Darcy's law predicts widespread forest mortality under climate warming

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Drought and heat-induced tree mortality is accelerating in many forest biomes as a consequence of a warming climate, resulting in a threat to global forests unlike any in recorded history[1-12]. Forests store the majority of terrestrial carbon, thus their loss may have significant and sustained impacts on the global carbon cycle[11,12]. We use a hydraulic corollary to Darcy's law, a core principle of vascular plant physiology[13], to predict characteristics of plants that will survive and die during drought under warmer future climates. Plants that are tall with isohydric stomatal regulation, low hydraulic conductance, and high leaf area are most likely to die from future drought stress. **Thus, tall trees of old-growth forests are at the greatest risk of loss, which has ominous implications for terrestrial carbon storage. This application of Darcy's law indicates today's forests generally should be replaced by shorter and more xeric plants,** owing to future warmer droughts and associated wildfires and pest attacks. The Darcy's corollary also provides a simple, robust framework for informing forest management interventions needed to promote the survival of current forests. **Given the robustness of Darcy's law for predictions of vascular plant function, we conclude with high certainty that today's forests are going to be subject to continued increases in mortality rates that will result in substantial reorganization of their structure** and carbon storage.

Rates of tree mortality have risen substantially throughout much of North America in recent decades[1,2]. Documentation of regional forest mortality events has increased globally[3] in regions as disparate as Alaskan and Amazonian rainforests[4,5], from boreal forests of North America[2] to semiarid forests of Southwestern USA[6], Mediterranean Europe[7] and Australia[8]. Forest loss often occurs rapidly whereas forest re-establishment and tree regrowth are much slower[9], and in many cases post-mortality succession is dominated by smaller trees or shrubs and grasses that store less carbon (ref. 10; Fig. 1). The identified culprit is warming temperatures that, when superimposed on episodic periods of low precipitation, result in severe water deficits[6]. Given forecasts of continued rising temperatures and more extreme droughts globally[11,12], there are increasing risks of massive disruption of today's forests during this century[6,10-12].

Here we predict the characteristics of vascular plants that are likely to survive and die under future warming and extreme droughts using a hydraulic corollary to Darcy's law, which is a core principle of plant physiology[13], and then apply this analysis to suggest forest management options that may help mitigate future tree mortality. The full version of Darcy's hydraulic corollary allows investigation of the constraints, and homeostatic compensating mechanisms, on canopy-scale water conductance G (mol m^{-2} leaf area s^{-1}):

$$G = \frac{A_s k_s (\Psi_s - \Psi_l)}{h \eta A_l D} \qquad (1)$$

in which A_s is conducting area (cm^2), A_l is leaf area (m^2), k_s is specific conductivity (m s^{-1}), h is plant height (m, a surrogate for total hydraulic path length), η is water viscosity (Pa s), $\Psi_s - \Psi_l$ is the soil-to-leaf water potential difference, and D is vapour pressure deficit (kPa) (ref. 13, see Supplementary Information 1,2, and Supplementary Figs 1–3 for assumptions and literature supporting the accuracy of equation (1)). The hydraulic corollary to Darcy's law is schematic of the response of G to both climate and plant structural variables.

Darcy's law predicts a future decline in G due to the greater D associated with warming surface temperatures (Fig. 2a). This is the most immediate hydraulic response to rising D considering the relatively limited and slow degree of acclimation of the other hydraulic factors such as leaf area, sapwood area and hydraulic conductance (Supplementary Information 3 and Supplementary Figs 2,3). This relationship is ominous because a rise from 30 to 35 °C gives a 20% increase in D after accounting for rising atmospheric humidity (Supplementary Information 2). Thus, warmer air demands greater amounts of water from soil and plant surfaces; hence, droughts that previously would have been tolerable may become deadly[6].

Using the hydraulic corollary of Darcy's law (equation (1)) we observe numerous vegetation characteristics that will enhance G and hence survival during extreme droughts. First, plants that minimize h and A_l will maintain the highest G with increasing D. Plants that enable $\Psi_s - \Psi_l$ to increase with D—that is, anisohydric behaviour—are more likely to maintain G during drought than those that maintain Ψ_l at an isohydric set point. Last, species that maximize k_s and A_s will be more likely to maintain G during drought.

In addition to allowing predictions of what plants will survive, Darcy's law also allows assessment of what vegetation will die. Acclimation has distinct limits within living plants, and when those limits are exceeded, chronically in this case owing to rising D with rising temperature, the most efficient and immediate mode of homeostasis at the ecosystem scale is to reduce A_l through canopy dieback and whole-plant mortality with replacement by new species whose hydraulic system is adapted to higher D (Supplementary Figs 2,3). Tall old-growth trees, and conifers in particular, are at greatest risk of loss globally. A tree is characterized as old-growth when it has achieved its site- and species-specific maximum height, thus G is already minimized relative to shorter, younger plants[14]. Most conifers are particularly hampered during

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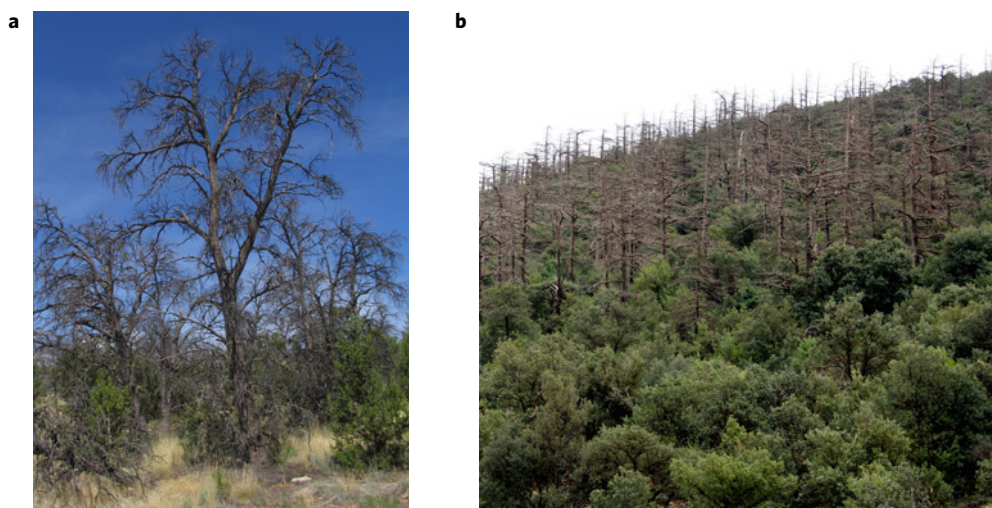
Figure 1 | Examples of mortality of taller trees and survival of shorter trees. a, *Pinus edulis* mortality, with surviving understory of *Juniperus monosperma*, in the Jemez Mountains, New Mexico, USA. **b**, *Cedrus atlantica* mortality, with surviving understory of *Quercus ilex*, *Fraxinus xanthoxyloides* and *Juniperus oxycedrus* in Belezma National Park (Aurès Région), Algeria. Note that the surviving trees and shrubs that now occupy these sites store much less carbon than the forests they have replaced. Images courtesy of: **a**, C. D. Allen; **b**, C. Gazi and A. Briki.
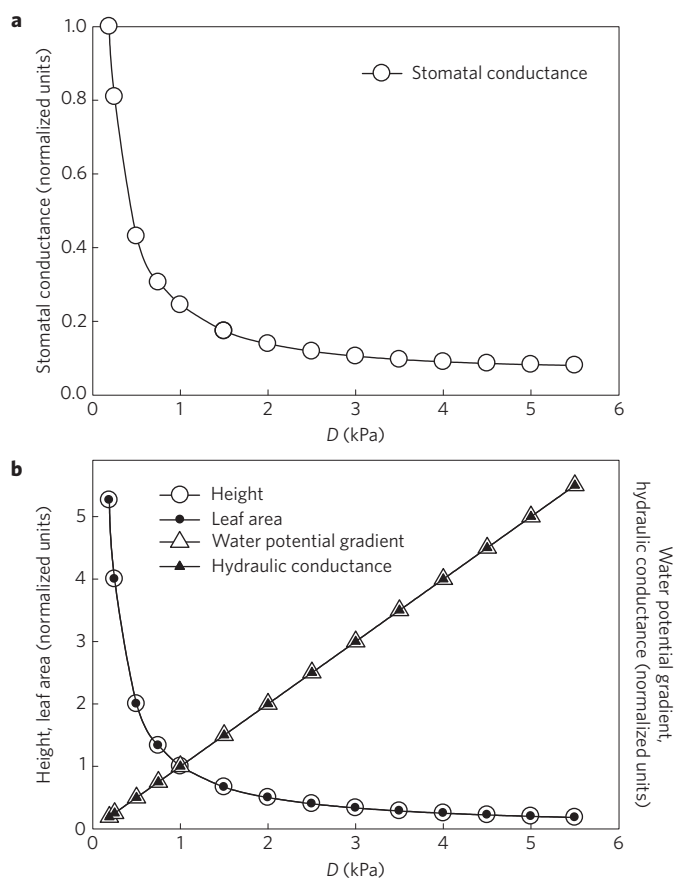
Figure 2 | The plant-hydraulic corollary to Darcy's law allows estimates of physiological and structural responses to climate change. a, Canopy-scale stomatal conductance declines with increasing D in accordance with the function $1/D$ from equation (1) in the absence of plant-hydraulic modifications to the other parameters within Darcy's law. **b**, If we assume that G is held constant with rising D, then the hydraulic parameters that must shift to accommodate the higher evaporative demand include reductions in height, leaf area, or A_l:A_s, and increases in hydraulic conductance and the soil-to-leaf Ψ gradient.

extreme droughts and associated stressors because of their isohydric behaviour, limited ability to drop leaf area rapidly, low k_s (ref. 15), and globally averaged, their greater height than angiosperms[16]. Indeed mortality of gymnosperms at present outpaces that of angiosperms in North America[1,2]. Coniferous trees also commonly lack the ability to epicormically resprout after mortality of their aboveground tissues relative to many angiosperm trees and shrubs. We note that widespread mortality of angiosperms also has been observed[9]; however, mortality even of resprouting trees in tall arboreal forms still occurs because of the vulnerability of such large, long-developing aboveground structures relative to the quick pace of climate warming, and because angiosperms (and resprouters) also obey Darcy's law. In general, large trees may become less competitive in a world of rapidly transitioning climate and disturbance conditions owing to their longer life spans and their lower fecundity relative to shrubs, grasses, and forbs. These predictions are consistent with observations of mortality of the tallest trees, isohydric trees, and trees that fail to resprout (see Supplementary Information 5 for examples). In addition, this result is consistent with the spatially widespread observation of accelerated mortality of gymnosperms and their replacement by shorter angiosperms during palaeo-warming periods in the Northern Hemisphere (see Supplementary Information 5). At the other end of the tree size-spectrum, seedlings and saplings also sometimes exhibit high drought-induced mortality rates owing to limited rooting depth (for example, ref. 17), as their ability to acquire resources is already constrained when a drought arises. Both empirical and quantitative model projections suggest that tall coniferous forests will increasingly be replaced by shorter shrubs and grasses over much of western North America in upcoming decades[6,10]. We note that although the absolute changes in A_l and h are smaller at higher mean D (Fig. 2b), the amount of leaf area and height that can be reduced is substantially lower in semiarid systems with higher mean D, thus the relative impact is still considerable.

Extreme droughts are expected to increase in the future not only in dry regions, but also in regions that will experience greater mean precipitation[11,12]. Historically, wet or cold forests commonly experienced long fire-return intervals even greater than 500 years with high-severity stand-replacing fires but with adequate time between fires for forest recovery[18]; warming conditions may drive more frequent and intense wildfire activity within this century (for example, ref. 19). Future warmer droughts will be significantly drier
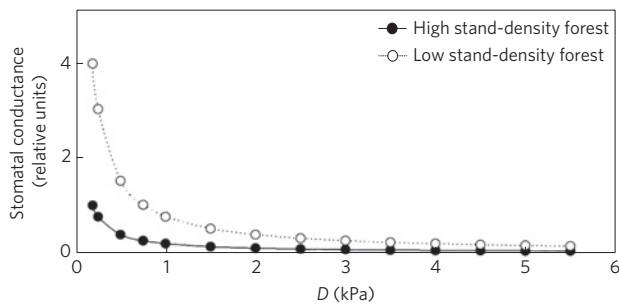
Figure 3 | Reducing stand density through sustainable harvesting can increase the resilience of forests to drought. Here we simulated a 50% reduction in stand density of a generic conifer forest, resulting in a substantial increase in stomatal conductance for the canopy that remains.

than conditions that the dominant trees in current forests have adapted to endure[15], because of greater D. In addition, warmer temperatures facilitate range expansion, growth acceleration and greater tree-killing success in tree pests such as bark beetles, with unprecedented beetle outbreaks recently affecting much of western North America[4]; in some cases, bark beetles are killing even previously unsuitable tree species[20]. Together these reasons may explain why some relatively moist forests are experiencing tree growth reductions and elevated mortality similar to drier regions during 'global change-type droughts'[1–9,11,21].

Management options to sustain current forests merit further attention given recent trends of growing severity and extent of climate-related forest disturbances[1–9], and increasingly ominous projections for the future[6,10,12]. Beyond the obvious but at present improbable mitigation solution of immediate massive reductions in greenhouse gas emissions[3,12], there are adaptation options for managing forests to ameliorate anticipated climate impacts. Under scenarios of increasing drought stress, the future persistence of many current forests could benefit from stand density reductions to improve the water balance for the remaining trees (see Supplementary Information 6 for references). For example, using equation (1), which includes the relevant parameters of soil water potential (Ψ_s) and structural features, we predict that halving stand density (specifically, halving A_s) increases G of the remaining trees by approximately 30% (after accounting for A_l adjustment to thinning[22], Fig. 3), consistent with the relationship between density and productivity (Supplementary Information 6). This predicted increase in G is associated with reduced risk of severe hydraulic failure and increased photosynthesis per plant, thus minimizing the risk of carbon starvation[23]. Stand density reductions also increase the production of defensive compounds used to protect against pest attacks[24], and can greatly reduce risks of stand-replacing high-severity fire[25]. Similar to mechanical thinning, recent and ongoing drought-induced tree mortality and canopy dieback events (Fig. 1) commonly leave shorter, more vigorous live trees after the mortality pulse[9], which can be seen as an incremental adaptation to reduce stand-level basal area (A_s), leaf area (A_l), and mean stand height (h) to better match G to the diminished level of water available to support tree growth and survival, thus improving the resistance of persisting stands to future climate stresses.

Vascular plants obey Darcy's law at the individual and stand levels (see Supplementary Information 1); thus, although the number of trees is reduced by thinning, the survival likelihood of the remaining trees is enhanced (Fig. 3). Even forests that traditionally were not exposed to frequent disturbances—and thus typically are not thinned—may benefit from reasonable stand density reductions when extreme drought conditions emerge, possibly including forests in wetter regions[25]. One important question is to determine benefits and consequences of stand density on stomatal conductance during

extreme drought conditions. Darcy's law again can be used to make such predictions if we have knowledge of mean annual precipitation, D, stand densities, and h (Fig. 3).

It is essential to maintain an awareness of historical disturbance regimes when applying management techniques[26]; however, it is apparent that previous forest disturbance patterns and processes may no longer be operative today or into the future (ref. 3, and see Supplementary Information 7), especially given the novel climate patterns of more extreme drought and heat projected for this century[12]. We do not advocate thinning in all forests, as for many reasons (ecological, ethical, aesthetic, economic, scientific, conservation, or logistical) some forests should be unmanaged or at least less manipulated—and, where thinning is implemented, low-disturbance techniques can be fostered. Similarly, although combinations of natural (lightning) and human-ignited fires historically have been essential to maintaining resilient lower-density forests in many semiarid regions[26], the appropriateness of future fire use will vary markedly by region and forest type[27].

Planting of southerly and low-elevation genotypes into more northerly or higher-elevation landscapes is another forward-looking adaptation approach to increase the resiliency of future forests to warming and extreme droughts[28]. Darcy's Law (equation (1)) predicts that shorter, more anisohydric plants with relatively higher k_s or greater $A_s:A_l$ are most likely to survive future droughts, and translocation of such genotypes should be considered for future planting.

Caveats to the predictions from the Darcy's law corollary are necessary. Equation (1) is an approximation of the real world, and fails to include some aspects of ecological realism regarding how trees die and survive[23,29]. For example, G may decline substantially with rising D, but in many forests insect attack is a critical last step to mortality; if relevant insect populations decline owing to negative feedbacks of climate change, then tree mortality rates may be buffered. Likewise the dependence of mortality on low G probably varies across taxa, geography and edaphic conditions, so predictions from equation (1) can be viewed only as a coarse level assessment. Nonetheless, the predictions from equation (1) are robust regarding the general patterns we can expect in forest responses to globally increasing D.

In conclusion, the hydraulic corollary to Darcy's law (equation (1)) predicts that as rising temperatures drive increasing vapour pressure deficits, the resultant greater water stresses will force major shifts in the dominant plants. Shrubby, low-statured plants are most likely to survive, whereas tall old-growth forests are particularly vulnerable to warming climate. Darcy's law can also inform forest management applications ranging from prescriptions for sustainable stand densities to more resilient tree species and genetic compositions to promote future forest survival in a strongly warming world. Overall, such applications of Darcy's law suggest that growing plant water stress from projected climate changes will increasingly drive the emergence of new global vegetation patterns.

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Author contributions

N.G.M. developed the theory, conducted analyses and wrote the manuscript. C.D.A. provided supportive data and co-wrote the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to N.G.M.

Competing financial interests

The authors declare no competing financial interests.