places over long periods of time, as the facilitation of adaptation to climate change requires detailed local and regional solutions that cannot be dictated from the top down.

Such an approach is exemplified by the work of Miller Hesed and Paolisso regarding the African American communities of St. Michael's, Crisfield, and rural Dorchester County, in Chesapeake Bay, Maryland. Through the lens of more standard quantitative measures, these communities might appear to be very similar, with respect to their risk for flooding as sea level rises, their histories and demographics, and their resource base. Yet, the integration of qualitative and quantitative methods allows a more nuanced understanding of the ways that these communities differ in their perceptions of risks as well as resources, affecting their ability to respond effectively to the impacts of a changing climate.

Miller Hesed and Paolisso conducted pile-sorts using terms related to climate change generated within the same region, asking respondents to group the terms that they found similar together, thereby generating a kind of mental map. No two people will sort the terms in the exact same way, but the cultural domains represented by the terms can be aggregated in ways that show the patterns of relationships across the sorted terms; a method called multidimensional scaling. The results of these analyses are then discussed in detail with the study participants in an iterative process that clarifies the outcomes. Very little has been done so far to engage with the African American experience of climate change, and this ethnographically grounded research brings the field forwards in a substantive way, providing a methodology that can be replicated in other marginalized places. Such an effort supports the quest for improving subnational sociocultural and economic datasets called for by Otto *et al.*<sup>2</sup>.

This work on vulnerable Chesapeake Bay communities also validates the conclusions presented by Barnes et al.6; that anthropological research approaches have a significant role to play as we work towards a more complete understanding of the human dimensions of climate change. As characterized in the contribution of Working Group II to AR5, in order to develop successful policies that can support resilience, policymakers and researchers generating data must consider the integrative nature of the social–ecological system under study<sup>1</sup>. Anthropological research describes local-scale phenomena that illuminate social structures and processes relevant to human cognition and behavior, past and present. By focusing on the broader socialecological system, Miller Hesed and Paolisso contribute to our understanding of these complex interactions through a holistic view

of human society that is integrally linked to environments as they change over time

It is not sufficient to identify only the climate impacts or hazards arising from our contributions to atmospheric warming, nor to focus only on the institutional and cultural values, policies, and actions that affect the severity of our experiences. An integrated approach is necessary, recognizing social–ecological systems as evolving wholes that cross and sometimes transcend national and other artificial boundaries, rather than placing human actions, beliefs, and engagements outside of the impacts on the non-human world. Miller Hesed and Paolisso's research is a step in the right direction.

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## Tall, leafy conifers lose out

A simple conceptual model helps to answer the question of which forests are more likely to die following droughts.

## Maurizio Mencuccini and Oliver Binks

he Rolling Stones famously sang "you can't always get what you want". However, it is not clear whether forests will be able to always get what they need under conditions of future climate change. This nicely sums up a current theme of research on how forests are expected to cope with the increased frequency and intensity of regional drought events and heat waves predicted under global climate change. Evidence of large-scale defoliation and mortality has been reported for forests around the world<sup>1</sup>, but our ability to predict these events remains weak<sup>2</sup>. When and where will droughts occur and what consequences will they have for the world's forests? Writing in Nature Climate Change, McDowell and Allen<sup>3</sup> discuss a conceptual tool that points out some of the vegetation

characteristics that predispose trees to drought-induced mortality.

Global air temperatures are rising. While the capacity of the atmosphere to hold humidity increases exponentially with temperature, climate models and observations show that absolute atmospheric humidity does not keep pace with warming<sup>4-6</sup>, especially over land areas<sup>7</sup>. The amount by which humidity increases with warming is a very important quantity as humidity strongly affects the terrestrial biosphere. Plant physiologists employ the concept of leaf-to-air vapour pressure deficit (VPD), the difference in vapour pressure between the humid air spaces inside plant leaves and the surrounding air. Leaf-toair VPD is predicted to increase strongly with warming<sup>4–7</sup>.

Plants routinely lose very large amounts of water from small pores in their leaves called stomata and this flux to the atmosphere is referred to as transpiration. The most direct response of vegetation to increased atmospheric dryness is to moderate water losses via transpiration. In the short term, plants regulate these losses by partial or complete stomatal closure. The downside of this is that photosynthesis is reduced because  $CO_2$  uptake is restricted. Therefore, plants are challenged by increased atmospheric dryness and also by the risk of starvation from declining carbohydrates<sup>8</sup>.

The short-term regulation of transpiration by stomatal closure remains one of the least understood aspects of plant physiology. Yet it has important implications for global-scale modelling of carbon and water cycles and of energy balance. This regulation is likely to involve responses to VPD<sup>9</sup>, which is therefore a key variable in the interactions between forests and the atmosphere. Increased global temperatures and VPD may therefore require plants to adjust their morphological and physiological traits.

Which plant traits are effective at enabling regulation of transpiration and avoidance of drought-induced mortality? Several groups have presented modelling and empirical analyses to distil this set of plant traits (for example, ref. 10). McDowell and Allen<sup>3</sup> employ a corollary of Darcy's law, a widely used principle of environmental biology linking water supply to demand within plants. As in traditional economic analysis, a break-even point must exist between how much water a tree can scavenge from the soil and how much it can spend via transpiration to maintain rates of photosynthesis.

Surprisingly, this principle also provides information on the characteristics acting when these physiological feedbacks break down under drought. In other words, the same variables that maintain balance (homeostasis) in response to background dryness also quantify the limits of homeostatic control and eventual mortality under extreme drought conditions. McDowell and Allen3 list a number of empirical observations where this breakdown applies, at scales from individual trees to forests.

Stomatal responses to atmospheric dryness help us to understand how plants cope with increased water demand in the short term. But what happens in the long term? The principle that leaf transpiration is regulated to moderate water losses also works to describe the long-term response of forests to atmospheric dryness. Darcy's law makes quantitative predictions about the reduction in the area of leaves necessary to maintain homeostasis within a forest.

The analysis of McDowell and Allen<sup>3</sup> predicts the emergence of shrubbier, shorter vegetation with a sparser canopy and more flexible stomatal control, which would therefore be more resilient to the drier climates expected in many regions under climate change. However, it would also be less capable of acquiring and storing large quantities of carbon. Needle-bearing trees appear to be more vulnerable than broad-leaved ones. Reductions in forest leaf area would also lead to reductions in evaporative cooling, with consequences for heat waves, and potentially for regional recirculation of precipitation in large forested regions such as the Amazon<sup>11</sup>. Perhaps the most menacing consequence



Figure 1 Tree stomata responses predicted to occur under the increased atmospheric dryness of various climate change scenarios. Increased air warming leads to increased leaf-to-air VPD, resulting in a smaller aperture of leaf stomata  $G_{s}$  (where  $G_{s}$  is the measure of the rate CO<sub>2</sub> enters, or water vapor exits, via the stomata; indicated by the blue line). This closure helps to reduce plant water losses. a-d, The consequences of increased VPD for four representative species are shown: two with broad leaves (chosen from a tropical (a) and a temperate (b) forest) and two with needle-like leaves (from a Mediterranean (c) and a boreal (**d**) forest). The value of  $G_s$  relative to current mean VPD values typical of the forest type is given by the green lines. The responses to three climate scenarios are given by the other coloured lines: changes expected for a reduction in air humidity over land<sup>7</sup> are indicated in red; for a temperature increase of +3 °C at current air humidity in grey; and for the changes suggested by McDowell and Allen<sup>3</sup> in yellow. The scenario used by McDowell and Allen could not be simulated for the tropical trees with broad leaves and it is therefore not plotted. Note that the maximum VPD on the x axis varies depending on the biome.

for biologists is the predicted loss of the tallest trees of key vulnerable species.

While this analysis<sup>3</sup> is useful as a bold first attempt to identify vegetation traits leading to mortality, much remains to be done. Several variables in the extension of Darcy's law are not independent of one another. For example, the capacity of trees to scavenge soil water may decline during drought, possibly leading to counterintuitive responses. Interactions with altered temperature, nutrient cycles and atmospheric CO<sub>2</sub>, and biotic relationships with fungi, insects and coexisting plants are minimally accounted for. McDowell and Allen3 assume that evaporative demand increases with warming (using a scenario of 5 °C of warming plus a 4% increase in relative humidity over land, see also refs 5-7), but measurements obtained by pan evaporation, a standard proxy for atmospheric evaporative demand, show a global declining trend<sup>12</sup>. If the trend shown by pan evaporation is correct, adjustments in stomatal conductance and leaf area are less critical. Finally, the dependency on plant height assumed in the corollary of Darcy's law implies that short seedlings with superficial roots are not generally threatened by drought, whereas the opposite is often found<sup>13</sup>.

Several questions remain to be answered, but the contribution from McDowell and Allen is a step forwards in efforts aimed at synthesis and improved understanding of drought-induced mortality in terrestrial vegetation.

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