Larger trees suffer most during drought in forests worldwide

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The frequency of severe droughts is increasing in many regions around the world as a result of climate change[1-3]. Droughts alter the structure and function of forests[4,5]. Site- and region-specific studies suggest that large trees, which play keystone roles in forests[6] and can be disproportionately important to ecosystem carbon storage[7] and hydrology[8], exhibit greater sensitivity to drought than small trees[4,5,9,10]. Here, we synthesize data on tree growth and mortality collected during 40 drought events in forests worldwide to see whether this size-dependent sensitivity to drought holds more widely. We find that droughts consistently had a more detrimental impact on the growth and mortality rates of larger trees. Moreover, drought-related mortality increased with tree size in 65% of the droughts examined, especially when community-wide mortality was high or when bark beetles were present. The more pronounced drought sensitivity of larger trees could be underpinned by greater inherent vulnerability to hydraulic stress[11-14], the higher radiation and evaporative demand experienced by exposed crowns[4,15], and the tendency for bark beetles to preferentially attack larger trees[16]. We suggest that future droughts will have a more detrimental impact on the growth and mortality of larger trees, potentially exacerbating feedbacks to climate change.

Climate change has been linked to water deficits in many parts of the world, and future climate projections suggest that droughts are likely to increase in severity because of changes in the timing and magnitude of precipitation and rising temperature[1,2,14,17]. Across a wide range of biomes, drought leads to changes in forest composition, structure, productivity and climate interactions[5,18,19]. Drought has many important consequences for forest communities, as species composition and dominance are shaped by water availability and can change rapidly in response to drought[19,20]. Drought-induced forest decline results in climate feedbacks including reduced CO_2 uptake, reduced carbon stocks, increased albedo and decreased evapotranspiration[21]. The impact of drought on forest structure and function depends on which trees are most adversely affected; greater mortality of small trees may modify future forest succession whereas mortality of large trees causes disproportionate losses of carbon and ecosystem function[5-7]. It has not been clear whether large or small trees would suffer more under drought stress. Several studies have documented a greater impact of drought on large trees at a single site[4,9,10], and a synthesis of data from the humid lowland tropics revealed a tendency for greater drought-related mortality increases in large trees[5], but these patterns have never been systematically reviewed for forests worldwide.

Here, we perform a meta-analysis of data from 40 drought events at 38 forest locations worldwide, ranging from semi-arid woodlands to tropical rainforests, to address whether trees of different size (seedlings excluded) respond differently to drought (Fig. 1 and Supplementary Tables 1 and 2). These included both natural and experimental droughts, the latter of which do not fully mimic natural droughts but nevertheless provide valuable insight into forest responses to water stress. Using published data from these forests, we analysed size-related variation in three response variables: (1) the ratio of diameter growth rate under drought to non-drought conditions ($n = 13$ droughts), (2) the ratio of mortality rate under drought to non-drought conditions ($n = 14$ droughts) and (3) the percentage of drought-related mortality ($n = 28$ droughts, 31 drought-species combinations; Supplementary Tables 3 and 4). Standardization of growth and mortality rates relative to non-drought conditions accounted for size-related variation in growth and mortality rates under baseline conditions[22] (Supplementary Fig. 1). In contrast, the percentage of drought-related mortality is not a rate and is not standardized relative to non-drought conditions; it represents the absolute, as opposed to the relative, impact of drought on tree mortality. Response variables were analysed in relation to the lower limit of diameter classes. To account for variation in study methods, site characteristics and the nature of the droughts (for example, intensity and duration), drought instances (unique combinations of site and year) were treated as random effects in a mixed-effects model with random intercepts and slopes. Analyses were performed using a variety of data inclusion criteria and analysis methods (henceforth, 'robustness analyses'; see Methods). Although a limited sample size precluded rigorous analysis across different forest types, a separate analysis was conducted for any of the following subsets represented by at least three droughts for the response variable of interest: tropical and temperate forests, climates with and without significant precipitation seasonality, broadleaf and needleleaf dominated forests, and droughts where bark beetles were and were not identified as a driver of mortality.

In forests worldwide, drought consistently had a more detrimental impact on the growth of larger trees (Figs 1 and 2a). Specifically, the ratio of diameter growth rate during drought relative to non-drought conditions consistently declined with increasing tree size ($P < 0.001$; $n = 13$ drought instances, 65 data points, where data point refers to drought response of a given size class in a given drought instance). This relationship was also significant at $P \leq 0.001$ in all robustness analyses (Supplementary Table 5), and a sensitivity analysis determined that this pattern would be effectively unchanged if basal area increment or biomass increment were used in place of diameter growth as the response variable (Supplementary Fig. 3). This pattern held true separately for all subsets of drought instances with at least three records: tropical

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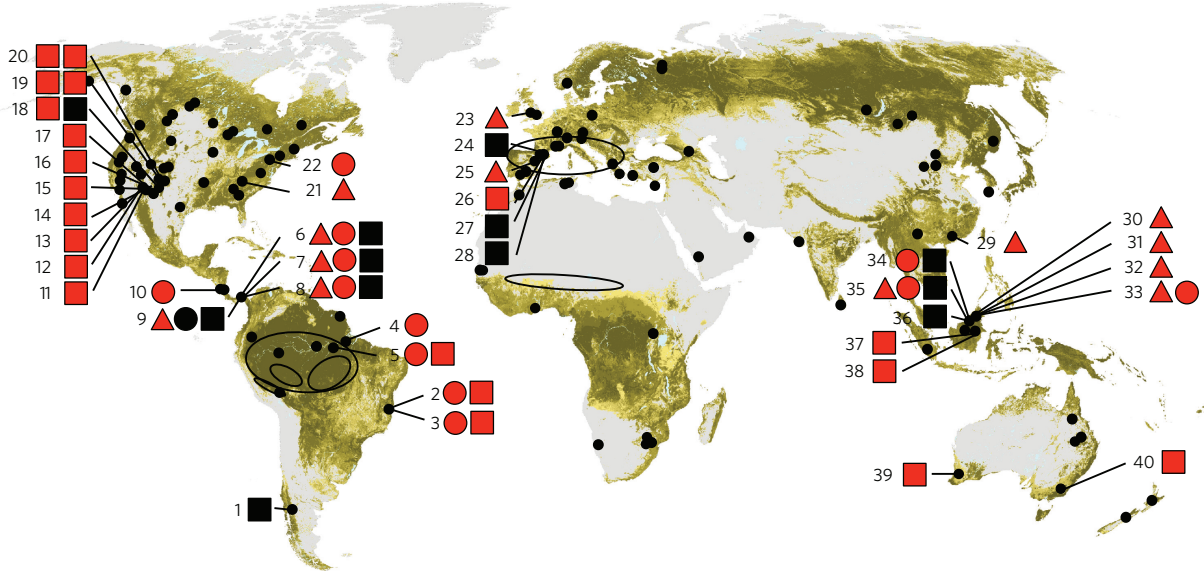
Figure 1 | Global distribution of instances of drought impacts on forests reviewed in this study. Drought typically had a more detrimental impact on larger trees (red symbols). Records of drought-induced tree mortality[3,18] (small black dots and ovals) and other forest drought response records were reviewed, and those reporting drought impacts on tree growth rate (triangles; $n = 13$), mortality rate (circles; $n = 14$) and per cent mortality (squares; $n = 31$) for multiple diameter classes were included in this analysis. Numbers correspond to drought instance numbers (Supplementary Tables 1–4). For instances 18–20, repeated symbols indicate separate results for two dominant species. Green shading indicates forested areas.

forests ($n = 10$ records, $P < 0.001$), temperate forests ($n = 3$, $P = 0.004$), climates with significant precipitation seasonality ($n = 7$, $P = 0.009$) and climates without significant precipitation seasonality ($n = 6$, $P = 0.009$). All of these drought instances were for broadleaf-dominated forests, and there were no instances where bark beetles were identified as a driver of mortality. Whereas growth rates of small trees sometimes increased and sometimes decreased in response to drought, growth rates of size classes with diameter at breast height (DBH) > 50 cm always decreased, and the ratio of growth under drought to normal conditions was consistently lower for large trees (Fig. 2a).

Larger trees also exhibited greater increases in mortality rate during drought in 13 of the 14 drought records analysed (Figs 1

and 2b). In the mixed-effects model, the ratio of mortality rate under drought to non-drought conditions increased with the lower limit of diameter class ($P = 0.004$, $n = 14$ drought instances, 73 data points; Supplementary Table 5). This pattern held for all robustness analyses (all $P < 0.02$; Supplementary Tables 5 and 6) and for all forest and drought type subsets with at least three records: tropical forests ($n = 12$, $P = 0.009$), climates with significant precipitation seasonality ($n = 8$, $P = 0.007$) and climates without significant precipitation seasonality ($n = 6$, $P = 0.051$). All drought instances were for broadleaf-dominated forests; there were only two records for temperate forests, and there were no instances where bark beetles were identified as an interactive driver of mortality.
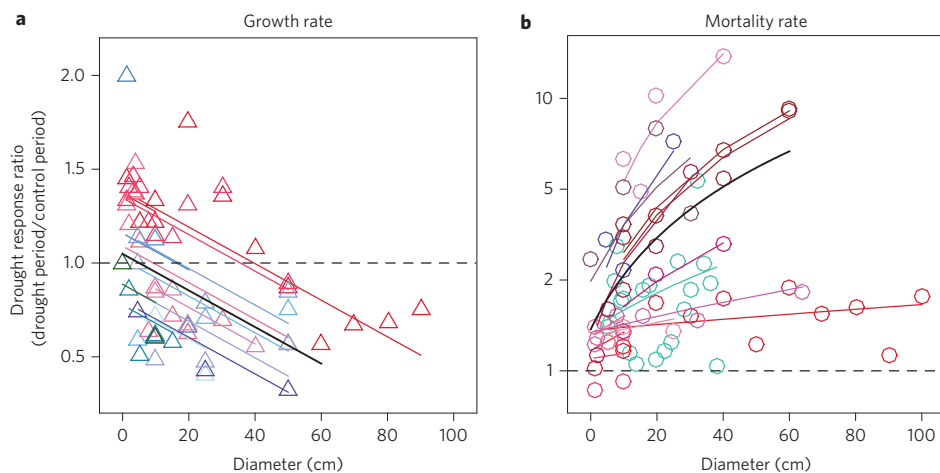
Figure 2 | Drought responses of diameter growth rate and mortality rate as a function of tree size. a,b, Larger trees exhibited greater decreases in growth rate and greater increases in mortality rate relative to non-drought conditions. Diameter refers to the lower size class limit. A solid black line represents the main effect in a linear mixed-effects model. Coloured symbols and lines represent unique drought instances ($n = 13$ for growth, $n = 14$ for mortality) and model fits. Colours correspond to those in Supplementary Fig. 2. A dashed line represents equality under drought and non-drought. In **b**, the log scale on the *y* axis is for display purposes.
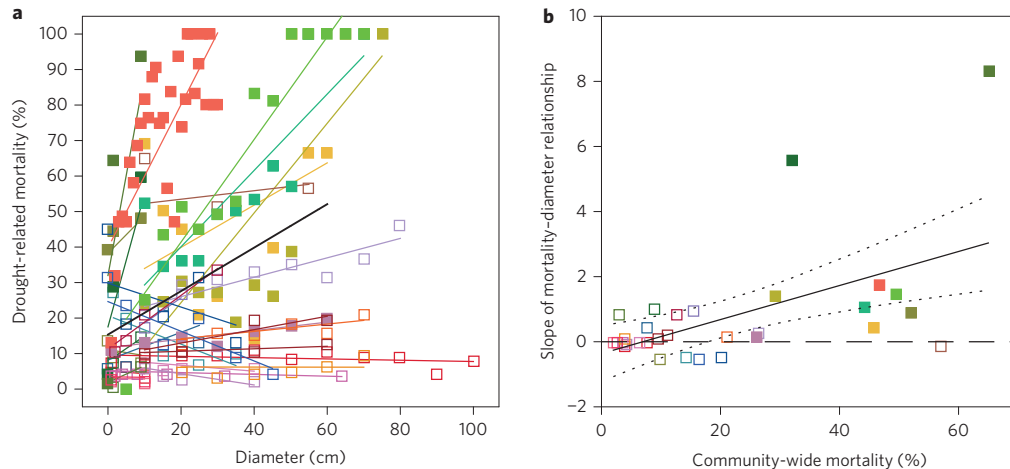
Figure 3 | Size dependence of drought-related mortality and its relationship to community-wide mortality. a,b, Drought-related mortality increased with diameter in 20 of 31 drought instances—a tendency that was particularly prevalent in the presence of bark beetles (solid symbols). In **a**, lines and symbols are as in Fig. 2. In **b**, the dashed black line represents no size bias to mortality, and positive values indicate greater mortality of large trees. Solid and dotted lines represent least squares model fit and its 95% confidence interval. Colours correspond to those in Supplementary Fig. 2.

The fact that drought results in a greater increase in mortality rates of larger trees does not necessarily imply that the percentage of individuals killed by drought should be highest in large trees, as baseline mortality rates generally decrease with increasing tree size across most of the diameter range[22] and the per cent mortality is not standardized relative to non-drought mortality patterns. Nevertheless, drought-related mortality increased with increasing diameter in the main analysis (Figs 1 and 3a; $n = 31$; $P = 0.017$; drought instances, 192 data points) and in all robustness analyses except two (in which cases $P < 0.07$; Supplementary Table 5). When records were subsetted by forest and drought type, results were mixed; the trend was significant for temperate forests ($n = 19$, $P = 0.025$), forests in climates with significant precipitation seasonality ($n = 23$, $P = 0.009$), needleleaf-dominated forests ($n = 17$, $P = 0.025$) and events where bark beetles were the proximate cause of mortality ($n = 9$, $P = 0.005$), but not significant for tropical forests ($n = 12$, $P = 0.11$), broadleaf-dominated forests ($n = 14$, $P = 0.11$), forests in climates without significant precipitation seasonality ($n = 8$, $P = 0.29$; Supplementary Table 6) or sites where bark beetles were not identified as an important contributor to mortality ($n = 22$, $P = 0.62$).

The tendency for the per cent mortality to increase with increasing diameter was particularly prevalent under extreme mortality events and when bark beetles were known contributors to mortality (Figs 1 and 3a). Specifically, there was a positive relationship between the per cent mortality and the tree size in 10 of 11 records of droughts with community-wide mortality >25%, 9 of which involved bark beetles. In the analysis including all droughts, the slope of the relationship between the per cent mortality and the diameter increased with community-wide mortality ($P = 0.002$, $R^2 = 0.30$; Fig. 3b)—a pattern that held in all robustness analyses except when data were subsetted by single versus multiple species (Supplementary Table 7). This pattern was largely dependent on the inclusion of sites with bark beetles (Supplementary Table 7), and was not significant across all sites with no known bark beetles ($n = 22$, $R^2 = 0.02$, $P = 0.52$). It did, however, also hold for tropical forests alone, none of which had known bark beetle activity ($n = 15$, $R^2 = 0.35$, $P = 0.02$). Thus, in contrast to the near-universal tendency for drought to have a relatively larger impact on growth and mortality rates of large trees (Figs 1 and 2), the size bias of the absolute mortality response was dependent on the nature of the drought (Figs 1 and 3).

These observed patterns may be underlain in part by differential responses of canopy and understorey species. As most of the drought instances analysed included multiple species (Supplementary Tables 3 and 4), it is not possible to determine whether the observed patterns apply consistently within species or whether they are driven by differential responses of species with different size distributions. Either way, it is apparent that fundamental physiological or ecological mechanisms make larger trees more vulnerable to drought.

The observed size bias of growth and mortality rate responses to drought contrasts with what would be expected if larger trees had more reliable access to water during drought. Despite their greater root mass, larger trees do not necessarily have deeper roots or rely more heavily on deep water than smaller trees[23,24]. Moreover, because increases in root mass with tree size are balanced by increases in transpiring leaf area[25], it is unlikely that greater root mass conveys a substantive hydraulic advantage to large trees during drought.

The primary driver of the observed greater sensitivity of large trees to drought may be greater physiological vulnerability. Basic principles of plant physiology predict that vulnerability to drought stress increases with tree height[13]; this theoretical prediction is confirmed by our results. Tall trees have to lift water to a greater height against the effects of gravity and pathlength-associated resistance, and therefore face greater hydraulic challenges[11–14]. Water-use efficiency increases with tree height globally as a consequence of both increasing hydraulic path length with greater height and higher evaporative demands in the upper canopy[14]. This benefits larger trees, but is a result of their more challenging hydraulic environment, and our results demonstrate that they remain more vulnerable when drought occurs.

Moreover, in closed-canopy forests, taller trees face a more challenging hydraulic environment. Large trees with crowns in or above the canopy are exposed to higher solar radiation and leaf-to-air vapour pressure deficits than those in the relatively buffered understorey[15]. This may become a liability under drought, when lower water availability and higher evaporative demand (natural droughts only) make it impossible for canopy-top leaves to simultaneously maintain hydraulic safety while opening stomata enough to maintain a positive carbon balance and regulate leaf temperature (through transpirative cooling). Biophysical challenges associated with maintenance of leaves at the top of the canopy during drought is consistent with, and may help to explain, observations

that drought deciduousness is more common in tropical forest canopy trees than in mid-storey or understorey trees[26].

In contrast to the large trees, understorey trees face less unfavourable, or even more favourable, conditions during drought. In closed-canopy forests, the understorey environment has lower leaf temperatures, specific humidity deficits and wind speeds[15], placing understorey individuals at a relative advantage during drought. In all seasonal tropical forests analysed here, the growth rate of small trees actually increased in response to drought (Fig. 2a). Presumably, this was driven by increased solar radiation reaching the understorey due to increased deciduousness of larger trees during drought[27]. Small trees also may benefit from release from competition with large trees for nutrients and water.

Finally, biotic agents commonly attack drought-stressed trees and may contribute to a size bias in drought-related decline. In particular, in cases where bark beetles are associated with drought-related mortality (for example conifer die-offs in the western United States; Supplementary Table 3), an additional driver may be that bark beetles preferentially attack larger trees[16]. Bark beetles were an important driver of both the size dependence of drought-related mortality and the tendency for the size bias to increase with community-wide mortality; these patterns were not significant when bark beetle sites were removed (Fig. 3 and Supplementary Tables 6 and 7). The size-dependence of the drought responses of growth and mortality rates (Fig. 2) had no drought instances in which bark beetles were identified as an important driver of mortality (Supplementary Tables 3 and 4).

The greater drought sensitivity of large trees has important implications for ecosystem-level carbon cycling responses to drought. Our results demonstrate that drought has more detrimental impacts on the growth of large trees (Fig. 2a), which translates directly to greater decreases in woody growth and associated carbon sequestration in long-lived woody tissues of large trees (Supplementary Fig. 3). Because woody productivity can be decoupled from gross primary productivity during drought through altered carbon allocation patterns[28], it remains unknown whether the observed size-biased decrease in woody growth reflects a parallel size bias in the response of gross productivity to drought or whether it is driven by differential drought responses in carbon allocation by large and small trees. Either way, drought disproportionately reduces carbon sequestration in the biomass of large trees and further reduces ecosystem-level carbon stocks associated with large size classes through higher mortality. The few studies that have quantified the implications of greater drought sensitivity of large trees on ecosystem-level productivity or carbon stocks demonstrate that the greater drought sensitivity of large trees has disproportionate impacts on the ecosystem carbon cycle[4,20,29].

As the climate warms and precipitation patterns change, leading to drier soils and more severe forest drought stress in many parts of the world[1,2], large trees are likely to suffer the most[13]. This implies several consequences for future ecosystem function and biodiversity. The fact that drought has a more detrimental impact on their growth and mortality suggests a greater drought-driven feedback to the carbon cycle than if their drought sensitivity were equal to the average community response[4,20,29]. In addition, large canopy trees can account for a greater proportion of ecosystem-level transpiration than smaller trees[8] and their drought-related decline could imply reduced latent cooling of the land surface and transpiration contributions to cloud formation[21]. Moreover, large trees have keystone ecological roles, creating unique above- and below-ground microenvironments on which many plant and animal species are dependent (for example nesting cavities, substrate for epiphytes), and their decline would impact other species[6]. Overall, our findings indicate that large trees will be most vulnerable to climate change-driven increases in drought stress frequency or intensity, impacting the climate regulation services and biodiversity of forests throughout the world. Our data set does not allow examination of how other climatic drivers may influence the size variation in growth and mortality, but given that drought has clear size-dependent impacts, it would be valuable in future research to extend this type of analysis to understand the impacts of other factors.

Methods

We compiled studies reporting growth or mortality rates under drought and non-drought conditions or the per cent drought-related mortality for trees in two or more size classes, as detailed in the Extended Methods section of the Supplementary Information. All events identified as drought by the study authors, including experimental droughts, were included regardless of their intensity or length. Drought severity, as reflected in community-wide mortality, varied substantially (Supplementary Tables 3 and 4). Standardization of drought severity was not required because it was effectively treated as a random effect in our analyses. We included drought response data for multiple (preferred) or individual taxa, as available. We included studies characterizing forest responses to natural drought with sampling area ≥0.5 ha and all controlled drought experiments. We excluded studies with major confounding anthropogenic or abiotic disturbances (for example logging, fire). Drought instances with interacting biotic disturbances (for example bark beetles, psyllid insects, mistletoe; Supplementary Tables 3 and 4) were included, as drought typically makes trees more susceptible to pests and pathogens[30], which are ubiquitous in forests.

A drought instance was a unique site–drought year combination, where site was a geographically distinct plot or set of plots. There were two cases where two separate droughts were recorded at the same site (drought instances 2, 3, 6 and 7; Supplementary Table 3). There was one study in which results were reported separately for two dominant species, in which case the two species were treated as separate instances (drought instances 18–20).

Data were obtained from tables or extracted from figures using WebPlotDigitizer v 3.4 (arohatgi.info/WebPlotDigitizer) and used to derive the variables used in our analyses. If not reported directly, the per cent mortality following drought was calculated from mortality rate when sufficient information was provided (that is sampling dates and formula used to calculate mortality rate). Original studies reported results by size classes defined by lower and upper diameter bounds, where diameter refers to breast height (most studies) or a lower height (studies in woodlands with smaller trees). The lower limit of the diameter size class was selected to characterize tree size for each size class because most studies did not report an upper diameter for the largest size class and because tree abundance would generally be skewed towards the lower end of a size class[22]. The number of size classes for each variable were as follows: mean = 5.2, range = 2–11 for the drought response ratio of growth rate; mean = 5.6, range = 2–20 for the drought response ratio of mortality; mean = 6.2, range = 2–30 for per cent mortality.

Some data were excluded based on considerations of lagged drought effects and sample size, as detailed in the Extended Methods section of the Supplementary Information.

The relationship of drought response ratio of growth and mortality rates and absolute drought-related mortality to diameter (both lower limit and standardized lower limit of diameter) was characterized using a linear mixed-effects model (fitlme in Matlab R2014b), where diameter was a fixed effect and instance was a random effect applied to both intercepts and slopes. To give all drought instances equal weight, data were weighted as 1/(number of size classes in instance).

To test the relationship between the slope of the drought-related mortality–diameter relationship and community-wide mortality (Fig. 3b), we first calculated the slope of the relationship between drought-related mortality and diameter for all drought instances independently using a linear regression model (LinearModel.fit in Matlab R2014b). Note that these calculated slopes differ from those calculated in a mixed-effects model. We then used a linear regression model (LinearModel.fit in Matlab R2014b) to examine the relationship between the slope of the drought-related mortality–diameter regression and the per cent community-wide mortality (all tree sizes combined, as reported by original studies; Supplementary Tables 3 and 4).

We conducted robustness analyses to test whether observed patterns held under a variety of analysis methods and data inclusion criteria (Supplementary Tables 5–7). These included alternative data analysis methods, excluding drought instances or data that may have been unreliable for a variety of reasons, separating records by whether multiple or single species were censused, and subsetting the drought instances by climate, forest type and the presence or absence of bark beetles. Additionally, because tree size distributions vary dramatically across the types of forests included in this analysis, all analyses were repeated using a standardized diameter for the lower limit of the size class as the independent variable (Supplementary Tables 5 and 6). These analyses are detailed in the Extended Methods section of the Supplementary Information.

Basal area increment or biomass increment provide more direct metrics of productivity than does diameter growth; however, these could not be reliably calculated for this data set because we are working with size classes and lack detailed information on numbers and sizes of trees. We conducted a sensitivity analysis,

detailed in the Extended Methods, to demonstrate that growth rate ratios are almost identical regardless of whether they are calculated based on diameter growth, basal area increment or biomass increment.

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Author contributions

K.A.T., A.C.B. and N.G.M. conceived and designed the analysis, A.C.B., C.D.A. and K.A.T. compiled data; K.A.T. and A.C.B. analysed data; A.C.B., K.A.T., N.G.M. and C.D.A wrote the paper.

Additional information

Supplementary information is available online. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to K.A.T.

Competing interests

The authors declare no competing financial interests.