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RESEARCH ARTICLE

Journal of Ecology



Local adaptation constrains drought tolerance in a tropical foundation tree

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Abstract

1. Plant species with broad climatic ranges might be more vulnerable to climate change than previously appreciated due to intraspecific variation in climatic stress tolerance. In tropical forests, drought is increasingly frequent and severe, causing widespread declines and altering community dynamics. Yet, little is known about whether foundation tropical trees vary in drought tolerance throughout their distributions, and how intraspecific variation in drought tolerance might contribute to their vulnerability to climate change.
2. We tested for local adaptation in seedling emergence and establishment with a full-factorial reciprocal transplant experiment including 27 populations and 109,350 seeds along a 3,500 mm precipitation gradient for a widespread tropical foundation tree, *Metrosideros polymorpha*, in Hawaii. To more precisely relate seedling performance to soil moisture, we conducted a complementary greenhouse experiment to test responses of the same focal populations to simulated drought.
3. In the reciprocal transplant experiment, we observed significant variation among populations and sites in germination and seedling establishment rates. Overall, there was a significant link between historical rainfall of populations and their performance under current rainfall at the study sites consistent with local adaptation. In particular, populations from historically wet sites demonstrated lower germination rates in currently dry sites compared to wet field sites, while populations from historically dry sites germinated well across all sites, with particularly high germination in dry sites. In the greenhouse, seedlings from wet populations survived fewer days without water, and succumbed at wetter soil conditions than populations from historically dry sites, corroborating results from the field experiment.
4. *Synthesis.* While climate change models project the greatest drying trends for historically dry areas in Hawaii, even moderate drying of wet sites could significantly reduce *Metrosideros polymorpha* recruitment given the sensitivity of seedlings to

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very slight changes in water regimes. Thus, although *M. polymorpha* demonstrates high seedling drought tolerance in some populations, providing evidence of resilience at the species-scale, there are nonetheless vulnerable populations that will likely decline under climate change. Our approach demonstrates that even trees with high dispersal abilities can show significant clines in drought tolerance, and suggests that similar intraspecific variation might be an important consideration for other tropical foundational tree species.

KEYWORDS

climate change, ecotypes, germination, Hawaiian Islands, phenotypic plasticity, seedling establishment, seedling recruitment

1 | INTRODUCTION

Predicting climate change effects on species distributions is a central focus of ecology and conservation today. Species distribution models are a popular approach that use historical occurrence data to generate climate envelopes that can be analysed in conjunction with climate change projections to predict future shifts in distributions. However, an important constraint of this approach is the assumption that species are homogeneous throughout their distributions (Elith & Leathwick, 2009), despite considerable evidence for clinal trends, intraspecific variation in climate stress tolerance (Alberto et al., 2013; Epperson, 2003) and examples for how incorporation of such intraspecific variation can improve accuracy and precision of species distribution models (Ikeda et al., 2017; Valladares et al., 2014). For instance, incorporating population-level data for phenotypic plasticity to warming revealed that *Pinus sylvestris* on the Iberian Peninsula is likely to experience even greater species contraction than predictions based on the species mean due to relatively strong effects of populations with very narrow thermal niches (Valladares et al., 2014). Foundation tree species, which dominate community and ecosystem dynamics and sustain a diversity of associated species, often have occurrences across a broad range of climates. It is essential to understand if these species have intraspecific patterns of climate stress tolerance, which might make some of their populations more vulnerable to climate-driven extinction than previously thought (Feng, Porporato, & Rodriguez-Iturbe, 2013; IPCC, 2014). While tests for clinal variation have been a focus of temperate and boreal forestry for decades, tropical trees remain poorly studied (Alberto et al., 2013).

Drought is one of the most pervasive climate change threats, affecting plants world-wide (IPCC, 2014). Even aseasonal tropical forests are experiencing altered frequency and intensity of rainfall (Chadwick, Good, Martin, & Rowell, 2016; Feng et al., 2013), so that drought is likely the greatest climate change threat to tropical trees (Allen et al., 2017; Schwalm et al., 2017). For example, the Hawaiian Islands are projected to have more days without rain, less precipitation overall and increases in extreme storms (Chu, Chen, & Schroeder, 2010; Frazier & Giambelluca, 2017; Timm, Giambelluca,

& Diaz, 2015; Zhang, Wang, Hamilton, & Lauer, 2016), which along with increased temperatures will make Hawaii more arid with increasing drought stress (Cook, Smerdon, Seager, & Coats, 2014; Giambelluca, Diaz, & Luke, 2008). Previous research has determined that drought tolerance, defined broadly with respect to maintained fitness under drought stress and regardless of underlying isohydric versus anisohydric mechanisms, is a key factor underlying tropical tree distributions (Esquivel-Muelbert et al., 2017; Gaviria, Turner, & Engelbrecht, 2017; Kursar et al., 2009), although these studies were conducted at the scale of species and genus and did not consider intraspecific variation in drought tolerance.

The most powerful approach to test for plant clinal variation is the use of reciprocal transplant experiments, which unlike the more commonly used common garden experiments, allow plant performance to be assessed at multiple sites throughout a species climatic range. Locally adapted populations are expected to have higher relative fitness at their home sites than they have at away sites or compared to immigrant seeds at the home sites (Blanquart, Kaltz, Nuismer, & Gandon, 2013; Kawecki & Ebert, 2004; Savolainen, Pyhajarvi, & Knurr, 2007). However, if some sites have greater resource availability, all populations may have greater absolute fitness at those sites (Lu, Parker, Colombo, & Man, 2016). For example, wet forest tree species showed no home-site advantage in Panama because all species performed better in sites with more moisture (Gaviria et al., 2017), and most experiments on tropical trees have detected positive responses in performance to supplemental irrigation (Comita & Engelbrecht, 2014). Thus, it is important to account for variation in site quality as well as genetic variation among populations in absolute performance in order to detect greater relative fitness of populations at their home site consistent with local adaptation (Blanquart et al., 2013). Linking relative fitness across sites to climatic variables such as precipitation or aridity provides evidence that local adaptation leads to intraspecific clinal variation (Gaviria et al., 2017; Lu et al., 2016). For local adaptation in drought tolerance, we would thus predict that plant performance would increase as precipitation increases across sites due to the general positive response of plants to greater soil moisture (Comita & Engelbrecht, 2014; Gaviria et al., 2017), but that populations from dry sites would have relatively high performance

also in dry sites, leading to a greater magnitude of response to precipitation for populations from wet sites due to their poor performance in dry sites (Figure 1a). This variation in the magnitude of response in performance across sites varying in precipitation could then be related to the historical precipitation at home sites to shed light on potential local adaptation. Specifically, we would expect a stronger positive response from historically wet populations than from historically dry populations, leading to a linear positive trend across populations (Figure 1b). Because plants may be locally adapted to other (biotic and abiotic) factors in addition to climate, combining reciprocal transplant experiments with additional experimentation that isolates performance responses to manipulations of climatic factors can provide more robust evidence for clinal variation.

To investigate clinal variation in a tropical foundation tree species, we assessed evidence for local adaptation along a rainfall gradient in *Metrosideros polymorpha* (Myrtaceae), the most widespread and abundant tree in the Hawaiian Islands (Craven et al., 2018). Growing across a broad rainfall gradient spanning from 300 to 9,000 mm mean annual precipitation (Giambelluca et al., 2013; Price et al., 2012), *M. polymorpha* provides critical habitat to rare and threatened plants, insects, snails and birds. It also dominates ecohydrology and carbon cycling in Hawaii, and its future persistence is critical for maintaining this biodiversity hotspot (Gotsch et al., 2014; Gruner, Taylor, & Forkner, 2005; Kagawa, Sack, Duarte, & James, 2009; O'Rorke et al., 2015; Percy, 2017; Santiago, 2000). As the species name suggests, *M. polymorpha* is highly variable phenotypically, and considerable genetic diversity has been detected across Hawaii's heterogeneous environments (Crawford, Hagen, Sahli, Stacy, & Glenn, 2008; Harbaugh, Wagner, Percy, James, & Fleischer, 2009; Stacy, Johansen, Sakishima, Price, & Pillon, 2014). Previous molecular and seedling studies have revealed locally adapted populations of *M. polymorpha* on Hawaii Island (DeBoer & Stacy, 2013; Morrison & Stacy, 2014; Stacy et al., 2014).

More recently, leaf anatomical traits have been used to characterize 10 morphotypes of *M. polymorpha* on Oahu Island (Sur, Keating, Snow, & Stacy, 2018), suggesting considerable genetic differentiation within this species on Oahu. Because *M. polymorpha* seeds are minute and wind-dispersed, they have large dispersal distances (Wright & Ranker, 2010), and biotic and abiotic interactions affecting germination, survival and growth at the seedling stage are likely to play a key role filtering out genotypes that are not locally adapted, thereby maintaining genetic differentiation and allowing for local adaptation. Observed bird and bee pollination (Cortina, Aslan, & Litson, 2019; Hanna, Foote, & Kremen, 2013) may further contribute to gene flow across the heterogeneous range of *M. polymorpha*.

We performed a full-factorial reciprocal transplant experiment to investigate local adaptation in drought tolerance of *M. polymorpha* across a 3,500 mm mean annual rainfall (MAR) gradient on Oahu Island (Figure 2, Table S1). Seedling recruitment is a critical life history process for population resilience, and because seedlings tend to be more susceptible to drought stress (Comita & Engelbrecht, 2014; Gerhardt, 1996; Marod, Kutintara, Tanaka, & Nakashizuka, 2002) given their limited carbohydrate storage, superficial roots and underdeveloped wood tissue, we focused on the seedling stage in this study. To more specifically attribute population variation in seedling performance to water availability, we conducted a complementary greenhouse experiment in which seedling tolerance to simulated drought was assessed for the same focal populations. We predicted that absolute performance across all populations would increase with precipitation, but that populations from historically dry sites would also perform well at dry sites leading to variation among populations in their relative performance across sites (Figure 1). This two-part approach offers a rigorous test for intraspecific variation in drought tolerance of a tropical foundation tree, providing important insights into potential resilience of this island endemic to future climate change.

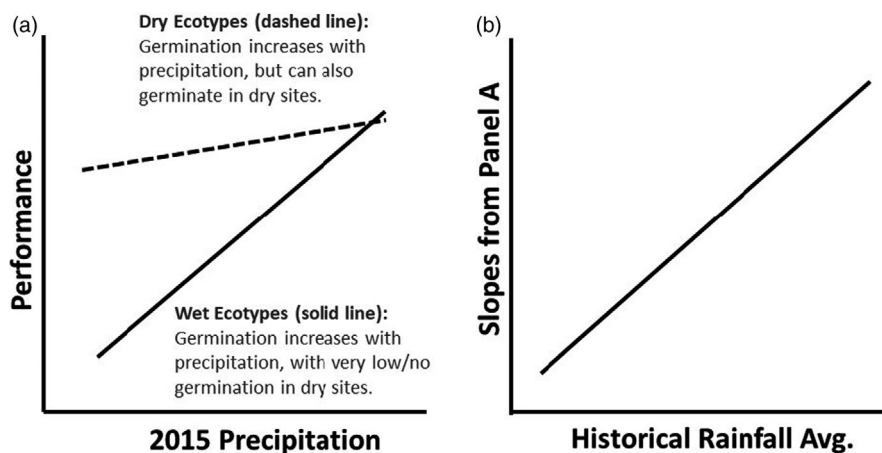
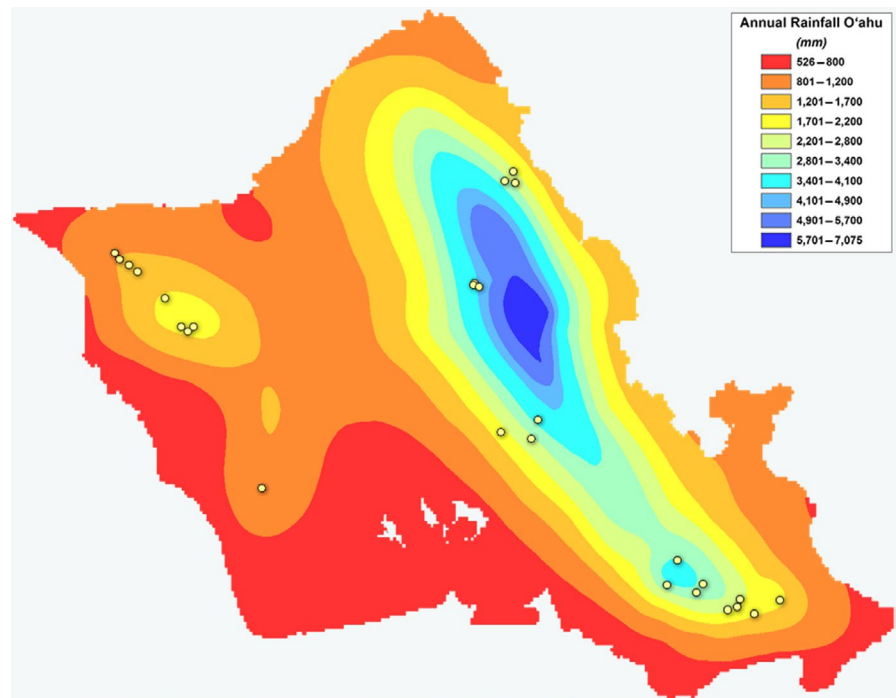


FIGURE 1 Predictive model for seedling performance in full-factorial field reciprocal transplant experiment. To test whether *Metrosideros polymorpha* populations are locally adapted to rainfall for seedling performance, we link rainfall during the experimental period (January–June 2015) with the historical rainfall trends (MAR) among the population sites. We predicted that rainfall will induce germination in all populations, resulting in positive slopes of performance (germination) on current rainfall across the 27 sites. Because of local adaptation, we predicted that populations from dry sites would have higher germination rates at dry sites than populations from wet sites, leading to variability in the population slopes of germination on current rainfall (a). This trend across populations should be detectable as a positive response of the germination slopes of the populations to historical mean annual rainfall (b)

FIGURE 2 Map of Oahu showing mean annual rainfall (Giambelluca et al., 2013) and the 27 field sites marked with yellow circles



2 | MATERIALS AND METHODS

2.1 | Field experiment

Selection of the 27 sites for the reciprocal transplant experiment (Figure 2) was based on the presence of *M. polymorpha* in the canopy (although dominance of *M. polymorpha* and other native trees varied across sites, Table S1), availability of germination sites provided by the cushion moss *Leucobryum gracile* and to span the largest possible range in MAR on Oahu Island. Sites occurred in both the Koolau and Waianae mountain ranges, ranging from 1,150 to 4,460 mm MAR (Table S1). Although we did not determine whether trees across the 27 sites were genetically differentiated, leading to detectable population structure, we refer to the seeds from these sites as “populations,” although we recognize that these may not be populations in the genetic sense. However, this practice allows us to easily differentiate the seed samples (‘populations’) from the field locations (referred to as ‘sites’). Because abiotic conditions shift dramatically across short spatial scales in Hawaii due to extreme elevational gradients and complex heterogeneity in land cover (Selmants, Giardina, Jacobi, & Zhu, 2017), sites near each other in space were not necessarily similar in terms of *M. polymorpha* dominance or climate (Table S1). For this reason, we did not use spatially explicit analyses, but rather examined how key climate variables influenced seedling performance.

In June–November 2014, seeds were collected from 10 randomly selected fruiting trees at each site. After removing inviable seeds with unfilled embryos, five seeds per tree were mixed together to produce 50-seed batches, and 81 replicate seed batches were prepared from each population. Seeds of *M. polymorpha* are minute (Drake, 1992), and potential variation among populations in

seed mass is beyond the precision of our lab balance and unlikely due to the highly consistent seed size and colour. A full-factorial reciprocal transplant experiment was conducted in which seeds from all 27 populations were planted back out into all 27 sites. At each site, seed batches were sown into 10-cm radius areas covered by *L. gracile* cushion moss, and marked with a plastic stake. Three replicate 50-seed batches were sown from each population at each site, giving a total of $N = 2,187$ seed batches (27 sites \times 27 populations \times 3 replicates) and a total of $N = 109,350$ seeds sown. Because all the seed batches were sown into a single general area at each site, the three batches sown for each population were thus pseudo-replicates, and we summed the seedling data across them to produce a single response for each population \times site sample. In addition, at each of the 27 sites, three 10-cm radius control areas were established into which no *M. polymorpha* seedlings were sown. These plots were used to calculate ambient seedling establishment from natural seed rain. No seedlings were observed in the control plots, indicating zero background germination at this scale.

Seeds were sown in the field during the first 2 weeks of January 2015. Plots were inspected every 2 weeks from February to June 2015, and the number of seedlings within each plot was counted. Due to the number of sites, it was not feasible to mark and follow individual seedlings, preventing us from quantifying growth rates, or calculating individual survivorship. From seedling counts, we can quantify maximum germination (highest number of seedlings in any census) and establishment in the last census (number of seedlings left in June). Because it is likely that some germination events went uncounted due to mortality between census dates, we consider calculations of germination and establishment to be conservative, and do not quantify rates of mortality.

To investigate whether populations of *M. polymorpha* may be locally adapted, we first tested whether seedling performance (germination and establishment) was higher for seedlings germinating into their original site ('home') compared to the other 26 sites where they had been planted ('away'). We used GLMMs (Bates, Maechler, Bolker, & Walker, 2015), in which location (home vs. away) was treated as a fixed factor, and population (where the seeds came from) and site were treated as a random factors (Blanquart et al., 2013). Because there were many instances in which a population had zero germination at a site, we analysed the data using a hurdle model (Edwards, Litchman, & Klausmeier, 2013; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We first used the occurrence of *any* germination (germination/no germination), for a population at a site, as a binary response variable modelled with a binomial error distribution. Second, we used the subset of the data in which germination was non-zero to test for patterns in the abundance of germinants, conditional on the occurrence of germination, in a model with the same predictors (home/away, population, and site). Abundance was modelled using a negative binomial distribution. Finally, the same subset of non-zero germination data was used to test whether establishment (the number of seedlings persistent at the final census) showed evidence of local adaptation, using a negative binomial distribution for the number of recruits.

We further examined the role of rainfall in underlying variation in germination and establishment among sites. Rainfall data were obtained from the National Oceanic and Atmospheric Administration Hawaii Rainfall Summary 90 Archive and from the NOAA National Center for Environmental Information Climate Data Online database (NOAA, 2018). Although there is an extensive system of rain gauges throughout Oahu Island, not all of these are measured every month. The closest rainfall gauge with data for the entire experimental period was identified for each of the 27 field sites, and in some cases, the same gauge had to be used for multiple sites. Using monthly rainfall data, we summed the total rainfall for the experimental period of January–June 2015 for analysis (Table S1).

To examine the link between historical climate of the populations to rainfall during the experimental period, we obtained MAR data for each of the 27 sites from the Rainfall Atlas of Hawaii (Giambelluca et al., 2013). In addition to MAR, we examined potential evapotranspiration which integrates combined effects of rainfall and temperature providing a metric of aridity that has been shown to limit plant performance via stomatal regulation (Keenan et al., 2013) and obtained mean annual potential evapotranspiration (MET) for our 27 sites from the Evapotranspiration Atlas of Hawaii (Giambelluca et al., 2014). Data for MET and MAR were scaled to have a mean of zero and variance of one before analysis. We fit GLMMs to test whether a population's response to 2015 precipitation across the 27 sites can be explained by historical precipitation (MAR) and potential evapotranspiration (MET) at the sites of origin. The predictors of the model for MAR were fixed effects for current precipitation at the sites, historical precipitation

of the populations and the interaction between current and historical precipitation; and random intercepts and slopes to allow the effect of current precipitation to vary across populations, and allow populations to differ on average. Thus, this model tests whether the slope of a population's response to precipitation is correlated with the historical rainfall experienced by that population (Edwards et al., 2013; Gelman & Hill, 2007). We predicted that populations from historically wet sites would have a more positive response to precipitation than populations from historically dry sites (Figure 1). The response distributions in the GLMMs were the same as those used when testing for local adaptation: a model for the occurrence of any germination (binary response), a model for number of germinants conditional on germination at that site (negative binomial), and a model for number of recruits conditional on germination (negative binomial). Similar models were run for MET.

2.2 | Greenhouse experiment

Because performance trends in the field could not be singly related to precipitation patterns, but could also reflect local adaptation to other factors, we followed the field experiment with a greenhouse experiment to directly test drought tolerance across the focal populations. In this experiment, drought tolerance is defined as similar performance (quantified via several metrics, detailed below) in drought-stressed seedlings compared to control seedlings. Seeds used for the greenhouse experiment were collected at the same time as those used in the field experiment. Seeds were germinated in the greenhouse by sowing them in germination trays filled with nursery mix covered with a thin layer of sphagnum moss to ensure that the tiny seeds did not fall into cracks in the soil. Germination trays were placed within shade cages and watered daily from January to June 2016 until no more seedlings emerged. Seedlings at the 2-leaf stage were transplanted into 1-gallon pots (4.4 L) filled with equal parts of Promix BX (65%–75% Canadian sphagnum peat moss, perlite, dolomitic and calcitic limestone, macro- and micronutrients and *Glomus intraradices* mycorrhizae inoculum) and black cinder and treated with a single application of slow-release fertilizer (Osmocote[®]). Although seeds from all 27 populations were sown, there was considerable variation among populations in the rates of germination in both the total number and the timing. As a result, sample sizes ranged from 10 to 75 seedlings per population, and seedlings germinating at the same time were grouped together into temporal blocks (eight blocks total).

Following germination, all seedlings were watered daily to 100% field capacity, determined as excess water dripping from the pots. After 4 weeks, half of the seedlings within each population were randomly assigned to a press drought treatment ('drought' plants hereafter) in which pots were watered three times a week at 80% field capacity (80% FC). To determine how much water to apply to the drought plants, 20 pots were randomly selected and weighed; the mean of this pot mass was used to calculate the water content gravimetrically as a percentage of the control pots at 100% FC, and

then the amount of water needed to bring those pots to 80% FC was calculated and applied to each drought pot by hand (Sack, 2004). Plants in the control treatment group were watered to 100% FC every other day.

The press drought treatment was applied for 6 weeks, at which time, half of the plants in both the control and drought groups were harvested. Shoot height was measured to the apical meristem, and shoots were clipped and dried to constant weight in a drying oven. Roots were extracted from the soil, washed of debris and dried to constant weight as well. Dried root and shoot tissues were weighed to 0.01 mg using an analytical balance. At the same time as half the plants were harvested, the remaining seedlings in the control and drought treatments were subjected to a terminal pulse drought during which time, seedlings received no water until they died. Seedlings in terminal drought were examined daily, and when they died, the date was recorded, and the pot was weighed so that the terminal soil water content could be calculated gravimetrically (as a percentage of 100% FC). Plants were considered dead when the shoot tissues were completely brown, and the stems had lost all elasticity (Engelbrecht & Kursar, 2003). The terminal soil water content represents a threshold of soil water content below which is lethal for these *M. polymorpha* seedlings. The number of days from the start of the terminal pulse drought to seedling mortality is referred to as longevity and represents the number of days without water the seedlings can survive.

Volumetric soil water content (VWC) was measured weekly using a HydroSense II (©Campbell Scientific) to quantify the effects of the press and terminal drought treatments on soil water and to characterize how these effect sizes changed over time. Although soil types vary considerably, the HydroSense manual reports that 'sandy/loam' soils most similar to the media used in this study are considered 'dry' when VWC ranges from 10% to 15%, and 'wet' soils range from 20% to 30%.

Greenhouse data were analysed using R 3.4.3 (R Core Team, 2017). Residuals were examined, and biomass and root/shoot ratio were log-transformed to meet assumptions of normality and homoscedasticity. Effects of experimental drought on seedling performance were assessed using multiple fitness metrics, including mortality, seedling height, total biomass, root/shoot ratio and longevity in terminal drought. The terminal soil water content was analysed to determine the critical threshold in soil water content beyond which populations of *M. polymorpha* seedlings cannot survive.

To characterize how the watering treatments influenced soil water content, soil VWC data were analysed using a mixed-model ANOVA with the main effects of drought and time, with block and ID included as random factors. Due to several instances in which seedlings were not sampled at all weekly censuses (thereby leading to missing data points), a repeated-measures analysis was not appropriate.

To test the effects of press drought on seedling performance, we used GLMMs (Bates et al., 2015) in which drought (control vs. 80FC) was treated as a fixed factor, and population, temporal block and the interaction between drought \times population were treated as random

factors. Mortality was analysed as a binary response variable modelled with a binomial error distribution, and the other fitness metrics were modelled as normally distributed.

Significance of fixed effects for normally distributed responses were tested with approximate *F*-tests (Kuznetsova, Brockhoff, & Christensen, 2017), and random effects as well as fixed effects for non-normal responses were tested with chi-squared likelihood ratio tests. Significant effects of drought in which control plants are significantly larger than drought-stressed plants will reveal low drought tolerance of seedlings. A null effect of drought would indicate similar growth of stressed and control plants, reflecting full tolerance. A significant interaction between population and drought stress would indicate significant variation among populations in their drought tolerance. If the drought treatment (and population \times drought) significantly influences the root/shoot ratio, this reflects a response of drought-stressed plants in allocation of growth below- versus above-ground. A greater root/shoot ratio in drought-stressed plants is generally interpreted as adaptive plasticity as it reflects greater allocation tissues that can capture the limited resource (Lloret, Casanovas, & Penuelas, 1999).

To assess whether significant variation among populations was linked to climate, additional models were analysed that included MAR and MET to test whether historical patterns of climate predict seedling responses to simulated drought. Full models included drought as a fixed factor, scaled MAR or MET, an interaction between MAR or MET and drought and a random intercept and random treatment effect of drought that vary by population.

3 | RESULTS

3.1 | Reciprocal transplant experiment

Germination rates were low, as is typical for *M. polymorpha* (Burton, 1982; Drake, 1993), and varied considerably among sites, ranging from 0% to 14% (Figure S1). Although some sites had no detected germination, seeds from all populations germinated in at least one site, confirming that viable seeds were sown.

Accounting for random variation among sites and populations, germination as a binary response (i.e. whether any germination occurred at that site for a population) did not differ between home versus away sites ($\chi_1^2 = 0.091$, $p = .7625$). When excluding sites without any germination, germination rates tended to be higher in home versus away sites (Figure S2), although this was not statistically significant ($\chi_1^2 = 1.992$, $p = .1582$). The number of seedlings at the end of the experimental period (% establishment) was similar in home versus away sites ($\chi_1^2 = 0.038$, $p = .8459$; Figure S2).

The analyses incorporating historical and current precipitation revealed that the incidence of germination (binary response $\chi_1^2 = 3.959$, $p = .0466$) and marginally, the germination rate ($\chi_1^2 = 3.757$, $p = .0526$) responded to precipitation during the experimental period. However, in contrast to our predictions, the number of germinants was generally

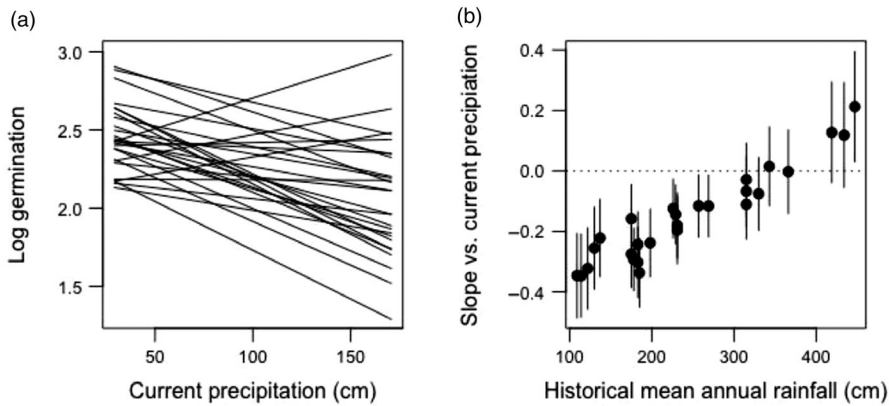


FIGURE 3 (a) Slopes of the response of germination (abundance) to experimental year (2015) precipitation varies among the 27 populations. (b) Historical mean annual rainfall for the population sites predicts the response in germination to current precipitation. Points are posterior means and error bars are ± 1 posterior SD

lower at high rainfall sites (Figure 3a). Most importantly, there was a significant interaction between historical and current precipitation for germination rate ($\chi_1^2 = 4.462$, $p = .0347$), revealing that the historical rainfall of a population predicts its germination response to current precipitation. As predicted, the slope of germination on current precipitation responded positively to an increase in historical rainfall, with populations from wetter sites having a stronger positive response to current precipitation (Figure 3b). By the end of the experiment, there was no detectable effect of current precipitation ($\chi_1^2 = 0.0634$, $p = .8011$), or an interaction between historical and current precipitation ($\chi_1^2 = 0.7455$, $p = .3879$) on the number of seedlings surviving. There was no interaction between historical and current precipitation for germination as a binary response ($\chi_1^2 = 0.4892$, $p = .4843$). Mean annual evapotranspiration did not predict the slopes of germination (binary: $\chi_1^2 = 0.0003$, $p = .9863$; germination abundance: $\chi_1^2 = 0.0050$, $p = .9435$) or seedling establishment ($\chi_1^2 = 2.983$, $p = .0842$) on current precipitation.

3.2 | Greenhouse experiment

Mortality rates in the greenhouse experiment were quite high, ranging among populations from 22% to 80% for seedlings in control water treatment (watered to 100% field capacity gravimetric water content daily), and from 27% to 75% for seedlings exposed to the 4-week press drought (watered to 80% field capacity gravimetric water content two times per week), with significantly higher rates overall for seedlings in drought ($\chi_1^2 = 16.814$, $p < .0001$). Mortality also varied significantly among populations ($\chi_1^2 = 5.143$, $p = .0233$), but populations did not vary in the effects of press drought on mortality ($\chi_2^2 = 1.05$, $p = .5916$).

Volumetric soil water content differed significantly between drought and control pots ($F_{1,3,557} = 51.37$, $p < .0001$), and the magnitude of this effect shifted over time (Figure 4), leading to a significant interaction between drought and time ($F_{20,4,032} = 63.28$, $p < .0001$). As expected, VWC was similar for drought and control pots during the first 4 weeks when both groups were watered daily, then differed considerably during the press drought treatment. Within a couple weeks of the terminal drought initiation, VWC was similar for pots in the control and press drought treatment groups (Figure 4).

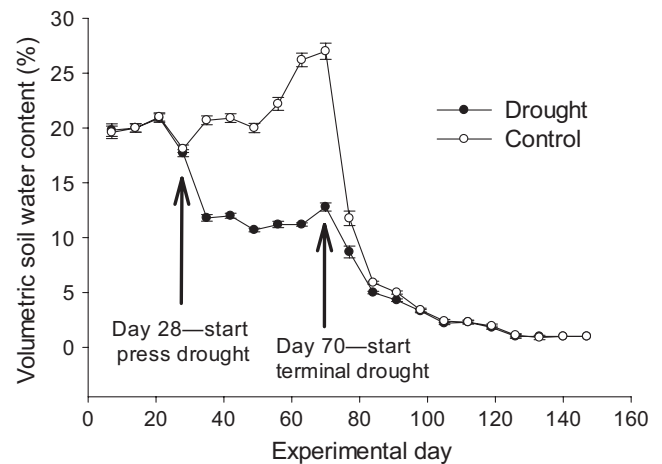


FIGURE 4 Trends in volumetric soil water content (%) during the experimental period. At Day 28, the 80% FC press drought was initiated. At Day 70, half of all plants were harvested, and the remaining (in both control and drought treatment groups) received no more water. The last day for seedling mortality under the terminal drought was at Day 147 (with 1 seedling in each group), representing 11 weeks with no water. According to the HydroSense II manual, VWC measured in control pots were consistent with or exceeded the 'wet' classification for sandy/loam soils (20%–30%), and the press drought reduced the VWC to levels consistent with the 'dry' classification (10%–15%). The terminal drought treatment dropped VWC well below the 'dry' classification, and many seedlings were able to persist below 3%–5%

Seedlings that survived the press drought treatment were able to grow at comparable rates to those in the control group, leading to no effect of drought on height, total biomass or root/shoot ratio (Table 1; Figure S3). Populations varied significantly for all growth metrics, and there was significant variation among populations in how drought influenced the root/shoot ratio (significant interaction, Table 1).

During terminal drought, seedlings that had previously been exposed to the 6-week press drought had a marginally significantly lower soil water content at the time of mortality ('terminal gravimetric soil water content': $48.8 \pm 1.1 M \pm 1 SE$) than seedlings from the control group (51.8 ± 1.1), suggesting that the 80% press drought pre-acclimated seedlings to the terminal pulse drought, or that

TABLE 1 Summary of results from the mixed-model ANOVAs for the greenhouse experiment. Seedling performance was measured as seedling final height (cm), total biomass (g), root/shoot ratio (unitless), % mortality during the 4-week press drought, number of days (longevity) until mortality in the terminal pulse drought (TD) and the final soil water content at mortality in the terminal pulse drought (terminal SWC). *F*-tests are reported for fixed (*F*) factors (degrees of freedom num, den), and log-likelihood ratio statistics compared to a chi-squared distribution (*df*) are reported for random factors obtained by running the models with and without the random factor of interest

Seedling performance	Drought treatment (<i>F</i>)	Population (<i>R</i>)	Block (<i>R</i>)	Population × Drought (<i>R</i>)
Height (cm)	0.32 _(1,12.2)	5.08 ₍₁₎ *	1.50 ₍₁₎	0.0 ₍₂₎
Total biomass (g)	0.01 _(1,74.9)	9.03 ₍₁₎ **	4.56 ₍₁₎ *	0.41 ₍₂₎
Root/shoot ratio	0.52 _(1,11.5)	0.05 ₍₁₎	3.75 ₍₁₎ +	16.70 ₍₂₎ ***
% Mortality	16.81 ₍₁₎ ***	5.14 ₍₁₎ *	6.19 ₍₃₎	1.05 ₍₂₎
Longevity in TD	0.10 _(1,6.6)	27.69 ₍₁₎ ***	1.34 ₍₁₎	0.84 ₍₂₎
Terminal SWC	2.96 _(1,24.5) †	26.37 ₍₁₎ **	6.60 ₍₁₎ *	2.41 ₍₂₎

Significance is given as *** $p < .0001$; ** $p < .01$; * $p < .05$; † $p < .10$.

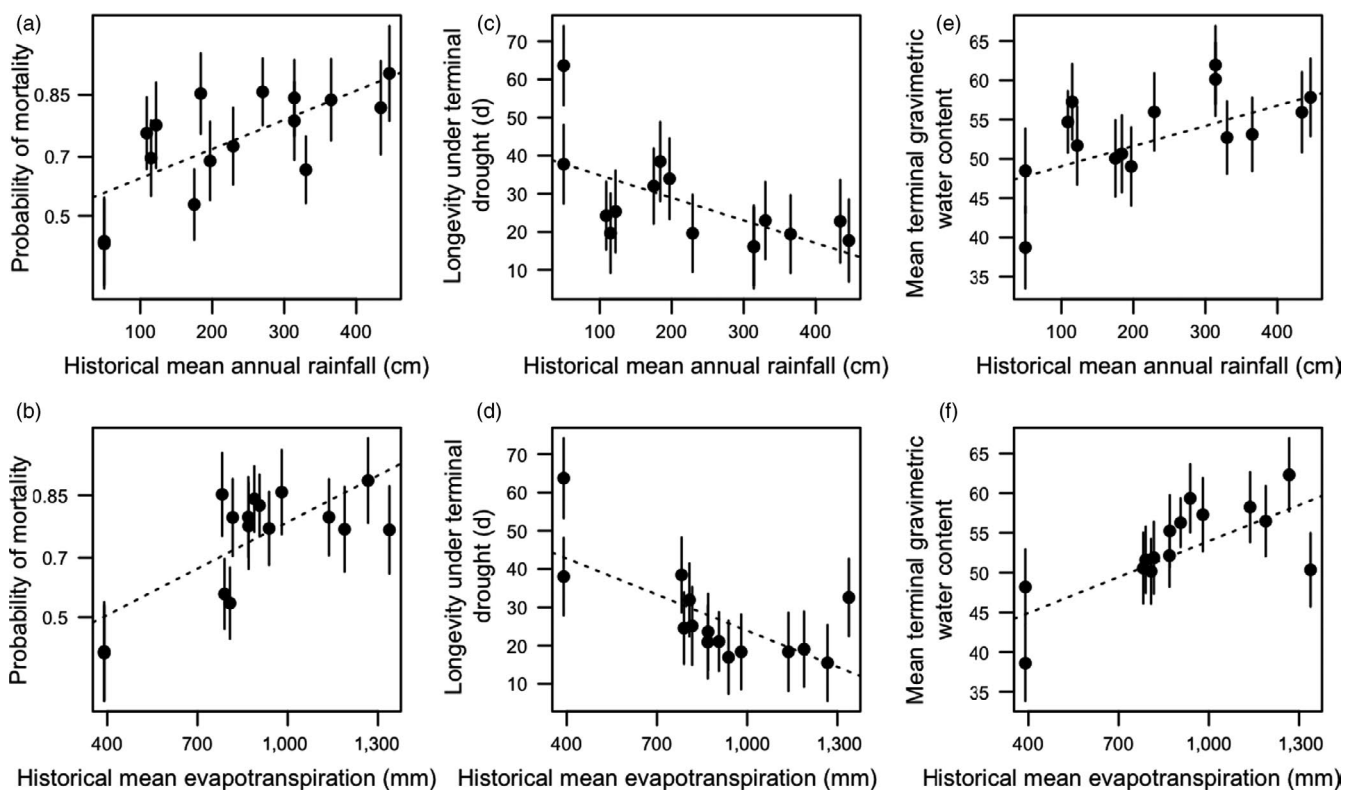


FIGURE 5 Relationship between historical climate (mean annual rainfall, a, c, e, and mean annual evapotranspiration b, d, f; Giambelluca et al., 2013) and seedling responses (probability of mortality: a, b; longevity under terminal drought: c, d; mean terminal gravimetric water content: e, f) to simulated drought in the greenhouse experiment. Dots are population means \pm 95% confidence intervals

seedlings surviving the press drought to reach the terminal drought treatment were highly drought tolerant (Table 1). Effects of the terminal drought on seedling longevity and terminal soil water content were highly variable among populations (Table 1).

Because populations varied significantly for all variables examined (Table 1), we predicted that climate (MAR and MET) may have played a role via local adaptation. Because initial analyses revealed no significant interactions between press drought and MAR or MET, we removed this interaction from the models, testing main effects of MAR and MET in models that also include population and block as random

variables. We found that % mortality during press drought was higher for populations from historically wet sites ($\chi^2 = 12.25$, $p = .0005$) and that seedlings from historically dry sites survived longer ($F_{1,9.4} = 7.11$, $p = .0249$) and persisted to a lower soil gravimetric water content ($F_{1,9} = 6.49$, $p = .0312$) in the terminal drought before dying compared to seedlings from historically wet sites (Figure 5). Similar trends were detected for MET (Table S2, Figure 5). We detected no significant relationships between MAR or MET with final seedling height, total biomass, root/shoot ratio or plasticity in root/shoot ratio (Table S2). These results corroborate patterns detected in the field experiment.

4 | DISCUSSION

Although local adaptation to climate has been well-documented in temperate and boreal trees, few such studies have focused on tropical trees (Alberto et al., 2013). Considering the pervasive threat of increasing drought (Corlett, 2016; IPCC, 2014), it is critical that intraspecific variation in tropical tree drought tolerance be examined in order to predict which populations will be most vulnerable to climate change, particularly for foundation species. Using a full-factorial reciprocal transplant experiment and a complementary simulated drought experiment, we demonstrated that climate predicts population responses for the tropical foundation tree, *M. polymorpha*, consistent with local adaptation to water availability. This two-part experimental approach provides compelling evidence for intraspecific variation in seedling drought tolerance of this island endemic. Although we did not detect greater germination and establishment in home versus away sites, this is likely because many sites had similar rainfall during the experimental period and because variation across sites in current rainfall did not coincide with the historical rainfall patterns. Germination and seedling establishment are thus linked more to rainfall, as detected using the GLMM analyses, than whether populations are at their home site. Specifically, populations from historically wet sites demonstrated lower germination rates in currently dry field sites, survived fewer days without water and succumbed at wetter soil conditions than populations from historically dry sites. While climate change models project the greatest drying trends for historically dry areas in Hawaii (Timm & Diaz, 2009), even moderate drying of wet sites under climate change could significantly reduce *M. polymorpha* recruitment given the sensitivity of seedlings to very slight changes in water regimes, as has been found in other species (Choat et al., 2012).

Surprisingly, most populations examined showed a negative germination response to increasing rainfall during the field experimental period, with the exception of the historically wettest populations which showed a strong increase in germination with greater rainfall. This result suggests that *M. polymorpha* seedlings are generally quite drought tolerant, and are even suppressed under very wet conditions, perhaps due to greater pathogen or herbivore abundances in wet sites (Baltzer & Davies, 2012; Comita & Engelbrecht, 2014). Low establishment in wet sites could imply that there is a trade-off underlying local adaptation such that higher drought tolerance increases susceptibility to whatever factor is reducing establishment in wet sites, or simply that tolerance to different and likely multiple sources of stress has evolved in historically wet versus dry sites. Multiple stressors (biotic and abiotic) often have non-additive effects on plant performance (Baltzer & Davies, 2012; Markesteijn, Poorter, Bongers, Paz, & Sack, 2011; Pellissier et al., 2013; Sthultz, Gehring, & Whitham, 2009; Uriarte, Muscarella, & Zimmerman, 2018), and untangling the complexity of naturally co-occurring stressors is challenging but fruitful for precisely predicting how plant populations will respond to climate change. Alternatively, low germination in wet sites could result from physical conditions associated with high

rainfall, such as burying or washing seeds away from the experimental plots. However, seeds were placed within cushion moss at all sites, and so it is unlikely that physical disturbance contributed to germination in some sites more than others.

Like other island species, *M. polymorpha* faces many threats in addition to climate change, including invasive plant competition, mortality from invasive pathogens and herbivores and habitat loss (Caujape-Castells et al., 2010). Reduced recruitment under elevated drought stress with climate change could lead to the eventual loss of this foundation species as standing trees die without replacement. Although such cohort dynamics have characterized *M. polymorpha* during primary succession on Hawaii Island (Mueller-Dombois & Boehmer, 2013), it remains unclear how current threats may alter population dynamics. While light competition from invasive plants have been shown to limit *M. polymorpha* recruitment (Funk & McDaniel, 2010; McDaniel & Ostertag, 2010), this is the first demonstration of drought effects on seedling performance. Future work simultaneously testing drought, light and also natural enemy pressure are needed to elucidate how *M. polymorpha* seedlings perform under multiple threats as their combined effects may be non-additive and complex.

The greenhouse drought experiment provides mixed evidence that *M. polymorpha* seedlings are drought tolerant. Although drought increased seedling mortality, suggesting weak drought tolerance, the surviving seedlings had similar total biomass and height as control seedlings, indicating that those seedlings expressing drought tolerance via survival are vigorous enough to maintain growth at comparable rates as control seedlings. These results highlight the value of considering multiple fitness metrics when characterizing stress tolerance. The ability of seedlings surviving pulse droughts to grow at comparable rates as well-watered plants could become irrelevant if mortality rates continue to be high, or even higher, under increasingly frequent and severe droughts. The recruitment of *M. polymorpha* onto young lava substrate with almost no soil on Hawaii Island supports the conclusion that *M. polymorpha* seedlings are able to tolerate very low soil water availability (Lohse, Nullet, & Vitousek, 1995). Seedlings also demonstrated adaptive plasticity through an increase in root/shoot ratio under simulated drought, although this response was found to vary across populations irrespective of historical MAR. Additional experimentation is needed to better understand population variability in phenotypic plasticity and the role this plays during early ontogenetic stages.

Given the small seed size of *M. polymorpha* (Drake, 1993), we might have predicted it to have low drought tolerance due to limited rooting potential. In general, small seed size is often associated with limited stress tolerance (Moles & Westoby, 2004), although previous research has revealed greater suppression of growth by drought for large- than small-seeded species consistent with high drought tolerance in small-seeded species (O'Brien, Philipson, Tay, & Hector, 2013). In general, seedling drought tolerance is linked to stored nonstructural carbohydrates (O'Brien, Leuzinger, Philipson, Tay, & Hector, 2014; O'Brien et al., 2013), low leaf turgor loss point (Kursar et al., 2009), stomatal regulation and high tissue density (Poorter & Markesteijn, 2008). Mature *M. polymorpha* trees express traits

consistent with drought tolerance, having high water use efficiency (Cavaleri, Ostertag, Cordell, & Sack, 2014; Kagawa et al., 2009), resistance to embolisms in dry sites (Cornwell, Bhaskar, Sack, Cordell, & Lurch, 2007; Fisher, Goldstein, Jones, & Cordell, 2007) and highly variable pubescence, gas exchange rates and wood density among sympatric populations (Cordell, Goldstein, Mueller-Dombois, Webb, & Vitousek, 1998; DeBoer & Stacy, 2013; Hoof, Sack, Webb, & Nilsen, 2008; Sur et al., 2018; Tsujii, Onoda, Izuno, Isagi, & Kitayama, 2016). In the single study to examine physiological responses of *M. polymorpha* seedlings to drought, continued performance under drought was linked to the maintenance of stomatal conductance, high chlorophyll content and high C/N ratios (Westerband et al., 2019). Whether these underlying seedling drought tolerance traits vary across *M. polymorpha* populations remains to be tested.

In addition to shifts in species distributions, climate change can reduce genetic diversity through the elimination of maladapted alleles and bottlenecks associated with range contractions (Lima, Ballesteros-Mejia, Lima-Ribeiro, & Collevatti, 2017). For *M. polymorpha*, long-range dispersal of the minute seeds could potentially maintain the current distribution under climate change through the replacement of vulnerable genotypes by more drought-tolerant genotypes. Essentially, this would represent an expansion in population size of the drought-tolerant populations with the simultaneous extirpation of drought-vulnerable populations. As a foundation tree, *M. polymorpha* provides critical habitat to associated plants, fungi, insects, snails and birds (Gotsch et al., 2014; Gruner et al., 2005; Kagawa et al., 2009; O'Rorke et al., 2015; Percy, 2017; Santiago, 2000). These complex community interactions vary across the distribution of *M. polymorpha* (Mueller-Dombois, Jacobi, Boehmer, & Price, 2013), and the loss of vulnerable populations could have important cascading effects, leading to the loss of associated organisms and reducing overall diversity. Thus, at the species level, *M. polymorpha* will likely be robust to climate change, given its climatically broad range, intraspecific variation in drought tolerance and high dispersal. But nonetheless local populations may suffer, at least before new genotypes show up, which could have ecosystem-wide effects.

More studies are needed to characterize intraspecific variation in climate stress tolerance of tropical species. The critical roles that tropical plants play in the global carbon and water dynamics emphasize the need to refine our predictions for species distribution shifts under climate change. Moreover, it will be important to consider life stage explicitly. While some authors have found stronger climate stress effects on older trees underlying species distributions (Esquivel-Muelbert et al., 2017), we and others have found seedling drought tolerance to be important (Fortunel et al., 2016; Kursar et al., 2009). Considering the dramatic shifts in ecophysiology across whole-plant ontogeny (Carlson, Adams, & Holsinger, 2016; Mason, McGaughey, & Donovan, 2013), it is not surprising that life stage contributes to variation in stress tolerance. Consideration of additional key factors such as life history strategy, reproductive status, germination type and biomass allocation patterns may also contribute to a better understanding of intraspecific variation in climate stress tolerance, leading to more precise and robust species distribution models and conservation plans.

5 | CONCLUSIONS

We have shown that despite small seeds with long-distance dispersal, *M. polymorpha* harbours significant intraspecific variation in drought tolerance consistent with local adaptation to historical climatic trends. Although previous research has demonstrated strong clinal variation in temperate and boreal tree species (Alberto et al., 2013), there are relatively few studies to test for clinal variation in tropical trees. While there is widespread evidence that plant populations are locally adapted (Leimu & Fischer, 2008), it has been difficult to identify factors that constrain local adaptation. Although breeding system (i.e. clonal vs. sexual reproduction), dispersal distance and phylogeny have all been examined, only population size has repeatedly been linked with the likelihood of local adaptation, with local adaptation more likely for larger population sizes (Leimu & Fischer, 2008; Leimu, Mutikainen, Koricheva, & Fischer, 2006). Thus, the fact that few examples of clinal variation in trees comes from the tropics likely reflects a bias in research site and not the absence of such intraspecific variation in the tropics. For widespread foundation species driving community interactions and ecosystem dynamics, it is likely that clinal variation similar to that described here is common and will be important for predicting which populations and species are most vulnerable to climate change.

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AUTHORSHIP

K.E.B., A.B.S. and T.K. developed the conceptual framework; K.E.B. and C.J. collected the data; K.E.B. and K.F.E. analysed data; K.E.B. was the primary writer of the manuscript; K.F.E., A.B.S. and T.K. provided feedback and contributed to the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n5tb2rbrz> (Barton, Jones, Edwards, Shiels, & Knight, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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