Increasing atmospheric humidity and CO₂ concentration alleviate forest mortality risk

Yanlan Liu, Anthony J. Parolari, Mukesh Kumar, Cheng-Wei Huang, Gabriel G. Katul, and Amilcare Porporato

Climate-induced forest mortality is being increasingly observed throughout the globe. Alarming, it is expected to exacerbate under climate change due to shifting precipitation patterns and rising air temperature. However, the impact of concomitant changes in atmospheric humidity and CO₂ concentration through their influence on stomatal kinetics remains a subject of debate and inquiry. By using a dynamic soil–plant–atmosphere model, mortality risks associated with hydraulic failure and stomatal closure for 13 temperate and tropical forest biomes across the globe are analyzed. The mortality risk is evaluated in response to both individual and combined changes in precipitation amounts and their seasonal distribution, mean air temperature, specific humidity, and atmospheric CO₂ concentration. Model results show that the risk is predicted to significantly increase due to changes in precipitation and air temperature for the period 2050–2069. However, this increase may largely get alleviated by concurrent increases in atmospheric specific humidity and CO₂ concentration. The increase in mortality risk is expected to be higher for needle-leaf forests than for broadleaf forests, as a result of disparity in hydraulic traits. These findings will facilitate decisions about intervention and management of different forest types under changing climate.

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Forest mortality can lead to irreversible change in vegetation cover, thereby affecting many processes pertinent to water, carbon, and nutrient budgets (1). Multiple studies (2–10) have noted close association between forest mortality and water and heat stress, owing to shifting precipitation patterns and rising air temperature. However, the influence of concurrent changes in specific humidity (SH) and CO₂ concentration, which affect plant response to stress by altering stomatal kinetics (11), have not received similar attention. Although elevated CO₂ concentration is expected to promote future forest productivity (12), the extent to which it affects forest mortality in the context of water and heat stress remains a subject of inquiry. Short-term records (3, 4) and long-term manipulative field studies in forests such as the Free Air CO₂ Enrichment experiments (13–15) have tried to fill the knowledge gap; however, they do not cover the entire manifold of projected climate conditions. The goals of this study are to evaluate the individual and combined influence of projected changes in precipitation, temperature, SH, and CO₂ concentration on forest mortality risk and to investigate whether the response of mortality risk differs among plant functional types (PFTs).

Tree mortality may occur through several mechanisms, including hydraulic failure, carbon starvation, phloem transport limitation, and biotic attack (16, 17). Hydraulic failure is characterized as the malfunction of xylem water transport associated with cavitation, which is induced by low xylem water potential under limited soil water availability. Carbon starvation occurs when carbohydrate supply and storage cannot meet demand (17), which could result from low photosynthesis due to stomatal closure in response to low plant water potential and high atmospheric vapor pressure deficit (VPD). Reduced photosynthesis and plant water potential also pose limitations for phloem to maintain turgor pressure and may further impair phloem transport (18). Intense and prolonged stresses could weaken the defenses of forests to biotic attack (5) and may alter plant adaptation, seed production, and germination (2). Despite these mechanisms being far from thoroughly understood (17, 18), they primarily result from low plant water potential and restricted photosynthesis.

To quantify the risk of mortality induced by low plant water potential, past studies (19, 20) used the safety margin (i.e., the difference between the minimum observed xylem water potential and the xylem water potential at 50% loss of conductivity (ψʾ)). Plants with narrower or more negative safety margins are considered to be more susceptible to hydraulic failure. The safety margin provides a static assessment of plant susceptibility to hydraulic failure, although its representativeness may be undermined by limited field observations. It has also been suggested that, instead of the minimum water potential plants reach, the duration plants operate under high percentage loss of conductivity could more likely distinguish mortality (21, 22). Here, a duration-based hydraulic failure risk (HFR) is introduced, which quantifies the fraction of days when the daily minimum xylem water potential (ψʾ,min) falls below ψʾ,50. Because stomatal closure restricts photosynthesis (6, 17, 23), a stomatal closure risk (SCR) can also be formulated as the fraction of days on which stomatal closure in response to low plant water potential and high atmospheric vapor pressure deficit (VPD).

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Significance

The significance of forest mortality on ecosystem services, and water, carbon, and nutrient cycling is indubitable. While there is a general agreement that climate change-induced heat and drought stress is expected to intensify forest mortality, the concurrent influence of changes in atmospheric humidity and CO₂ concentration remains unclear. Here, the response of mortality risk to projected climate change is evaluated in 13 biomes across the globe. Our results show that increasing specific humidity and CO₂ concentration partially offset the intensification of risk by changing precipitation and air temperature. The risk response is also mediated by plant hydraulic traits. The study provides a mechanistic foundation for estimating future responses of forest mortality risk, which can facilitate ecosystem management.
are completely closed (SI Appendix, section S1). The aggregated mortality risk is then defined as the fraction of days with occurrence of either hydraulic failure or stomatal closure, two physiological states contributing to dieback and eventual mortality. Alternative quantifications of risk that account for stress duration and severity are also considered to test the robustness of the analysis here (SI Appendix, section S3).

The mortality risk is evaluated by using a soil–plant–atmosphere continuum (SPAC) model, which computes hourly dynamics of xylem water potential and stomatal conductance (Materials and Methods and SI Appendix, section S1). By comparing against observed mortality at four sites, the modeled risk is shown to capture the temporal variation of mortality in response to climate stressors (SI Appendix, section S3). The risks under historical and future climate scenarios are then evaluated for 13 temperate and tropical forest biomes across the globe (Fig. 1). The selected biomes cover a variety of climates and PFTs, including evergreen needleleaf forest (ENF), deciduous broadleaf forest (DBF), and evergreen broadleaf forest (EBF). The response of mortality risk to changes in the following climate characteristics is analyzed: mean annual precipitation (MAP), precipitation seasonality (PS), mean annual air temperature (T), mean annual atmospheric SH, and atmospheric CO$_2$ concentration. PS is quantified as the fraction of MAP that falls within the growing season. Changes in these climate conditions are obtained from the projection of Coupled Model Intercomparison Project Phase 5 (CMIP5) (Table S2) from 1986–2005 to 2050–2069.

**Influence of Individual Changes in Climate Variables**

Mortality risk is found to increase with reduced annual precipitation and a lower fraction of precipitation in the growing season. Reduced precipitation decreases plant water potential via low soil moisture, hence increasing HFR (Fig. 2D, horizontal axis). Meanwhile, low plant water potential also restricts stomatal conductance, hence increasing SCR (Fig. 2A, horizontal axis). Plants experience higher risk in the growing season than in the nongrowing season, due to low plant water potential and atmospheric aridity imposed by a high VPD. Given the same annual precipitation, more growing season precipitation (higher PS) generally decreases the risk (Fig. 2A and D, vertical axis).

Reduced precipitation during the nongrowing season typically does not increase the risk, as the stressed conditions mostly occur in the growing season.

Sensitivity of mortality risk to precipitation amount and seasonality varies across soil, plant, and climate conditions, as expected. For ENF in the western United States (Fig. 2A and biome 1 in Fig. 1), the risk is primarily controlled by annual precipitation amount when $<400$ mm. For wetter climates (MAP $>800$ mm) with low growing season precipitation (PS < 0.2), seasonality becomes the dominant factor. Under the historical climate in this region, both precipitation amount and seasonality play significant roles in mortality risk. Although large uncertainties exist in the projected annual precipitation, CMIP5 models mostly predict lower PS in this region, which is likely to increase mortality risk. For DBF in the southeastern United States (Fig. 2D and biome 3 in Fig. 1), both precipitation amount and seasonality affect the risk over a wide range of climatic conditions. Although the risk generally decreases with higher PS when PS $<0.7$, the trend reverses for PS $>0.8$. As CMIP5 projections point to an increase in precipitation with little change in seasonality, mortality risk of this biome is expected to decrease under future precipitation patterns.

Modeled mortality risk increases with warming air temperature, but decreases with rising SH (Fig. 2B and E) and CO$_2$ concentration (Fig. 2C and F). Elevated temperature promotes water loss through higher VPD. Although stomata close in response to high VPD to prevent excessive water loss, the same action increases the risk of full stomatal closure. Increasing SH, on the other hand, offsets the increase of VPD by air temperature, hence attenuating intensified risks caused by warming. Under higher atmospheric CO$_2$ concentration, plants can operate at lower stomatal conductance to meet their biochemical demand for CO$_2$. This so-called “carbon fertilization effect” allows plants to enhance water-use efficiency, hence reducing the risks of both hydraulic failure and stomatal closure simultaneously. All three climate variables exhibit significant influence on mortality risk of ENF in the western United States and DBF in the southeastern United States. For the projected changes in temperature and SH (Fig. 2B and E), the intensifying influence of rising air temperature overwhelms the opposing influence of rising SH, leading to higher VPD, and thus

![Fig. 1. Distribution of PFT and locations of the 13 investigated biomes. Biomes are the areas within the selected rectangular regions that are covered by a given PFT. PFTs shown in the map include evergreen broadleaf forest (EBF), deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF), and deciduous needleleaf forest (DNF).](image-url)
Fig. 2. Responses of mortality risk to individual changes in MAP, PS, T, SH, and CO₂ concentration for ENF in the western United States (A–C) and DBF in the southeastern United States (D–F). PS is quantified as the fraction of MAP that falls within the growing season. Changes in MAP and PS are incorporated in daily precipitation time series through their impact on the statistical distribution of stochastic precipitation; changes in T, SH, and CO₂ are incorporated uniformly throughout the year, keeping the intraannual patterns unchanged. Numbers on the contours denote risk magnitude (%). Predicted ranges by multimodels under the four representative concentration pathway (RCP) scenarios are illustrated by rectangles. Blue and green contours represent risks due to hydraulic failure and stomatal closure, respectively.

Influence of Combined Changes in Climate Variables

Based on the CMIP5 projections of four RCP scenarios in all 13 biomes (SI Appendix, Fig. S6), the response of mortality risk to changes in three combinations of climate conditions are examined (Fig. 3): (i) P+T; (ii) P+T+SH; and (iii) P+T+SH+CO₂. Here, changes in P include combined changes in MAP and PS. For the 13 investigated biomes, on average, shifting precipitation patterns and rising temperature projected by RCP4.5 are found to intensify the risk by 158.8% for the period 2050–2069 relative to the historical risk. This increase in risk is consistent with previous studies highlighting the exacerbating effects of higher temperature (1, 3–7). However, by incorporating increases in SH, the risk decreases by 46.6%. More remarkably, the risk drops an additional 91.2% under the added influence of elevated CO₂ concentration. In aggregate, changes in all four climate conditions increase the risk by 21.0% on average, which is much lower than the increase of 158.8% when only the changes in precipitation and air temperature are considered. Under high emission scenarios (RCP6.0 and RCP8.5), elevated humidity and CO₂ concentration might even overwhelm the effects of higher temperature, possibly resulting in a lower risk than the historical level (Fig. 3). These alleviating effects are robust across alternative risk measures (SI Appendix, Table S6 and Fig. S14). The alleviating effect of increasing atmospheric CO₂ concentration is in line with a reported decrease in stomatal conductance and increase in water use efficiency across various climate regions and species (2, 25–29).

On average, the combined changes of P+T+SH+CO₂ in RCP4.5 are found to increase the mortality risks by 101.1%, −18.3%, and 19.6% for ENF, DBF, and EBF biomes respectively (Fig. 4). The significantly higher increase for ENF compared with the other two PFTs results from their distinct risk sources (Fig. 4). SCR, the primary risk source for ENF, shows notably higher sensitivity to air temperature rise than HFR. Specifically, for a 1 °C increase in air temperature from historical climates, HFR and SCR are estimated to increase by 23.5% and 125.1%. Remarkably, the increase in SCR is close to the

higher risk. Remarkably, elevated CO₂ concentrations offset the intensified risk imposed by elevated temperature (Fig. 2 C and F).

Despite the similar patterns of response to climate change, sources of risk in the two biomes (Fig. 2) are markedly different. Under both historical and projected climates, the risk for the ENF in the western United States mostly originates from stomatal closure. The risk for the DBF in the southeastern United States mostly originates from hydraulic failure. However, under extremely high air temperature (annual mean > 23 °C) in the DBF, high VPD induces full stomatal closure, resulting in a switch from HFR to SCR (Fig. 2 E and F). The different sources of risk for these two biomes can be attributed to their response strategies under stress, which are controlled by their hydraulic traits. ENF consists of conifers, which mostly operate with a wide safety margin ($\psi_{x, \text{min}} - \psi_{50}$) (19) and exhibit an isohydric strategy under stress (16) (i.e., restricting transpiration by reducing stomatal conductance while maintaining high water potential to prevent runaway cavitation; SI Appendix, Fig. S3). Owing to this conservative water use strategy and the wide safety margin, isohydric conifers are more susceptible to SCR than HFR. In contrast, DBF consists of angiosperms, which operate with a narrower safety margin (19) and largely use an anisohydric strategy under stress (16) (i.e., stomata remain open to sustain photosynthesis at the expense of decreased water potential; SI Appendix, Fig. S3). With this less conservative water use strategy and a narrow safety margin, anisohydric DBFs are more susceptible to HFR than SCR. These contrasting stress responses have been widely reported (16, 19, 24). Previous studies have also suggested hydraulic failure as the major mechanism in an aspen (angiosperm) mortality event (8) and near-zero stomatal conductance as the main contributor to conifer mortality events (16, 23). It is to be noted that large variations in hydraulic traits exist within each PFT, and the results presented here are based on the average traits of species falling within a PFT and climate type in a given biome.
previously reported 116.3% °C⁻¹ increase in die-off events of Pinus edulis (4), a conifer species likely threatened by SCR. From a mechanistic perspective, elevated temperature increases VPD and reduces stomatal conductance. This restricts carbon assimilation but promotes water loss, which results in a higher probability of full stomatal closure (i.e., higher SCR). The increase in HFR is smaller, as the reduction in stomatal conductance partly alleviates the increase in water loss due to increased VPD. Under projected changes of precipitation and VPD in RCP4.5, HFR increases by 135.5% on average, while SCR increases by 305.8%. When CO₂ is also considered, the aggregate changes are −8.6% and 83.7% for HFR and SCR, respectively. These findings imply a larger increase in mortality risk of ENFs, more specifically of isohydric species, than other PFTs under changes in the considered climate conditions.

Discussion and Implications

The study evaluates how projected climate change will affect mortality risks and how the risks may be mediated by different PFTs across the globe. In this regard, the study introduces a measure of mortality risk that accounts for the duration that plants operate under high percentage loss of conductivity or stomatal closure. Although large uncertainty exists in the exact physiological mechanisms that cause mortality (17, 18), the proposed mortality risk measure captures two of the fundamental causes (i.e., low water potential and severely restricted carbon assimilation) which contribute to the downstream mortality mechanisms. Notably, the quantification of mortality is made possible by synergistic coupling of multiple prior submodels connecting plant physiological status to hydrological and meteorological conditions. This coupling allows the SPAC model to resolve hourly dynamics of xylem water potential and stomatal conductance, the variables required to evaluate mortality risk (SI Appendix, sections S1 and S5). For example, by accounting for the feedback between evapotranspiration and atmospheric boundary layer (ABL) development, the SPAC model is able to simulate a physically consistent hourly dynamic of air temperature and SH during droughts. During drought, when evapotranspiration is restricted by low soil moisture, the model partitions a larger fraction of incoming energy into sensible heat, thus enhancing the ABL and raising the temperature during daytime. This evapotranspiration–ABL coupling allows SPAC to consider the cooccurrence of extreme drought and heat stress, which has been pointed out as the main environmental trigger of tree mortality (3–5, 7). The SPAC model also uses an optimization-based stomatal conductance representation that accounts for the effect of plant hydraulic limitation (SI Appendix, section S1). The representation is an advantage over several widely used dynamic global vegetation models, where...
the stomatal regulation is disconnected or empirically connected with soil water stress (6, 21). Many of these semiempirical models are derived from observations under ambient CO₂ concentration, and their parameter values are subject to change in an elevated CO₂ environment (11), thus undermining their efficacy under future climate. In contrast, the optimization-based stomatal regulation model used here has been demonstrated to predict stomatal response to stress under both historical and elevated CO₂ concentration (30).

Although the modeled risk shows strong correspondence with observed mortality (SI Appendix, section S3), the estimated risk should be interpreted with care. Given the uncertainties inherent in model structure and parameters, and the complexity of the forest ecosystem, it is unrealistic to accurately assess the exact magnitude of mortality risk. Large variations in plant hydraulic traits, tree height, diameter at breast height, and stand density (31, 32) may impact the actual mortality risk. Sensitivity of mortality risk to aforementioned factors and to uncertainties in model structure are examined (SI Appendix, section S4). Results indicate that, despite their influence on the magnitude of mortality risk, the alleviating effect of increasing SH and CO₂ concentration is still found to be robust. Notably, actual mortality risk may also be altered by forest fire frequency and insect outbreak, rooting profile, seed production, community-level competition, local acclimation to drought, and adaption to long-term climate change (33–36), factors whose characterization is still fraught with uncertainties (37). Their impacts in relation to the direct influence of climate conditions discussed here deserve further investigation. However, independent of these indirect influences, results reported here demonstrate a ubiquitous and robust alleviating effect of elevated atmospheric humidity and CO₂ concentration, which is comparable in magnitude to the intensifying effect of changes in precipitation patterns and air temperature. The combined influence of changes in these climate variables on mortality risk is also strongly mediated by plant hydraulic traits. These results highlight that ignoring the influence of elevated atmospheric humidity and CO₂ concentration may lead to overestimation of future forest mortality risk.

Materials and Methods

**SPAC Model.** The SPAC model consists of three process components: a soil–water balance; a plant water transport that is based on cohesion–tension theory and associated hydraulic properties; and an ABL development model that permits evapotranspiration to alter the height, temperature, and SH of the boundary layer (SI Appendix, section S1 and Fig. S1). Soil is characterized as a two-layer bucket, where the soil moisture is controlled by precipitation, interception, evapotranspiration, soil evaporation, and plant root extraction. Water transport within plants is modeled as a resistance system with no capacitance. Water vapor and CO₂ exchange at the leaf level are modeled by combining Fickian diffusion of gases and the Farquhar photosynthesis model (38, 39), where the stomatal kinetics are determined by optimizing carbon gain while minimizing water losses (11). The stomatal conductance is affected by both atmospheric conditions and plant water status. The water flux through the soil–plant–atmosphere system is solved given soil and atmospheric conditions. Subdaily temperature and SH are obtained from the ABL development model. The energy and mass components in ABL development are affected by feedback of total water flux from the ground surface (40), including interception, soil evaporation, and plant transpiration. The coupled SPAC model simulates ecohydrologic states at an hourly interval.

**Soil and Vegetation Properties.** Based on the global land cover type from the moderate imaging spectroradiometer (MODIS; MCD12C1) (41), 13 forest biomes were selected across the globe. The biomes cover three PFTs and a snow-dominated climate (43) were avoided, as the influence of ground-water and snow is not considered in the model. The SPAC model in each biome was parameterized with local soil and representative plant properties. Soil texture compositions were obtained from the Harmonized World Soils Database (44). Soil hydraulic properties were calculated based on the generalized statistical relations (45). The annual cycle of the Leaf Area Index (LAI) was extracted from the level-4 MODIS global LAI and Fraction of Photosynthetically Active Radiation product (MCD15A2) (46). Plant hydraulic traits were obtained from a global database containing hydraulic traits of 866 species (47). Photosynthetic parameters were derived from a cross-species study (48). Stomatal optimization parameters were obtained based on a metaanalysis study across PFTs and climates reported in a previous study (49). These plant properties were obtained at a biome level by averaging the properties of trees belonging to the same PFT and climate type (47) as found in the given biome.

**Historical and Projected Climates.** The SPAC model in each biome is forced by local daily climate, including stochastic precipitation, net shortwave radiation, and initial and boundary conditions of potential temperature and SH of ABL. At the beginning of each day, the ABL is reset with the corresponding initial and boundary conditions. The stochastic precipitation is represented as a marked Poisson process characterized by frequency and mean precipitation amount, which are site-specific statistics (50). Daily historical climates are calculated based on the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) reanalysis data (51) from 1986 to 2005. Projected climate changes are obtained from multimodel outputs of CMIP5 experiments under four RCP scenarios (Table S2). For each model under each RCP scenario, changes in climate variables are quantified as the difference between the averages for 1986–2005 and 2050–2069. Future precipitation statistics and other climate forcings for the model are generated by incorporating these changes into the historical climates from NCEP/NCAR (SI Appendix, section S2) to eliminate the influence of biases in climate model outputs (52). Historical and future atmospheric CO₂ concentrations under the four RCP scenarios are provided in ref. 53.

**Experimental Design and Statistics.** The mortality risk under a given climate was quantified based on plant dynamics by running the SPAC model at hourly resolution for 30 annual ensembles after a 5-y warm-up period. Influence of changes in each individual climate variable was analyzed by keeping the others the same, while only changing the target climate variable. Influence of combined changes in climate variables as projected by multimodels were grouped together to evaluate the overall response of mortality risk under each RCP scenario. Each reported change in risk is the average of changes of all of the biomes, unless stated otherwise. Change in each biome was calculated as the difference between the historical risk and the future risk (i.e., the average risk based on multimodel projections), in proportion to the historical risk. Biomes with historical risks <0.01% were excluded from the statistics.

**Note.** Details on model formulation, data processing, model validation, sensitivity analyses, and alternative quantifications of risks are provided in SI Appendix.

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Supporting Information Appendix for “Increasing atmospheric humidity and CO$_2$ concentration alleviate forest mortality risk”

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Section S1: Soil plant atmospheric continuum (SPAC) model formulation

The SPAC model consists of three components, i.e., soil water balance, plant water transport and atmospheric boundary layer (ABL) development (Figure S1). Model formulation of each component is as below.

Soil water balance. Assuming negligible lateral flux due to the effects of topography and contribution from groundwater, the vertically averaged relative soil moisture in the first layer \((s_1)\) is recharged by throughfall \((P_T = P - I)\), and depleted by leakage \((L_1)\) to the second layer, surface runoff \((Q)\), soil evaporation \((V)\) and plant root extraction \((E_1)\). The second layer soil moisture \((s_2)\) is recharged by \(L_1\) and depleted through leakage to deeper soil \((L_2)\) and root extraction \((E_2)\). Here \(P\) is precipitation and \(I\) is interception loss. The soil water balance at an hourly scale for the two layers is expressed as

\[
\begin{align*}
  n_1 Z_{r1} \frac{ds_1}{dt} & = P_T - L_1 - Q - V - E_1 \\
  n_2 Z_{r2} \frac{ds_2}{dt} & = L_1 - L_2 - E_2
\end{align*}
\]

where \(n_j\) and \(Z_{rj}\) \((j = 1, 2)\) denote soil porosity and root zone depth of the two layers, respectively. Daily precipitation is modeled as a marked Poisson process \([1]\), with a frequency parameter of \(\lambda_P\) and rainfall depth drawn from an exponential distribution with a mean of \(\alpha_P\). Daily precipitation is randomly assigned within an hour. Interception is quantified as

\[I = \max(P - I_s, 0),\]

where \(I_s = 10^{-4}\text{LAI (m)}\) \([2]\) is the interception storage and LAI is leaf area index. According to Darcy’s law for unsaturated flow, the water flux between the two soil layers is

\[
L_1 = K \frac{\psi_{s1} - \psi_{s2}}{\rho_w g \Delta l}
\]

where \(\rho_w\) is water density; \(g\) is gravitational acceleration; the soil vertical unsaturated hydraulic conductivity \((K)\) and flow path \((\Delta l)\) are taken as the harmonic mean of the two layers, i.e.,

\[
K = \frac{(Z_{r1} + Z_{r2})}{(Z_{r1}/K_1 + Z_{r2}/K_2)}, \quad \Delta l = (Z_{r1} + Z_{r2})/2,
\]

where \(K_1\) and \(K_2\) are the unsaturated hydraulic conductivities of the two layers.

Leakage from the second layer occurs only when \(s_2 > s_{fc,2}\) with a rate of \(K_2\) \([1]\), where \(s_{fc,2}\) is the field capacity of the second layer corresponding to \(\psi_{s2} = -0.03\) MPa \([3]\). \(Q\) is generated when the first layer is fully saturated. Soil evaporation is controlled by the potential evaporation rate \((V_p)\) and the limitation induced by top soil moisture \((s_1)\). \(V_p\) is calculated using the adapted Penman-Monteith equation \([4, 5]\), i.e.,

\[
V_p = \frac{\Delta R_n^b + \rho_a c_p (e_s - e_a) / r_a}{\rho_w \lambda_w [\Delta + \gamma (1 + r_s / r_a)]}
\]
where $\Delta$ is the saturation vapor pressure function with respect to air temperature at 2 m height $T$ ($^\circ$C); $R_n^b$ is the below-canopy shortwave net radiation, which depends on shortwave net radiation ($R_n$) and an exponential decay function given by $R_n^b = R_n \exp(-b_0\text{LAI})$ [6]; $\rho_a$ is air density; $c_p$ is the constant-pressure specific heat capacity of air; $e_s$ and $e_a$ are saturated and actual vapor pressure; $\lambda_w$ is the latent heat of vaporization; $\gamma$ is the psychrometric constant; $r_a = 50 \text{ s m}^{-1}$ and $r_s = \exp(8.206 - 4.255s_{fc,1}) \text{ s m}^{-1}$ [7] are the aerodynamic and soil resistance to water vapor transport, respectively. The actual soil evaporation $V$ is calculated using the following piecewise linear function:

$$V = \begin{cases} V_p & \text{if } 1 \geq s_1 > s_{fc,1} \\ (s_1 - s_{h,1})/(s_{fc,1} - s_{h,1}) \times V_p & \text{if } s_{fc,1} \geq s_1 > s_{h,1} \\ 0 & \text{if } s_{h,1} \geq s_1 > 0 \end{cases}$$  \hspace{1cm} (5)$$

where $s_{h,1}$ is the hygroscopic point of the top layer soil, i.e., the soil moisture corresponding to $\psi_s$ of $-3 \text{ MPa}$ [3].

**Plant water transport.** Soil water is extracted by roots in both layers, i.e.,

$$E_j = g_{sr,j}(\psi_{s,j} - \psi_r)$$  \hspace{1cm} (6)$$

where $\psi_r$ is the root water potential; the soil-root conductance ($g_{sr}$) is computed using a cylindrical root model [8]:

$$g_{sr,j} = \frac{K_j \sqrt{\text{RAI}_j}}{Z_{rj} \pi \rho_w g}$$  \hspace{1cm} (7)$$

in which $\text{RAI}_j$ is root area index in each layer. Assuming negligible plant water storage, according to continuity, the total transpiration ($E$) is

$$E = E_1 + E_2$$  \hspace{1cm} (8)$$

$$E = 2g_p \left[ \psi_r - (\psi_x + \frac{1}{2} \rho_w g H_c) \right] = g_p [\psi_r - (\psi_l + \rho_w g H_c)]$$  \hspace{1cm} (9)$$

where $\psi_x$ and $\psi_l$ are xylem (located at half the canopy height ($H_c$)) and leaf water potential respectively; the plant conductance $g_p$ depends on the most negative water potential in plant, i.e., $\psi_l$ [9],

$$g_p = g_{p,\text{max}} \left[ 1 + (\psi_l/\psi_{50})^a \right]^{-1}$$  \hspace{1cm} (10)$$

where $g_{p,\text{max}}$ is the maximum plant conductance; $\psi_{50}$ is the xylem pressure at 50% loss of conductivity; $a$ is the shape parameter of plant vulnerability curve.
CO₂ and water vapor transfer between leaves and atmosphere can be described by Fickian diffusion through the stomata:

\[
f_c = g_s(c_i - c_a) \quad (11)
\]

\[
f_e = a_0 g_s(e_i - e_a)/P_0 \approx a g_s D \quad (12)
\]

where \( f_c \) and \( f_e \) are CO₂ and water vapor flux; \( g_s \) is the stomatal conductance to CO₂; \( a_0 = 1.6 \) is the relative diffusivity of water vapor with respect to CO₂; \( c_i \) and \( c_a \) are intercellular and ambient CO₂ concentration; \( e_i \) is intercellular water vapor pressure; \( D \) is the vapor pressure deficit normalized by atmospheric pressure \( P_0 \), i.e. \( D = (e_s - e_a)/P_0 \). Here, for the sake of simplicity, saturated water vapor pressure at the leaf surface is approximated as \( e_s \), without considering the influence of leaf size and wind speed on leaf temperature.

According to the Farquhar photosynthesis model [10], the assimilation rate of CO₂ is described as a function of \( c_i \) (when ignoring the mesophyll conductance), \( R_n \) and \( T \). Accounting for the limitation by RuBP (\( J_E \)), Rubisco (\( J_C \)) and sucrose synthesis (\( J_S \)), the carbon assimilation rate is computed as

\[
f_c = A(c_i, R_n, T) = \phi(J_E, J_C, J_S) - R_d \quad (13)
\]

Representations of gross assimilation \( \phi(J_E, J_C, J_S) \) and the respiration from the leaf \( (R_d) \) come from the model by [11]. Based on the stomatal optimization theory [12], the net carbon gain for the leaf is defined as

\[
f(g_s) = f_c - \lambda f_e \quad (14)
\]

The stomata is assumed to operate under a trade-off between maximizing \( f_c \) and minimizing \( f_e \) in order to achieve the maximum net carbon gain with the optimal \( g_s \) subject to \( df(g_s)/dg_s = 0, f(g_s) \geq 0 \). \( \lambda \) is the marginal water use efficiency (mWUE), i.e., \( \lambda = df_c/df_e \). To account for the responses of stomata to water stress, \( \lambda \) is quantified as [13]

\[
\lambda = \lambda_{WW} \frac{c_a}{c^*_a} \exp(\beta_0 \bar{\psi}_l) \quad (15)
\]

where \( \lambda_{WW} \) is the mWUE under well-watered condition at \( c_a = c^*_a \); \( c^*_a = 400 \) ppm is the reference ambient CO₂ concentration; \( \beta_0 \) is the slope parameter; \( \bar{\psi}_l \) is the average leaf water potential in the previous day. Increase of \( \lambda \) with \( c_a \) was validated in previous studies [13, 14].

The stomatal conductance \( (g_s) \) can be solved by combining Equations (11) – (15). The water flux at a leaf scale \( (f_e) \) can then be obtained based on Equation (12). By upscaling the water flux to a canopy scale based on continuity, i.e., \( E = f_e \text{LAI} \), and combining with Equations (6), (8), (9), the plant hydraulic system is closed.
**ABL development.** The hourly dynamics of the soil-plant system above is coupled with the development of the ABL to obtain diurnal mean air temperature and humidity that are consistent with land-atmosphere heat and mass exchange [15]. The ABL is represented as a well-mixed slab of air with a height $h$ and constant potential temperature $\theta$ and specific humidity $q$. At the ground surface, neglecting the ground heat flux, available solar energy is partitioned into latent heat and sensible heat ($H$),

$$R_n = \lambda_w \rho_w ET + H$$

(16)

where $ET = E + V + I$ is the total water flux from the soil-plant system. Within ABL, temperature and humidity are governed by energy and water balance [16]. According to the first law of thermodynamics and mass conservation, the energy and water balance are

$$\rho_a c_p \frac{d\theta}{dt} = H + \rho_a c_p (\theta_f - \theta) \frac{dh}{dt}$$

(17)

$$\rho_a h \frac{dq}{dt} = \rho_a ET + \rho_a (q_f - q) \frac{dh}{dt}$$

(18)

where $\theta_f$ and $q_f$ are the potential temperature and specific humidity of the free atmosphere at height $h$ respectively. In the free atmosphere, potential temperature and specific humidity are assumed to vary linearly with height [17],

$$\theta_f = \theta_{f0} + \gamma_\theta h$$

$$q_f = q_{f0} + \gamma_q h$$

where $\gamma_\theta$ and $\gamma_q$ are the lapse rate of potential temperature and specific humidity in the free atmosphere, respectively.

$\theta_{f0}$ and $q_{f0}$ are the intercepts of the assumed linear profiles, which can be obtained by inserting the initial conditions. Following [16], the simplified ABL growth rate is expressed as

$$\frac{dh}{dt} = \frac{H}{\rho_a c_p \gamma_\theta}$$

(19)

The dynamics of $\theta$, $q$ and $h$ are solved by Equations (17) – (19). At the beginning of each day and during precipitation events, ABL is reset to the daily initial conditions based on daily climate data (see Section S2 for details). The diurnal development of ABL, in response to the feedback of heat and water vapor flux from the soil-plant system, provides dynamic forcing of temperature and humidity to the soil-plant system.

Figure S1: Processes and states in the SPAC model. See the text for notations.
Section S2: Details on data processing

Soil and plant properties. The global distribution of plant functional type (PFT) was obtained from MODIS (MCD12C1) [18] with a spatial resolution of $0.05^\circ \times 0.05^\circ$. Multiple regions covered by forests were selected across the globe, with a variety of climate types (Table S1). Each biome corresponds to the areas covered by a given PFT within a selected region. Soil texture compositions were obtained from the Harmonized World Soils Database [19]. Based on the major soil texture in each biome, the soil hydraulic properties, i.e., saturated and unsaturated conductivity, soil water potential, pore-size distribution index and porosity, were calculated using the generalized statistical relations [20].

Leaf Area Index (LAI) was extracted from the level-4 MODIS global Leaf Area Index and Fraction of Photosynthetically Active Radiation (FPAR) product (MCD15A2) [21], with a spatial and temporal resolution of $1 \text{ km} \times 1 \text{ km}$ and 8-day respectively. In the SPAC model, LAI is a seasonally varying parameter. After re-sampling LAI to $0.05^\circ \times 0.05^\circ$ grids and linearly interpolating to a daily scale, the intra-annual variation of LAI was represented by the average of pixels within each biome over the period of 2003 to 2015. Root zone depth for the first and second layer were taken as 0.3 m and 1.0 m for all the biomes [1, 9, 22]. For each biome, RAI in the first layer was obtained from the biome-level average reported in [9] (Table S1). Because of lack of data, RAI in the second layer was taken as 1. Plant properties controlling internal water transfer, including leaf-specific conductivity ($k_{p,\text{leaf}}$), $\psi_{50}$, and $a$, were obtained from a global database containing hydraulic traits of 866 species [23]. These plant hydraulic traits were classified into categories based on combinations of PFT and climate type [24]. Each biome in this study was then assigned with the mean value of the category that has the same PFT and climate type. $g_{p,\text{max}}$ in Equation (10) was estimated according to $g_{p,\text{max}} = k_{p,\text{leaf}} \overline{\text{LAI}}/(H_c \rho_w)$ [9], in which $\overline{\text{LAI}}$ is the long term average LAI; $H_c$ is the 90th percentile canopy height extracted from a global map [25] and averaged across the biome. Large tree height, i.e., 90th percentile instead of 50th percentile, was used since tall trees are associated with low plant conductance, and hence are likely to be the main target during mortality events [26]. The parameters in the biochemical model (Equation (13)) and their temperature corrections came from the cross-species study by [27]. Parameters for all species were grouped by PFTs and the means for each PFT were used to parameterize the model. The response of leaf gas exchange to water availability (Equation (15)) was parameterized according to a recent study based on cross-biome meta-analysis [13]. Due to large range of these parameters, starting from the biome-average values reported in [13], $\lambda^*_W$ and $\beta_0$ were calibrated to match the modeled monthly potential evapotranspiration (PET) and ET against the PET and ET dataset derived from MODIS [28].
respectively (Figure S2), making sure that the magnitudes among PFTs and climate types are in the same order as reported in [13]. $\lambda^*_{\text{WW}}$ was first calibrated with the goal to match PET. Modeled PET equals the ET under presumptive conditions of $s_1 = s_2 = 1$ and $\lambda = \lambda^*_{\text{WW}}c_a/c_a^*$, where $c_a$ is equal to the historical ambient CO$_2$ concentration. Then $\beta_0$ was calibrated according to annual actual ET, where soil moisture and mWUE were allowed to vary under actual climate conditions. It should be noted that in PET calculation, the model was decoupled with ABL and the climate forcings came from ABL development in the ET calculation, which represents the actual climate conditions. In this way, the soil-plant system in each biome is physiologically and hydrologically reasonable in representing the overall properties at a biome scale. The biome-specific soil and plant properties are listed in Table S1.

Given the soil and plant properties in each biome, we analyzed the responses of stomatal conductance and plant water potential during dry down processes. Starting from a soil moisture at field capacity, the soil was allowed to consecutively dry down with zero precipitation. As shown in Figure S3, ENF biomes generally operate with wider safety margins than DBF and EBF biomes. Most ENF biomes adopt an isohydric leaning strategy under stress, i.e. they decrease $g_s$ while keeping a relatively wide safety margin even when $g_s$ gets close to zero. In contrast, most DBF biomes adopt an anisohydric leaning strategy under stress, i.e., they tend to decrease water potential while keeping stomata open even when the safety margin drops near zero or negative. The response of EBF biomes could be either one or a hybrid of these two strategies. The exact response of each biome depends on their hydraulic traits. The typically wider safety margin and isohydric strategies for ENF compared to the other two PFTs are consistent with observations [29, 30], which indicates representativeness of the plant parameterizations and enables inter-comparison among PFTs.
Figure S2: Comparison between modeled and MODIS based monthly ET and PET. Modeled monthly ET and PET are the average of 30 annual ensembles after a 5-year warming up period. MODIS ET and PET are the average across the available time range of 2000–2014.

Figure S3: Variation of stomatal conductance $g_s$ and safety margin ($\psi_{x,\text{min}} - \psi_{50}$) during dry down processes for ENF, DBF and EBF biomes. $\psi_s$ denotes soil water potential. These dry down processes were plotted for a constant air temperature of 20 °C, VPD of 1.5 kPa, and daily maximum net shortwave radiation of 700 W/m².
Table S1: Location, soil texture, climate conditions and vegetation parameters for the investigated biomes.

<table>
<thead>
<tr>
<th>ID</th>
<th>Latitude range</th>
<th>Longitude range</th>
<th>Major soil texture</th>
<th>Climate type</th>
<th>PFT</th>
<th>RAI</th>
<th>LAI</th>
<th>$H_c$ (m)</th>
<th>$k_{p,leaf}$ (kg/m/s/MPa)</th>
<th>$\psi_{50}$ (MPa)</th>
<th>a</th>
<th>$\lambda_{WW^*}$ (mmol/mol)</th>
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<td>EBF</td>
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<td>Mediterranean</td>
<td>ENF</td>
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<td>DBF</td>
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<td>4.4</td>
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**Historical climate forcing.** Historical climate forcings for the SPAC model, including stochastic precipitation, net shortwave radiation, and initial and boundary conditions of ABL, were obtained from the NCEP/NCAR reanalysis data (2.5° × 2.5°) [31] for 1986 to 2005. The two statistics for stochastic precipitation, i.e., precipitation frequency ($\lambda_P$) and mean precipitation depth ($\alpha_P$) were computed from the 20-year daily precipitation. To account for precipitation seasonality, $\lambda_P$ and $\alpha_P$ were computed for two periods separately, i.e., April to October and November to March, which correspond to the growing season and non-growing season for biomes in the northern hemisphere and the opposite for those in the southern hemisphere. Stochastic precipitation in the two seasons was then generated separately for the two seasons using the corresponding statistics [1]. Daily net shortwave radiation, which varies with day of year (DOY), was calculated as the average over the 20 years. Radiation for days with and without precipitation were calculated separately to account for cloud coverage on rainy days. Daily net shortwave radiation was distributed into an hourly diurnal cycle using a sine function consistent with local sunrise and sunset time, calculated from DOY and local latitude. Initial conditions of ABL include initial ABL height ($h_0$), potential temperature ($\theta_0$) and specific humidity ($q_0$). $h_0$ was set as 100 m [32]. $\theta_0$ and $q_0$, which also vary with DOY, were obtained from the 4-time daily data of 2 m air temperature and near surface specific humidity, linearly interpolated to the sunrise time of each day and averaged over the 20 years. Similar to radiation, humidity for days with and without precipitation were evaluated separately as humidity is generally higher on rainy days. Boundary conditions of ABL, i.e., the lapse rates of potential temperature ($\gamma_\theta$) and specific humidity $\gamma_q$, which reflect the stability of ABL, were extracted from the daily pressure level data within the troposphere. Daily mean values and the lapse rates are mostly linearly correlated [33] (Figure S4). Though some tropical biomes (biome 4, 5, 8, 12) showed low $R^2$ values, their lapse rates had small variation range, as such using these linear relations do not impair their representativeness as much. The fitted linear relations were used to represent lapse rates under given temperature and humidity. These representations of climate forcing enable the model to readily incorporate projected changes in climate conditions.

**Climate projections.** We calculated projected climate changes for multi-models of CMIP5 experiments under four RCP scenarios (Table S2). Under each RCP scenario, changes projected by each model were quantified as the difference (percentage for MAP and magnitude for others [34]) of the ensemble means for 2050 – 2069 relative to those for 1986 – 2005. These changes were incorporated in the historical climates from NCEP/NCAR reanalysis data to generate future climate forcings for the model. Changes in daily initial conditions of potential temperature and specific humidity were assumed to be identical to the changes in their annual means. Future
Figure S4: (a) Relation between daily mean surface potential temperature ($\theta$) and the lapse rate of potential temperature in the free atmosphere ($\gamma_{\theta}$); and (b) relation between daily mean surface specific humidity ($q$) and the lapse rate of specific humidity in the free atmosphere ($\gamma_{q}$) based on daily NCEP data from 1986 to 2005.
boundary conditions were obtained based on the linear relationships in Figure S4. Future precipitation amount in the growing and non-growing seasons were obtained by incorporating changes in MAP and PS. For the two seasons, precipitation amount was separated into mean precipitation depth ($\alpha_P$) and precipitation frequency ($\lambda_P$) by keeping $\alpha_P \lambda_P$ equal to the future daily mean precipitation, and the ratio $\alpha_P / \lambda_P$ to be constant [35]. As these statistics change in the projected climate, the occurrence frequency and duration of drought with a given severity will change accordingly. However, possible changes in the spectrum characteristics of long-term climate oscillations, such as change in El Niño Southern Oscillation which is still under debate [36], is not included in the model.

It is to be noted that the risk was found to be dominated by precipitation amount with little sensitivity to the separation approach (Figure S5). Hence, the results are not affected by using a different combination of $\alpha_P$ and $\lambda_P$. Future initial conditions of ABL were obtained by adding changes in annual mean air temperature and specific humidity uniformly throughout the year, assuming intra-annual and diurnal variation patterns remain unchanged. Future boundary conditions of ABL were changed accordingly based on the fitted linear relations with $\theta$ and $q$ respectively (Figure S4). Figure S6 shows the historical climates and ranges of multi-model projections for each biome, including mean annual precipitation amount, precipitation seasonality, mean annual air temperature and mean annual specific humidity. Identical future atmospheric CO$_2$ concentration under each RCP scenario was used for all the biomes. The ranges shown in Figure 2c, f correspond to the values from 2050 to 2069, which were obtained by linear interpolation of the values reported in [37].

Figure S5: Responses of mortality risk to individual changes in mean annual precipitation (MAP) and mean precipitation depth ($\alpha_P$) for (a) ENF in the western US and (b) DBF in the southeastern US. Numbers on the contours denote risk magnitude. Blue and green contours represent risks due to hydraulic failure and stomatal closure, respectively.
Table S2: List of CMIP5 model outputs included in this study. The used RCP scenarios of each model are denoted with “x”.

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Figure S6: Historical and future climate conditions of (a) mean annual precipitation (MAP), precipitation seasonality (PS), (b) annual mean air temperature (T) and annual mean specific humidity (SH) in the 13 biomes as projected by the CMIP5 models. Ranges of multi-model predictions under each RCP scenario are illustrated by rectangles.
Section S3: Model validation

Multiple components of the SPAC model have been previously examined and validated. For example, the soil water balance under stochastic precipitation was demonstrated to be able to capture observed probablistic characteristics of soil moisture dynamics [1]. An ecohydrological model forced by stochastic precipitation in the previous study [38] was shown to capture the frequency of canopy loss across a precipitation gradient. The resistance based plant water transport model has been widely examined and applied [8, 9]. The optimization based stomatal function was shown to be able to predict the observed stomatal response in both ambient and CO₂ enriched atmosphere [12, 14]. The constraint of water availability on leaf gas exchange was examined in [13]. Feedbacks between vegetation and ABL dynamics were compared with observed data in [15].

To examine the efficacy of the modeled mortality risk, observed mortality in two temperate and two tropical forests were compared to modeled mortality risk.

(1) Needleleaf forest in southern Sierra, California, USA

The United States Forest Service Pacific Southwest Region Aerial Detection and Monitoring Program (ADMP) conducts annual aerial survey over the forested areas in California [39]. Areas with new mortality since last survey were delineated as polygons. The surveyed area in southern Sierra (119.28° W – 118.20° W, 35.41° N – 37.57° N), which belongs to biome 1 in this study (Fig. 1, Table S1), was considered for comparison as it underwent massive mortality in 2014 and 2015. The aerial survey data from 2006 to 2015 were first converted to raster data with

![Figure S7: Comparison between modeled mortality risk of evergreen needleleaf forest and observed mortality area in southern Sierra, CA.](image)
grid resolution of 3 km and then used to calculate the area that underwent mortality in a given year. The model was parameterized with local soil properties and plant hydraulic traits, as described in Section S2, and forced with climate time series of the concerned period [40]. Figure S7 compares the temporal variation of modeled mortality risk and the observed area with mortality. The temporal variation in the area with mortality can be interpreted as the temporal variation in the probability of mortality of a tree within the selected area. Result shows that the temporal variation of modeled mortality risk ably captures the variations in areal cover that underwent mortality. Notably, the modeled risk captures the increase in mortality area from 2006–2008 to 2009–2011, a non-increase in mortality area from 2009–2011 to 2012–2013, and a significant increase in mortality area from 2012–2013 to 2014–2015. It is to be noted that reasonable correspondence between modeled and observed data is captured despite using an average representative soil, vegetation and climate properties for modeling the mortality risk.

(2) Deciduous forest in Bond Park, North Carolina, USA

A recent study [41] reported mortality of deciduous broadleaf forest in Bond Park, NC. The area belongs to biome 3 in this study (Fig. 1, Table S1). Within the surveyed area, 14% of Acer rubrum had died in 2007 while no mortality was observed in 2008. We examine if the difference in mortality between these two years can be captured by the modeled mortality risk. The model was again parameterized with local soil properties, and plant hydraulic traits specifically for Acer rubrum from the TRY database [23]. Using the daily historical climate [40] for the site, the model evaluates the risk for each year from 1990 to 2008 (Figure S8). It can be seen that

![Figure S8](image_url)

Figure S8: Modeled annual mortality risk in deciduous broadleaf forest in Bond Park, NC from 1990 to 2008.
Figure S9: Comparison between modeled and measured plant water potential of *Acer rubrum* in Bond Park, NC, reported in [41].

The risk in 2007 is abnormally high (18.4%), and is largest between 1990 to 2008. The modeled risk in 2008 is zero, which agrees with the observation that there was no observed mortality in 2008. Figure S9 further shows that the model was able to capture the plant water potential during 2007 and 2008 [41]. Notably, during the intense drought period in 2007, plant water potential fell below $\psi_{50}$ suggesting that the observed mortality would likely have been induced by hydraulic failure, which is consistent with the conclusion in [41]. These results highlight the effectiveness of model in capturing both the temporal variations in mortality risk and its mechanistic control.

(3) Evergreen broadleaf forest on Barro Colorado Island, Panama

Mortality rates in tropical forest of Barro Colorado Island (BCI) were measured for two census periods viz. 1982–1985 and 1985–1990 in a previous study [42]. Based on survey of 205 species, the average forest–wide mortality rate was observed to be 3% yr$^{-1}$ and 2% yr$^{-1}$ during the two census periods, respectively. The higher mortality rate during the first period was attributed to low precipitation and high temperature [42] during the unusually severe dry season of 1983. To examine if the modeled mortality risk in this study is able to distinguish observed mortality during these two periods, the SPAC model was parameterized with local soil properties and average plant hydraulic traits for species found on BCI from the TRY database [23]. Forced with deterministic climate conditions [40], the model shows a higher mortality risk of 2.2% during the first period, compared to 1.7% during the second period (Figure S10). The higher risk during 1982–1985 is primarily due to the notably high risk in 1983 (Figure S10), which is consistent with the finding in the previous study [42].
(4) Evergreen broadleaf forest in Lambir Hills National Park, Malaysia

The tropical evergreen forest in Lambir Hills National Park, Malaysia, experienced a severe drought in 1998, which resulted in the observed forest–wide mortality rate to increase to 7.63% yr\(^{-1}\) from a mere 2.40% yr\(^{-1}\) [43] during pre-drought (1993–1997) years. This area belongs to biome 12 in this study (Fig. 1, Table S1). Annual mortality risk during 1993–1998 was estimated using the SPAC model to examine its ability to capture the response to drought. Soil properties provided in [43] were used to parameterize the model. As complete set of plant
hydraulic traits of only two species from the region are included in the TRY database [23], the average plant properties over all the evergreen species in tropical wet climate were used for simulation. In agreement with the observation, the model shows higher mortality risk of 3.3% in 1998, compared to the pre-drought average risk of 1.1% (Figure S11).

The aforementioned comparisons between modeled mortality risk and observed mortality in the field indicate the effectiveness of the model in capturing the temporal variation of mortality in response to climate for different PFTs under a range of climate settings.
Section S4: Sensitivity analyses

Sensitivity to plant hydraulic traits. Given that plant hydraulic traits may vary significantly within each biome [9, 44] (Figure S12), sensitivity analyses of risks to magnitude of plant hydraulic traits are performed to test the robustness of the main conclusions of this study. In this regard, the historical mortality risks and relative change in them in response to projected climate was evaluated for 25%, 50% and 75% quantiles of the plant hydraulic traits for each biome. Table S3 shows the estimated historical risk, the relative changes in risk under projected changes of precipitation and temperature only, and then with additional consideration of changes in specific humidity and CO₂ concentration. Higher leaf specific conductance ($k_{p,leaf}$) promotes water loss, hence increasing the magnitude of historical risk. Variations in the absolute value of $\psi_{50}$ and $a$ also alter the historical risk by influencing the shape of vulnerability curve (Equation (10)). Notably, for all considered magnitudes of the three hydraulic traits, relative change in risk significantly reduces when the effects of projected changes in specific humidity and CO₂ concentration are considered (Table S3).

Table S3: Sensitivity of historical risk and relative changes (difference between historical and future risk divided by historical risk) under projected climate to plant hydraulic traits. “HR” denotes historical risk; “P+T” denotes relative change of risk under projected changes in precipitation and temperature; “All” denotes relative change of risk under projected changes in precipitation, temperature, specific humidity and CO₂ concentration. Values are the average over all the biomes (%). Biomes with historical risk less than 0.01% were excluded from calculating the average relative change.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>25%</th>
<th></th>
<th>50%</th>
<th></th>
<th>75%</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HR</td>
<td>P+T</td>
<td>All</td>
<td>HR</td>
<td>P+T</td>
<td>All</td>
</tr>
<tr>
<td>$k_{p,leaf}$</td>
<td>1.2</td>
<td>224.4</td>
<td>31.0</td>
<td>2.4</td>
<td>158.8</td>
<td>21.0</td>
</tr>
<tr>
<td>$\psi_{50}$</td>
<td>7.0</td>
<td>115.9</td>
<td>12.2</td>
<td>2.4</td>
<td>158.8</td>
<td>21.0</td>
</tr>
<tr>
<td>$a$</td>
<td>3.5</td>
<td>123.2</td>
<td>11.0</td>
<td>2.4</td>
<td>158.8</td>
<td>21.0</td>
</tr>
</tbody>
</table>
Figure S12: Range of plant hydraulic traits for each biome. The range is obtained by mapping hydraulic traits of all species that belong to the same PFT and climate type as the given biome, using the TRY database [23]. The horizontal line in each box denotes the median, and the upper and lower boundaries of each box denote the 25% and 75% quantiles respectively.
Sensitivity to tree sizes. In addition to the plant hydraulic traits, sensitivity analysis was also performed for variations in tree height, diameter at breast height (DBH) and stand density. These variables influence the plant conductance according to \( g_{p,max} = k_{\text{sap}} SAI / (H_c \rho_w) \), where \( k_{\text{sap}} \) is the sap wood conductivity; SAI is the sapwood area index; \( H_c \) is the canopy height; and \( \rho_w \) is the water density. Higher canopy height reduces the plant conductance, whereas larger DBH and higher stand density increase the plant conductance via larger SAI. Table S4 lists the sensitivity of risks to plant conductance. 20% increase in plant conductance can result from 20% decrease in canopy height or 20% increase in SAI due to either larger DBH or higher wood density. For all the biomes, on an average, 20% increase in the plant conductance raises the historical risk from 2.4% to 3.8%, suggesting that trees with larger DBH and higher wood density have higher mortality risk, all else being equal. This trend is consistent with previous studies suggesting tight correspondence of observed mortality with large DBH [45] and high wood density [46]. Though the magnitude of risk could differ due to variations in tree sizes and wood density within each biome, the increasing extent of mortality risk under projected climate is still found to be robustly alleviated by increasing specific humidity and CO\(_2\) concentration (Table S4).

Table S4: Sensitivity of historical risk and the alleviating effect of specific humidity and CO\(_2\) concentration to maximum plant conductance (%). Refer to Table S3 for abbreviations.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>-20%</th>
<th>0%</th>
<th>+20%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HR</td>
<td>P+T</td>
<td>All</td>
</tr>
<tr>
<td>( g_{p,max} )</td>
<td>1.8</td>
<td>189.0</td>
<td>64.3</td>
</tr>
</tbody>
</table>
Sensitivity to model structure uncertainties. Although multiple components of the SPAC model have been previously examined and validated, given that a model is just an approximate representation of the complex reality, latent structural uncertainties (apart from parameter uncertainties) still exist. For example, the model in this study adopts a big-leaf representation, which could result in different canopy water and carbon flux compared with a two-big-leaf model or a multilayer model that explicitly considers shading effects on flux exchanges [47, 48]. Notably, computing gas exchange using a multilayer model at canopy scale still remains challenging because of the difficulty associated with accurately resolving the within canopy turbulence [49, 50], which generally requires large eddy simulation. Accurate estimation of the influence of leaf texture, size and inclination angle [48] on incident direct and diffused radiation is challenging as well. To evaluate how sensitive the main results in this study are to the structural uncertainty inherent in the model, the modeled mortality risks for all the biomes under both historical and future climate scenarios were re-evaluated for ±20% uncertainty in the stomatal conductance. As stomatal conductance is influenced by leaf temperature, photosynthetically active radiation (PAR) at each leaf, humidity, air temperature, mesophyll conductance and turbulent flow right outside the stomata, ±20% uncertainty could be due to any of these controls. Table S5 indicates that although lower stomatal conductance would lead to a lower mortality risk, it is still significantly intensified by changes in precipitation and warming temperature. Also, this increase in risk can again be largely alleviated by rising specific humidity and CO\textsubscript{2} concentration.

Table S5: Sensitivity of historical risk and the alleviating effect of specific humidity and CO\textsubscript{2} concentration to uncertainties in stomatal conductance, on the average of all investigated biomes. -20% denotes the case where the ‘actual’ canopy level stomatal conductance should be 20% lower than the model estimates, and vice versa. Values are in %. Refer to Table S3 for abbreviations.

<table>
<thead>
<tr>
<th></th>
<th>-20%</th>
<th>0%</th>
<th>+20%</th>
</tr>
</thead>
<tbody>
<tr>
<td>HR</td>
<td>0.5</td>
<td>2.4</td>
<td>7.7</td>
</tr>
<tr>
<td>P+T</td>
<td>283.1</td>
<td>158.8</td>
<td>84.2</td>
</tr>
<tr>
<td>All</td>
<td>44.9</td>
<td>21.0</td>
<td>14.6</td>
</tr>
</tbody>
</table>

Therefore, although the exact magnitude of risk is difficult to estimate accurately due to uncertainties in parameters and model structure, the sensitivity analyses suggest that trend of response of mortality risk to projected climate are still robust.
Section S5: Analyses based on alternative quantifications of risk

Considering that stress thresholds leading to actual mortality vary among sites and species, here we consider the following alternative metrics that employ different thresholds of stress intensity and/or duration to evaluate the proneness to mortality. (1) Mortality risk is quantified as the probability of occurrence of either hydraulic failure ($\psi_{x,\text{min}} < \psi_{50}$) or full stomatal closure. This is the risk analyzed in the main text. (2) Cavitation risk is the probability of $\psi_{x,\text{min}} < \psi_{12}$. $\psi_{12}$ is the plant water potential at 12% loss of conductivity when conduit cavitation starts to occur and may not be easy to be fully repaired [51, 52]. (3) Hydraulic failure risk is the probability of $\psi_{x,\text{min}} < \psi_{50}$. (4) Long-duration cavitation risk is the probability of $\psi_{x,\text{min}} < \psi_{12}$ existing for more than two weeks. The time threshold of two weeks was selected based on the distribution of duration for $\psi_{x,\text{min}} < \psi_{12}$ (Figure S13), indicating that most duration are within two weeks. (5) Cavitation risk considering intensity is quantified as $\int_0^T \min(\psi_{x,\text{min}} - \psi_{12}, 0)dt/T/\psi_{12}$, i.e., the integrated difference between $\psi_{x,\text{min}}$ and $\psi_{12}$ (only when $\psi_{x,\text{min}} < \psi_{12}$) over time normalized by total time length and $\psi_{12}$. (6) Stomatal closure risk is the probability of full stomatal closure. (7) Long-duration stomatal closure risk is the probability of full stomatal closure that lasts for more than two weeks.

Figure S14 illustrates the combined impacts of climate change on the alternative risks for the thirteen biomes, indicating a robust alleviating effect by increasing specific humidity and CO$_2$ concentration. Note that EBF biomes in tropical wet climate (biome 5, 8 and 12) show $\psi_{x,\text{min}} < \psi_{12}$ almost all the time (Figure S14a) owing to their high $\psi_{12}$, which can be seen from the high $\psi_{50}$ of EBF in tropical climates, as listed in Table S1. Table S6 summarizes the cross-biome averaged response of each risk. Results based on different risk quantifications confirm a profound intensifying effect of changes in precipitation and temperature, which however can be significantly alleviated by rising humidity and CO$_2$ concentration. It is also found that combined change in climate variables tends to increase the risks associated with stomatal closure relative to that associated with low water potential. Agreement in results based on alternative quantifications of risk indicate remarkable robustness of the findings in the main text.
Table S6: Changes in risk using alternative quantifications, under the influence of changes in precipitation pattern and air temperature (P+T), additional changes in specific humidity (SH), additional changes in atmospheric carbon dioxide concentration (CO₂) and combined changes in all the considered climate variables (P+T+SH+CO₂) based on RCP4.5. Changes are quantified as the difference between historical and future risk divided by historical risk, and averaged across all the biomes with historical risks higher than 0.01%.

<table>
<thead>
<tr>
<th>Risk type</th>
<th>P+T</th>
<th>SH</th>
<th>CO₂</th>
<th>P+T+SH+CO₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality risk</td>
<td>158.8 %</td>
<td>-46.6%</td>
<td>-91.2%</td>
<td>21.0%</td>
</tr>
<tr>
<td>Cavitation risk</td>
<td>174.2%</td>
<td>-98.8%</td>
<td>-87.1%</td>
<td>-11.7%</td>
</tr>
<tr>
<td>Hydraulic failure risk</td>
<td>163.4%</td>
<td>-27.9%</td>
<td>-144.1%</td>
<td>-8.7%</td>
</tr>
<tr>
<td>Long-duration cavitation risk</td>
<td>43.6%</td>
<td>-9.9%</td>
<td>-33.6%</td>
<td>0.1%</td>
</tr>
<tr>
<td>Cavitation risk considering intensity</td>
<td>54.6%</td>
<td>-8.3%</td>
<td>-47.6%</td>
<td>-1.3%</td>
</tr>
<tr>
<td>Stomatal closure risk</td>
<td>445.7%</td>
<td>-139.9%</td>
<td>-222.1%</td>
<td>83.7%</td>
</tr>
<tr>
<td>Long-duration stomatal closure risk</td>
<td>794.0%</td>
<td>-313.4%</td>
<td>-390.0%</td>
<td>90.6%</td>
</tr>
</tbody>
</table>
Figure S13: Probability density of the duration of (a) $\psi_{x,\min} < \psi_{12}$ and (b) full stomatal closure. Bin width in the bar plots is one week.
Figure S14: Combined climate impacts of changes in climate on the (a) cavitation risk, (b) hydraulic failure risk, (c) long-duration cavitation risk, (d) cavitation risk considering intensity, (e) stomatal closure risk and (f) long-duration stomatal closure risk in the 13 biomes. Gray dashed lines show the risks under historical climate. Upper and lower boundaries of the boxes correspond to the 25th and 75th quantiles of the risk based on multi-model projections in each RCP scenario.
References


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