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REVIEW ARTICLE

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Consequences of widespread tree mortality triggered by drought and temperature stress

William R. L. Anderegg[1,2]*, Jeffrey M. Kane[3] and Leander D. L. Anderegg[2]

Forests provide innumerable ecological, societal and climatological benefits, yet they are vulnerable to drought and temperature extremes. Climate-driven forest die-off from drought and heat stress has occurred around the world, is expected to increase with climate change and probably has distinct consequences from those of other forest disturbances. We examine the consequences of drought- and climate-driven widespread forest loss on ecological communities, ecosystem functions, ecosystem services and land–climate interactions. Furthermore, we highlight research gaps that warrant study. As the global climate continues to warm, understanding the implications of forest loss triggered by these events will be of increasing importance.

Forest ecosystems cover approximately 30% of Earth's land surface (42 million km^2)[1]. They provide numerous ecological, economic, social and aesthetic benefits across many spatial scales[1,2]. On local scales, forests structure communities and regulate ecosystem processes and services. On global scales, they serve as strong and persistent carbon sinks and exert substantial influence on biogeochemical cycles and climate regulation. Forests store 45% of the carbon found in terrestrial ecosystems, comprise 50% of terrestrial net primary production and may sequester as much as 25% of annual anthropogenic carbon emissions to the atmosphere[1,3].

Growing evidence suggests that many forests could be increasingly vulnerable to climate- and associated infestation-induced tree-mortality events[4]. Extensive tree mortality ('forest die-off') triggered by dry and hot climatic conditions has been documented on every vegetated continent and in most bioregions over the past two decades (Fig. 1)[4–6]. Although forest die-off has concerned ecologists since before the 1990s[7], at present no data set exists to assess the area and severity of widespread forest die-off globally over time. Changes in temperature, precipitation, insect and pathogen (termed collectively here as infestation) dynamics and more extreme climate events such as drought are expected to lead to increased instances of widespread forest die-off in the future[4,8,9]. Several dynamic global vegetation models have simulated the widespread die-off of some forest biomes by the mid- or late-twenty-first century, leading to a weakening of the terrestrial carbon sink or a positive feedback to climate warming, though recent simulations do not suggest such a severe die-off[10–12].

The physiological mechanisms through which drought drives tree death and forest die-off are a rapidly growing research area[13–15], but the impacts of forest die-off remain less well studied. Climate-induced forest mortality seems to be an emerging global phenomenon, yet there is no synthesis of the ecological, societal and climatological consequences of dying forests at present. Although research into forest-gap dynamics and other forest disturbances (for example, fire, forest harvesting or clearing, wind throw and storm damage) may inform the effects of climate-driven forest mortality, there are probably distinct consequences of forest die-off that justify independent consideration and synthesis.

We review current literature on the consequences of widespread forest die-off events — which we define as a substantial pulse of tree mortality (typically >10% loss of dominant canopy trees or 'stand-level' die-off[7]) on a regional scale (>250 km^2) — triggered directly by drought/heat stress or indirectly through infestation-induced mortality. We do not explicitly consider forest decline (that is, increased levels of tree mortality occurring over longer periods of time, typically >10 years) or mortality owing to fire, though die-off and decline probably represent two ends of a complex mortality spectrum. We focus primarily on North America, where much of the recent research has been done, but draw on mortality events and consequences across the globe. Our main objectives are to: (1) provide a synthesis of the direct research on the consequences of climate-induced tree mortality; (2) explore the distinct impacts of forest mortality relative to other forest disturbances; and (3) highlight key gaps in our understanding on the topic of the impacts of forest die-off. Our review of the ecological and societal consequences is structured by spatial scale, from stand-level alterations of forest communities to global biogeochemical cycle perturbations.

Forest structure and ecological communities

Tree mortality is a natural ecological process[16]; however, drought- and heat-induced mortality, including associated infestation-related forest die-off, is often a selective force that differentially affects tree species and rapidly alters the size, age and spatial structure of forests. Numerous studies throughout many forest types have demonstrated that mortality events tend to be taxonomically biased, where some species succumb more readily than others[6,17–21]. Because particular life stages of trees can be differentially susceptible to various disturbances, tree size and age structures of forests are altered by mortality. For example, in Queensland, Australia, drought triggered increased levels of large-stem mortality in the *Eucalyptus crebra–Eucalyptus xanthoclada* species complex, altering forest size structure, though differential size-class mortality didn't occur in four other species in the region[21]. In some instances, this mortality could be similar to stand-thinning surface fires (but not stand-replacing canopy fires), where smaller or younger trees are more often affected[6]. However, in many instances drought- and infestation-induced mortality have driven forest structural changes that differ markedly from those caused by fire by killing primarily larger or older trees[22]. Major mortality episodes also influence the density and spatial arrangement of trees in forests, although these effects are not well understood[23–25].

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Figure 1 | Images of climate-induced forest die-off from around the world. Clockwise from top left: Spain, Colorado, New Mexico and Argentina. Top right and the two lower images are reproduced with permission from ref. 4 © 2010 Elsevier.

Widespread tree-mortality events and subsequent alterations to forest structure will probably have strong impacts on community composition that differ from other disturbances. Selective mortality of particular tree species can drive long-term shifts in the dominant species and their associated communities[19,26,27]. In northern Patagonia, Argentina, for instance, drought-killed tree gaps favoured the recruitment and survival of *Austrocedrus chilensis* seedlings as opposed to *Nothofagus dombeyi* in co-occurring forests, altering the forest composition trajectory[19]. *A. chilensis* has previously experienced die-off from droughts[28], whereas tree-ring analysis from 1850 to present has documented widespread *Nothofagus pumilio* mortality in southern and northern Patagonia triggered by defoliator outbreaks related to warming trends[29]. Field data and modelling suggest that the subalpine fir (*Abies lasiocarpa*) may replace the lodgepole pine (*Pinus contorta*) in stands that suffered extensive mortality from the mountain pine beetle in Colorado, USA, accelerating forest succession in this system[27]. Drought-caused alterations in forest species composition can drive vegetation-type conversions, such as forests to savanna in northeastern Australia[30], promote new plant-community assemblages and reset or shift successional trajectories[31,32]. Widespread drought-induced tree mortality may also result in rapid species range contractions[33,34]. Furthermore, climate-change-induced tree mortality can induce shifts in understorey communities and soil biota. For example, drought-induced tree-mortality events drove changes in the understorey plant community beneath dead juniper (*Juniperus monosperma*) trees for at least seven years after drought[35]. Gap-dynamic principles suggest that these shifts in understorey plant communities will result in a greater proportion of species that are shade intolerant and possibly shorter lived, although the duration of these changes is less well understood. Moreover, theoretical and empirical studies suggest that some of the additional plant species and cover will be non-native in some ecosystems[35,36].

Changes in the cover and diversity of understorey vegetation will be highly dependent on environmental conditions (for example, climate, soils, topography) as well as the type and strength of species interactions at a particular site. For example, plant species in water-limited environments often depend more on facilitative relationships from other plants to aid establishment and growth[37,38] (but see ref. 39 for a counter argument). The loss of a foundation species (such as a dominant tree species) that acts to stabilize conditions and processes that promote the coexistence of other species can have a disproportionately large effect on biodiversity loss in an ecosystem[40]. In light-limited environments, understorey vegetation may be released owing to a reduction in overstorey trees.

Although extreme drought can directly alter fungal, microbial and animal communities, it can also influence food webs, as demonstrated by the effect of recent droughts on forest food webs in Spain[41]. Changes in the structure and composition of forests owing to rapid forest mortality can also have cascading indirect effects on associated communities by changing habitat structure and quality. Ecosystem impacts of forest mortality are likely to be

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largest in systems dominated by one or a few foundational tree species, where plant and animal community structure is often defined by a small number of strong interactions[40]. Research on the effect of resource pulses on bird communities following outbreaks of mountain pine beetle in Canada suggest that it is often possible to make qualitative predictions of the short-term impacts of tree mortality on species or functional groups, such as cavity-nesting birds, for which habitat requirements are well known[42,43]. However, this requires some knowledge of the time course of changes in the forest habitat structure following forest mortality, such as how quickly dead snags fall and decompose. Long-term predictions of species abundance, diversity and richness are ultimately constrained by uncertainty about the successional trajectories of affected forests.

We emphasize that the changes in ecological communities following forest die-off are crucial to understanding what the subsequent ecosystem consequences will be; however, such changes are poorly documented at present. Post-disturbance ecological community shifts certainly influence forest ecosystem functions, ecosystem services and land–atmosphere interactions (all reviewed below) in complex ways. Yet post-mortality successional trajectories are not known for most forest die-off events[4] and these trajectories will themselves be affected by emerging changes in climate and infestation dynamics. These trajectories thus represent a large uncertainty in the long-term impacts of climate-induced forest die-off.

Ecosystem function

The loss of a dominant species has many effects on ecosystem processes and functions (Fig. 2). Extensive forest die-off will alter the fluxes of energy and water in affected regions because trees play a large role in these processes. Loss of canopy cover from tree mortality directly decreases transpiration and canopy interception of precipitation, sometimes leading to increases in soil moisture, run-off and recharge[44]. However, increased radiation and wind following tree mortality at the ground surface can also increase soil evaporation and understorey transpiration, which would partly offset decreased transpiration and interception[45]. Thus, forest die-off can have substantial indirect and secondary effects on hydrological processes such as run-off, infiltration, groundwater recharge and stream flow that vary by ecosystem[46]. Depending on forest type and climatic zone, water yields are generally expected to change little or increase following widespread tree mortality[46,47], although recent data from southwestern US pine–juniper woodlands suggest that yields could decrease in dry ecosystems[48]. Canopy loss has large and spatially complex effects on near-ground solar radiation. Greater canopy openness will substantially increase the radiation load and the amount of direct rather than diffuse radiation[45]. Changes in the microclimate influence understorey species composition[35], which can in turn feed back to affect ecosystem function, such as nutrient cycling[45].

Forest nutrient cycling is likely to be affected by tree mortality through many pathways, although this has yet to be examined in depth[46,49]. Principles of forest nutrient cycling suggest that changes in radiation, soil moisture, infiltration and temperature owing to decreased forest leaf area will alter the cycling of nutrients[50,51], mycorrhizal activity[52] and erosion[53,54]. Yet these changes will occur mostly in tandem with large inputs of litter, dead roots and woody debris from standing and fallen dead trees. Two studies examined soil biogeochemistry following widespread forest die-off in lodgepole pine forests in Colorado, USA, and documented the initial increases in nitrogen inputs owing to fallen needles, followed by rapid carbon and nitrogen losses from soil organics, and an increase in inorganic nitrogen leading to highly altered soil food webs[55,56]. This is an active area of research, but greater geographic and taxonomic breadth is needed. Studies on wind throw and hurricane

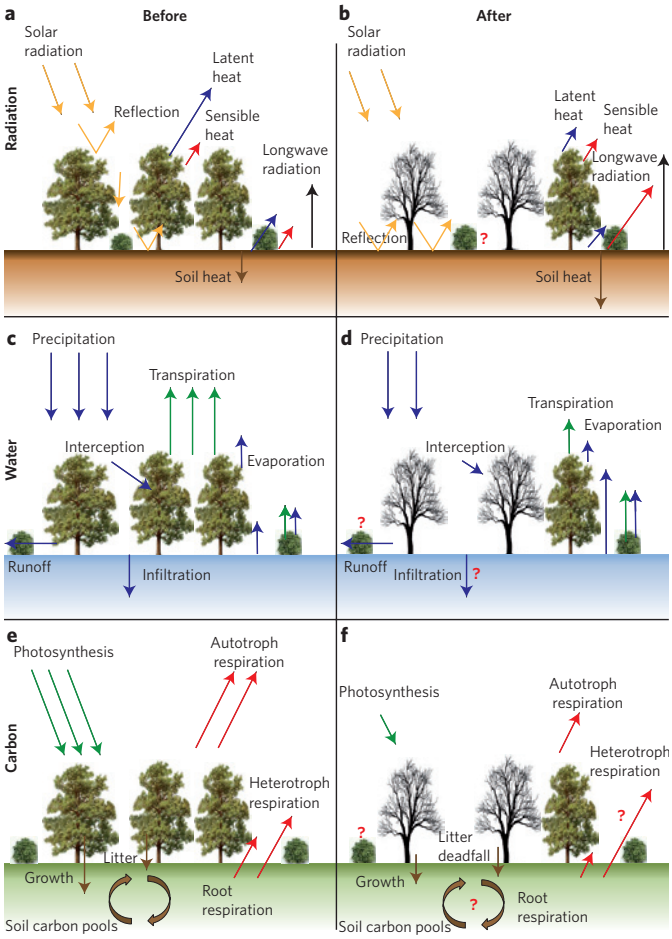

Figure 2 | Fluxes of radiation, water and carbon before and after widespread forest die-off. a,**b**, Radiation; **c**,**d**, water; and **e**,**f**, carbon. Increases or decreases in the number and length of arrows indicate general expected and/or observed increases or decreases in those fluxes following forest die-off, respectively. Question marks highlight key uncertainties in system response (for example, understorey species response) or changes in the fluxes themselves.

damage from tropical forests in Mexico and Puerto Rico may provide relevant perspectives, highlighting that tree mortality resulting from wind damage leads to short-term increases in fine litter and coarse woody debris[57,58] and increased levels of soil nitrogen and phosphorous[57,59], eventually followed by increased immobilization and thus lower soil nitrogen availability and lower primary productivity for many years following a hurricane[59,60].

Furthermore, forest die-off is likely to alter other ecosystem disturbance processes that play a primary role in the structure and function of forests[61], such as fire. In particular, tree death and the accompanying increase of fine litter and coarse woody debris could influence the fuel conditions and fire risk of forests[49,62]. The extent to which tree death increases fire risk is still debated, although it will probably vary among ecosystems. Fire risk owing to forest mortality has been studied only in high-elevation conifer forests after beetle infestation and has suggested that pre-fire disturbance history and stand condition can influence fire severity[63,64]. Such changes would occur within the broader context of direct climate effects on disturbance, such as the recent climate-driven increase in the frequency of large wildfires in western US forests[65]. At present, the effect of severe weather (drought and heat) on fire activity is expected to be more substantial than fuel-loading increases attributed to forest mortality alone[66].

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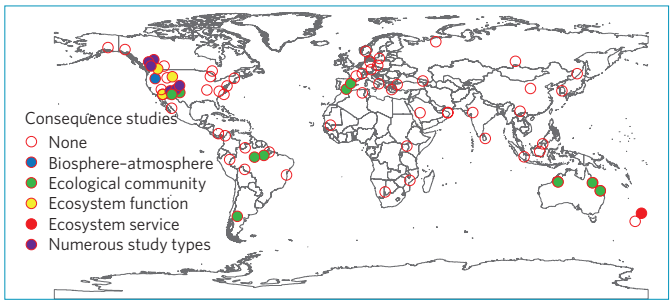

Figure 3 | Global distribution of studies documenting climate-induced widespread forest die-off events and consequences, from the English language scientific literature. Studies documenting climate-induced widespread forest die-off events are represented by red circles, taken from ref. 4. Studies documenting the consequences are shown by different fill colours, explained in the legend.

Ecosystem services

Ecosystem services, or the goods and services provided by ecosystems to society, have been broadly divided into four categories: provisioning (for example, food, timber); regulating (for example, climate control, water quality); supporting (for example, soil formation, nutrient cycling); and cultural services (for example, recreation, aesthetic benefits)[2]. The effects of forest die-off on many ecosystem services, such as pest or air quality control, have been little studied and in many cases (particularly for services derived from forest animals rather than directly from plants) have few reasonable analogues from which to extrapolate. Other services such as water purification and property value are just beginning to be investigated and may be more comparable to other disturbances such as logging and wind throw. However, because forest mortality is typically widespread but not necessarily uniform, analogues should be employed with caution.

Owing to its economic importance to the United States and Canada, timber production has been the best-studied provisioning service altered by forest die-off. Large reductions in both short- and mid-term timber stocks have resulted from the regional scale of recent die-offs. For example, more than 630 million m^3 of merchantable lodgepole pine were killed in British Columbia alone in a recent outbreak of mountain pine beetle[67]. Initially, short-term production losses for some economically valuable timber species can be offset by salvage logging after a mortality event, although salvage operations often reach only a fraction of the affected forests[68] and can be ecologically detrimental[69]. As many mortality events preferentially affect mature trees and leave living saplings and seedlings, mid-term (~20–50 years) timber losses may be somewhat offset by rapid stand regeneration, although overall losses still are likely to be substantial[70]. The long-term potential of wood production is often uncertain because it is largely dependent on the regrowing species composition and the impacts of future climate on growth of the post-mortality forest regeneration[27,71]. There has been little research, however, on the consequences of extensive tree mortality in areas where resource extraction other than timber may be economically important. Theoretically, other provisioning services, such as fruit or nut collection, may become patchier in availability, reducing the sustainability of production for local harvesters[72].

For regulating services, forest mortality can in some cases increase the overall yield of the watershed, although changes to the rate and timing of runoff owing to tree canopy loss can increase flooding risk[46]. In locations that receive snowfall, research from the literature on timber harvest has shown that the reduction of tree canopy cover leads to earlier, faster and more synchronous snow melt[73,74]. As forest-mortality events often surpass logging operations on the spatial scale, similar hydrological responses to such mortality could pose serious difficulties for catchment management. Furthermore, there is some evidence that forest mortality could decrease water quality by increasing nutrient leaching[56,75] and that tree die-off can increase erosion and stream siltation in steep terrain[76]. Disease risk could also be altered by tree die-off. For example, widespread drought-induced mortality of trembling aspen (*Populus tremuloides*) increased the prevalence of Sin Nombre virus in deer mice (*Peromyscus maniculatus*) as a result of altered community structure[77]. Widespread forest die-off such as recent lodgepole pine mortality is expected to lead to an array of public health impacts from the effects of increased runoff, water turbidity and forest fires on respiratory health[78].

Other major effects of forest die-off on regulating services include climate stabilization through carbon sequestration. The stochastic nature and potential for the substantial reduction of carbon sequestration in forests owing to die-off events (see Biosphere–atmosphere interactions) has important implications for carbon markets and policy[79]. Policies and institutions that regulate carbon credits must remain cognizant of the significant uncertainty that forest disturbances such as insect outbreak add when calculating present and future forest-carbon balances[80].

Substantial tree mortality can also decrease many cultural services or non-market values of forests, such as aesthetic values, particularly in protected areas such as national parks[81]. Economic studies quantifying the importance of trees to property values have found significant decreases in property value following both sudden oak death in California[82–84] and woolly adelgid infestation in New England[85,86]. Although these two events are not known to be climate related, they reveal that valuation losses can be as high as 15% of the total value for properties containing dead or dying trees and can spill over to nearby properties and those near affected forests[83,85]. In a county in Colorado, USA, the impacts of lodgepole pine die-off on property values were an estimated decline of US$648, US$43 and US$17 for every tree killed within a 0.1, 0.5 and 1.0 km buffer, respectively[87].

Biosphere–atmosphere interactions

Forest ecosystems play an important role in the climate system and global biogeochemical cycles[1]. Thus, widespread forest mortality can be expected to influence land-surface properties, biosphere–atmosphere exchanges of water and energy, and ecosystem productivity, altering carbon uptake and sequestration of forest ecosystems (Fig. 2)[4,5].

Scientists have long recognized that changes in land cover can substantially influence land-surface properties and their coupling with climate[88]. Forests affect the regional and global climate directly through biophysical attributes such as the land-surface albedo and roughness, and biophysical processes such as latent- and sensible-heat-driven energy exchanges (Fig. 2a,b)[89,90]. Widespread forest die-off is generally expected to increase land-surface albedo, decrease roughness and shift the exchange of heat towards less latent- and more sensible-heat transfer, leading to local temperature changes that vary by latitude[91]. One recent study examined the albedo changes resulting from lodgepole pine mortality and documented large increases in winter albedo owing to exposed snow, leading to a local cooling effect[92]. Changes in land cover can also affect regional circulation patterns over short- and long-term time periods[93,94]. Thus, biophysical changes coupled with decreased forest transpiration following tree die-off could potentially influence regional precipitation patterns as well, although so far no studies have examined this (Fig. 2c,d). These biophysical feedbacks of forest mortality will also depend on the land-surface properties underneath the forest, the response of understorey plant communities and the seasonality and timing of snow cover[94,95]. This contrasts with potential analogues of fire

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and harvest, which typically include more direct disturbance of understorey plant communities.

Forest die-off can also affect the global carbon cycle through changes in ecosystem exchange and the sequestration of carbon (Fig. 2e,f). Loss of canopy is expected to lead to sharp declines in net primary production following mortality, which can persist for decades. In lodgepole pine forests of western North America, the post-mortality recovery time of net primary production has been estimated at between 10 and 21 years, depending on many factors[5,96]. Furthermore, the decomposition of standing and fallen aboveground biomass and belowground roots can lead to substantial carbon emissions from dead and dying forests[5,9]. Relatively few studies have examined the loss of carbon from forests and most have been focused on conifer forests of the western United States and Canada[95]. Modelled carbon emissions from the lodgepole pine die-off in Canada over a 20-year period were roughly equal to those from Canada's transportation sector over five years, although this is based on carbon pools, not measured carbon fluxes. Recovery of biomass to premortality levels has been suggested through simulations to take many decades in this species[97]. Similarly, the estimated carbon loss from a die-off of aspen forests in the same region were equivalent to around 7% of Canada's annual anthropogenic carbon emissions[98].

Two studies have directly measured net ecosystem exchange following widespread forest die-off using eddy covariance methods over numerous years. These studies found that lodgepole pine forests constituted substantial carbon sources for three to seven years following die-off, although net ecosystem exchange increased steadily owing to increases in gross ecosystem photosynthesis from regrowth and the remaining trees[99,100]. Another study[101] examined net ecosystem exchange using eddy covariance methods throughout North American forest types that experienced natural and anthropogenic disturbances (fire, insects, hurricanes and silvicultural treatments) and demonstrated that the net ecosystem exchange of most forests recovered within 20 years, with the exception of a post-wildfire ponderosa pine (*Pinus ponderosa*) forest. The response of understorey forest plants and successional trajectory following die-off will influence longer-term carbon cycling in affected ecosystems. Yet these responses are largely unknown and constitute a significant gap in our understanding of the climate feedbacks of forest die-off.

A long history of research on land-cover change and deforestation suggests that the net effect of biophysical and biogeochemical feedbacks of forest die-off on the regional and global climate will vary greatly depending on forest type, latitude, land-surface properties, snow cover and ecosystem response[90]. In general, decreasing tree cover is expected to lead to net cooling in boreal systems and semi-arid systems with high radiation loads owing to biophysical changes, net warming in tropical systems owing to loss of carbon sequestration and little net effect in most temperate forests[90,91]. Furthermore, the relative importance of various forcings will be time-scale dependent. For instance, many components of forest die-off, including biophysical properties and carbon emissions, could be transient and reversible over a period of decades as a forest regenerates. This highlights that the ultimate climate effects of forest die-off are highly sensitive to: (1) severity of mortality; (2) post-die-off forest regrowth and regeneration; (3) species composition and structure of the regenerated forest; (4) frequency of the climate-related disturbance (for example, drought or pathogens); and (5) future resistance to disturbances.

Summary and future research needs

Although recent advances have been made in understanding the consequences of severe forest die-off, many critical research gaps remain. We posit that placing drought- and heat-triggered forest die-off in the broader frameworks of ecological succession and disturbance can facilitate and guide future research. At present we lack a clear understanding of how mortality will impact the composition of most forests. Research is needed to examine whether mortality resets the successional clock, shifts the entire successional trajectory, accelerates succession, or even triggers a change in ecosystem type. These different pathways have strong implications for alterations in biodiversity, ecosystem structure, ecosystem functions, ecosystem services and land–atmosphere interactions. Furthermore, the extent to which the impacts of forest die-off will parallel, differ from and interact with other disturbances such as high-severity fire or intensive harvesting is uncertain but could be important for management and policy decisions. Although many disturbances can cause long-term type conversions in ecosystems with many steady states, climate-induced forest mortality may be unique in that it could represent a permanent range contraction for tree species whose climate niche has moved. We are in only the early stages of studying drought- and heat-triggered die-off as a forest disturbance, though it is expected to occur more frequently in coming decades[4,8]. Our literature search identified 41 studies around the world that focused explicitly on the consequences of drought- and heat-induced forest mortality (Fig. 3), in contrast to more than 150 studies in a recent review documenting the global trend of forest mortality[4].

Most research concerning the consequences of drought-induced widespread forest die-off has been conducted in western North America, particularly on *Pinus* spp. and other conifer species, although our literature review covered only English language journals. Thus, greater geographic, ecosystem and taxonomic breadth will provide important avenues for future research. Cross-system comparisons of consequences have been conducted in only a few cases but have the potential to illuminate broader patterns of how impacts may differ across forest types[9,92]. Although large-scale die-off events are considered to be undesirable for numerous reasons, they provide a unique opportunity to test ecological theories and to promote a greater understanding of many ecosystems.

The varied nature of the consequences of forest mortality discussed here necessitates multidisciplinary and interdisciplinary engagement, including ecologists, biogeochemists, hydrologists, economists, social scientists and climate scientists. More studies are needed that examine changes in a wide array of ecosystem functions across a variety of ecosystems. This includes how forest die-off affects nutrient cycling, decomposition, hydrological cycles and habitat on other trophic levels. Research on changes in ecosystem services has only begun to illuminate how services change in dying forests. Many services such as non-timber provision, erosion control, disease control, tourism/aesthetic impacts and land-valuation impacts remain largely unstudied.

The effects of forest mortality on ecosystem–climate feedbacks have been better studied, but key knowledge gaps persist. The effects of forest die-off on regional albedo, surface roughness, water and energy exchange, and their influence on regional circulation and precipitation are important future research directions. Studies are also needed to understand the role of understorey plants, soils and decomposition on carbon budgets following mortality. The timescales on and degree to which dying forests will regrow leave much uncertainty over the timescales on which climate forcings and feedbacks of forest mortality will operate. Better regional and global monitoring of forest health and composition with plot and remote sensing methods would provide much needed data to address some of these questions, though at present these methods are limited by available field data for validation and time-series data to detect trends[4,9,95].

Human societies rely on forest ecosystems for numerous goods and services. Yet recent decades have revealed how forests may be increasingly vulnerable to variations in drought and temperature

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with climate change. As well as understanding the patterns and mechanisms by which trees die as a result of changes in climate, we must also understand the consequences of these events. A better understanding of the consequences of forest die-off owing to climate change can inform forest management, business decisions, mitigation and adaptation policy.

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