providing thus opportunities to refine our predictive understanding of large-scale forest dynamics, and develop and implement mitigation and adaptation strategies during coming decades.

Note: data and code used can be found in Zenodo repository (https://doi.org/10.5281/zenodo.7120609). Data is also available at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/default.aspx.

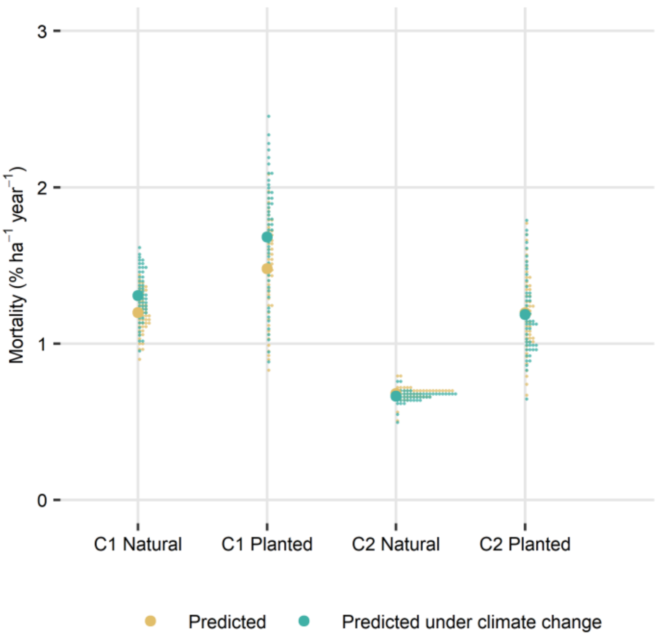


Figure I (Box 1). Planted-origin stands have higher tree mortality risk than natural-origin stands in Iberian Scots pine forests. Quantile dotplot representing model-predicted tree mortality (yellow) and model-predicted tree mortality under a climate change scenario (green) assuming a 20% reduction in water availability (WAI) and 20% increase in drought conditions (SPEI) for each forest type defined by stand origin (planted or natural) and forest structural typology (C1 and C2). *Note: Mortality was estimated in terms of percentage of dead basal area at the plot level. Large dots represent the median values and small dots represents approximately a 2% (1/50) chance. The climate change scenario is based on the IPCC predictions for the Mediterranean basin* [19].

Glossary

Anthropogenic land-use: human-driven exploitation of land with impacts on forest ecosystems, including complete tree cover loss due to land-cover changes, partial tree cover loss due to forest management practices, and tree cover increase due to tree planting (reforestation and afforestation).

Anthropogenic land-use legacy: persistent effect on forest properties following the cessation of anthropogenic land-uses.

Impacts of climate change on forests: abrupt or progressive climate-related shifts in forest dynamics and functioning, including forest die-off events, megafires, and forest degradation.

Conspecific negative density-dependence: population-level processes that occur when population growth is negatively influenced (e.g., tree mortality) by population density.

Forest properties: Genetic-, population-, community-, or ecosystem-level factors and processes that underlie forest dynamics.

Great acceleration: continuous and exponential growth rate of human activities since mid-20th century that are accompanied by substantial changes in ecosystems.

Human-modified forests: forest ecosystems shaped by past and current anthropogenic land-uses.

Land-use cessation: temporary or permanent stopping of a given land-use.

Resilience to climate change: the ability of forest ecosystems to cope with- and adapt to climate change stressors.

Secondary forests: forests that have re-established after the complete or partial loss of the original tree cover.

Table 1. Hypotheses regarding detrimental anthropogenic land-use legacies. Each specific hypothesis is framed considering the interaction outcomes between climatic stressors and contemporary forest properties resulting from anthropogenic land use-driven alteration in forest distribution, structure, and composition.

Altered forest pattern	**Affected forest property**	**Cause**	**Hypotheses on detrimental anthropogenic land-use legacies**	**Refs**
Distribution	Species range re-expansion	Land-cover change	Secondary forest expansion towards stressful climatic conditions relative to species climatic niches	[16,28–32]
		Management practice	Forest recovery occurs under an unfavourable climatic context relative to species niches	[31,33,34]
		Plantation	Forest plantations decline and are highly impacted at the edge or out of the species natural range	[24,35–38]
Structure	Stand-level tree size distribution	Land-cover change, management practice	Climatic stressors exacerbate conspecific negative density-dependence processes and fire impact in secondary forests	[32,39]
		Plantation	Climatic stressors exacerbate conspecific negative density-dependence processes and fire impact	[20,24,36,37,40]
Composition	Within-species phenotypic, functional, and genetic properties	Land-cover change	Soil legacies result in within-species functional shifts towards tree phenotypes with reduced resilience capacity to increased climatic stressors	[48,49]
		Management practice, plantation	Shifts toward tree phenotypes with reduced resilience capacity to increased climatic stressors	[12,21,39,41–47]
		Management practice, plantation	Reduced genetic diversity and genetic-induced functional changes reduce the resilience capacity of populations	[24,52–60]
	Interspecific functional traits and interactions	Land-cover change, management practice, plantation	Novel tree functional assemblages with reduced resilience capacity to increased climatic stressors	[33,39,61]
			Increased forest vulnerability as a result of shifts in species interactions involving mutualisms and antagonisms	[42,48,54,62–73]

Figure 1. Examples of anthropogenic land-use legacies emerging from alterations in forest distribution, structure, and composition in Iberian forests. Description of photos: (A) Forest landscape with stands of reforested and afforested Stone pines (*Pinus pinea*). Pines are today declining in response to drought and biotic stressors (photo: F. Vilà-Carbonell. Maresme, Catalonia, Spain). (B) Over-dense and structurally homogeneous Scots pine (*Pinus sylvestris*) abandoned plantation in a drought stressed area (photo: A. Vilà-Cabrera. Parque Natural de la Sierra Norte de Guadalajara, Spain). (C) Pollarded beech trees (*Fagus sylvatica*) today overgrown and with altered phenotype because of the cessation of the traditional management practice (photo: J. Astigarraga. Oñati, Gipuzkoa, Spain). (D) Secondary beech (*Fagus sylvatica*) forest established following the cessation of agricultural use (photo: J. Astigarraga, Oñati, Gipuzkoa, Spain). (E) *Pinus radiata* plantation surrounding a native stand of sessile oak (*Quercus petraea*; photo: J. Astigarraga. Oñati, Gipuzkoa, Spain). (F) Abandoned plantation of *Eucalyptus nitens* with regenerating native oaks (photo: J. Astigarraga. Oñati, Gipuzkoa, Spain).

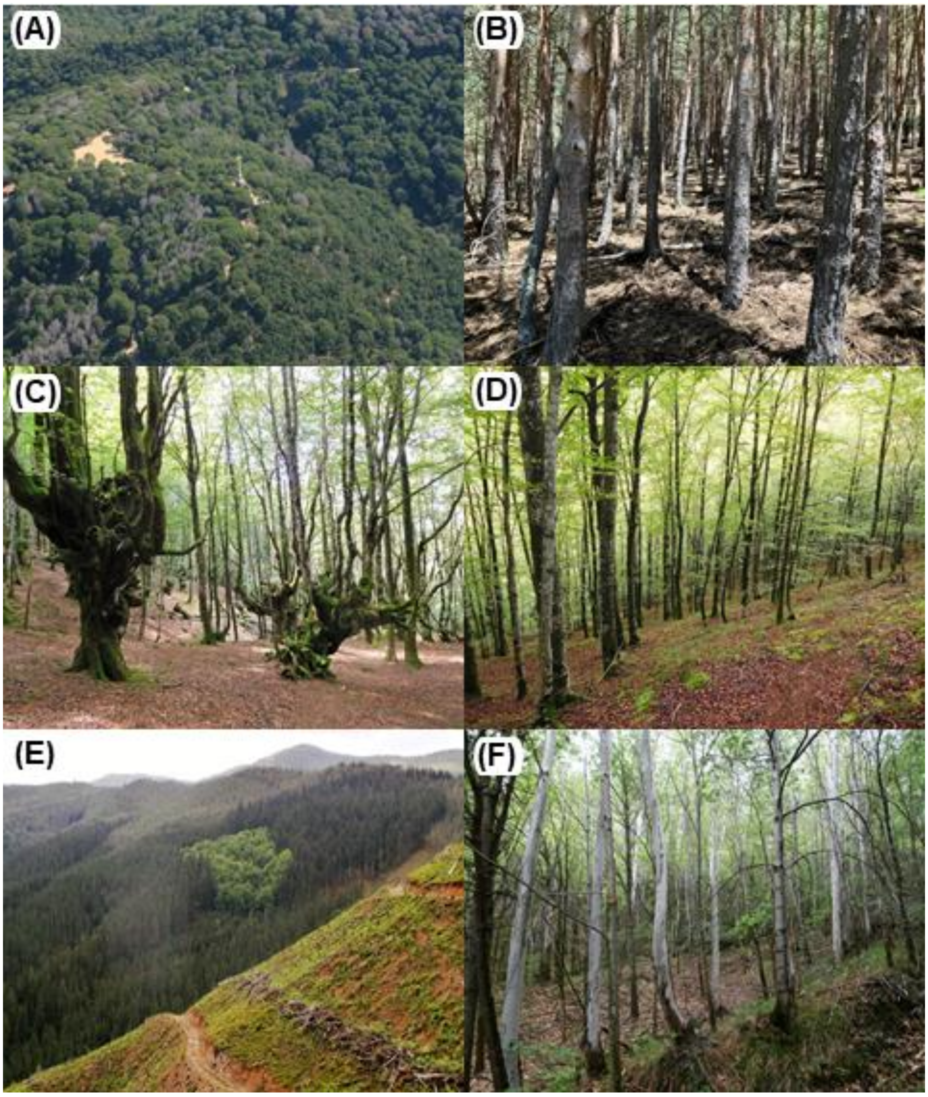
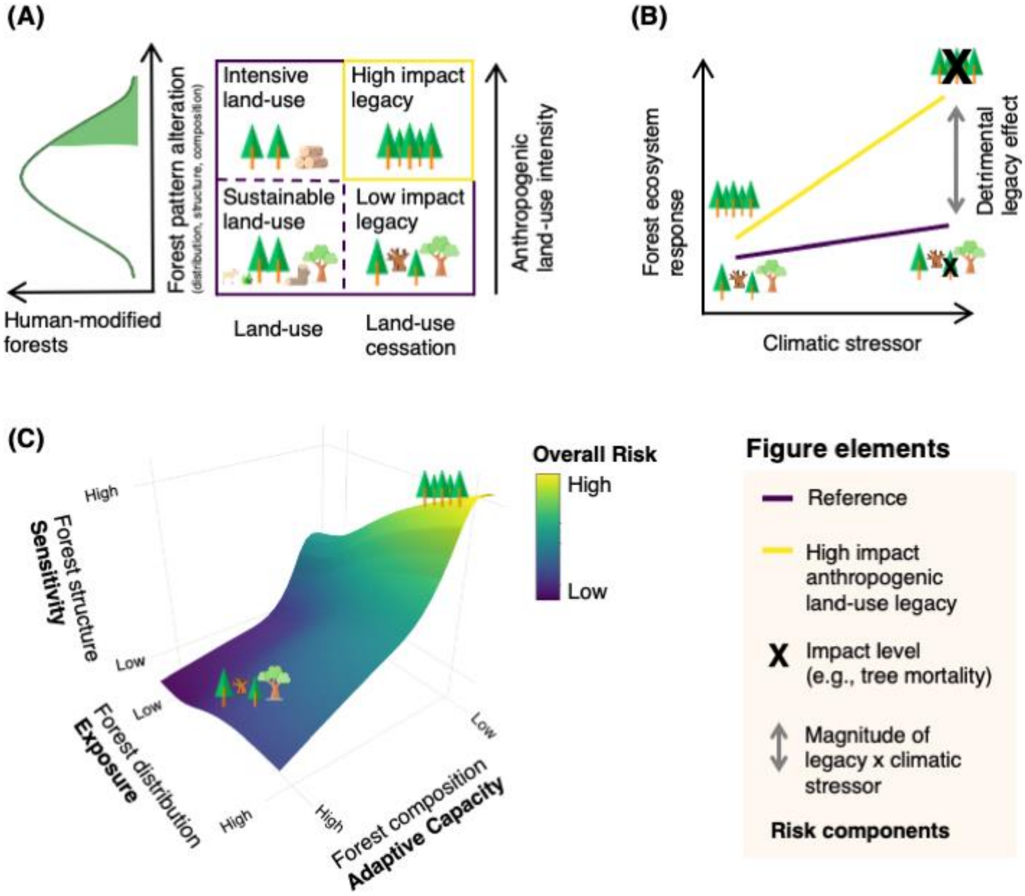

(A)
(B)
(C)
(D)
(E)
(F)

Figure 2 (Key figure). Risk-based framework using the concept of anthropogenic land-use legacy. We adapt the IPCC framework [19] to forest ecosystems considering the impact risk to forests as the potential response to a climate-related hazard (e.g., increased drought-induced mortality [82]). Risks to forests from climate-related hazards can be exacerbated by anthropogenic land-use legacies due to the interaction between exposure (ecological settings that expose forests to hazards, e.g., drought stress at the driest edge of species distributions [18]), sensitivity (the degree to which a forest ecosystem is affected, e.g., increased tree mortality due to exacerbated conspecific negative density-dependence [12]), and adaptive capacity (the capacity of forest trees, populations, and communities to counteract and cope with climatic stressors due to functional and genetic properties and interspecific interactions, e.g., where reduced functional diversity reduces the capacity of forest ecosystems to cope with climate change [83]). In this conceptual figure, a hypothetical region of pine-dominated forests is represented. Four- (in A) and two forest types (in B and C) are represented for simplification: intensively managed pine plantation, pine plantation following cessation of intensive land-use, sustainable managed natural pine forest, natural forest following sustainable land-use cessation. (A) Anthropogenic land-uses shape the main patterns in forest distribution, structure, and composition (i.e., human-modified forested areas). High-impact anthropogenic land-use legacies may derive after the cessation of high-intensity land-uses, e.g., high-density, and structurally homogeneous pine plantations for wood extraction. The characterisation, identification, and contextualisation of high impact anthropogenic land-use legacies in regions dominated by human-modified forests is of key urgency as these forests may be highly vulnerable to climatic stressors. (B) Testing interaction effects between anthropogenic land-use legacies and climatic stressors on forest ecosystem responses. The prevalence of increased detrimental anthropogenic land-use legacies leads to increased climate-related impacts on forests. (C) Linking detrimental anthropogenic land-use legacies in forest properties (derived from changes in forest distribution, structure, and composition) with climate-related risk components can support the predictive understanding of forest dynamics in regions dominated by human-modified forests. *Note: vector icons are from https://www.flaticon.com*


(A)
Human-modified forests
Forest pattern alteration
(distribution, structure, composition)
Intensive land-use
High impact legacy
Sustainable land-use
Low impact legacy
Land-use
Land-use cessation
Anthropogenic land-use intensity
(B)
Forest ecosystem response
Climatic stressor
Detrimental legacy effect
(C)
High
Low
Forest structure
Sensitivity
Low
High
Forest distribution
Exposure
High
Low
Forest composition
Adaptive Capacity
Overall Risk
High
Low
Figure elements
Reference
High impact anthropogenic land-use legacy
X Impact level (e.g., tree mortality)
Magnitude of legacy x climatic stressor
Risk components