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RESEARCH ARTICLE

Evolutionary history constrains heat tolerance of native and exotic tropical Zingiberales

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Abstract

1. Tropical wet forest plants experience relatively stable temperatures throughout the year. However, tropical forests represent a mosaic of habitats characterized by different temperatures. Heat tolerances are expected to be adapted to temperatures specific to their habitats. Although heat tolerance of species sharing similar environments is expected to be similar, it is also possible that heat tolerance is constrained by evolutionary history because closely related species usually display similar physiologies. When exotic species are introduced to novel communities, colonization may be facilitated by their previous adaptation to high temperatures and other physiological, genetic and demographic traits, which may grant them some competitive advantage. Increasing temperatures may represent a strong environmental filter affecting community assembly, and higher heat tolerances could facilitate the persistence of exotic species in novel environments.
2. Using a community of 32 native and 7 exotic Zingiberales species from different tropical habitats in Costa Rica, Central America, we aim to answer the following questions: (a) does evolutionary history constrain heat tolerance? (b) do plants in the same habitat display similar heat tolerances? (c) do the heat tolerances of exotic species differ from those of native species?
3. We measured temperature-dependent changes in photosynthetic fluorescence to determine the temperature at which the first sign of damage to photosystem II is observed (T_{15}), and the temperature at which the fluorescence of photosystem II is reduced by 50% (T_{50}). Using a community phylogeny, we tested for phylogenetic signal in T_{15} and T_{50}. In addition, we tested for differences in heat tolerance among Zingiberales from old growth, secondary forests and open areas, as well as between native and exotic species.

4. Our results support (a) a significant phylogenetic signal (Pagel's λ) for both T_{15} and T_{50}, (b) communities from open areas displayed similar photosynthetic heat tolerance compared to species from old growth and secondary forests, and (c) exotic Zingiberales are marginally tolerant to high temperatures than native species, but only for T_{15}. Our results suggest that evolutionary history constraints heat responses of native and exotic Zingiberales in a warming world.

KEYWORDS
chlorophyll fluorescence, climate change, global warming, heat tolerance, phylogenetic signal, temperature, thermal tolerance, tropical plants

1 | INTRODUCTION

Tropical lowland rainforests are the most speciose terrestrial ecosystems in the world and among the most vulnerable to climate change (Corlett, 2011; IPCC, 2021). Recent evidence suggests that in some tropical regions, carbon assimilation (Doughty & Goulden, 2008; Mau et al., 2018; Slot & Winter, 2018) and maximum photosynthetic quantum yield (Sastry et al., 2018; Slot et al., 2019, 2021; Tiwari et al., 2020) are already operating at or above their thermal thresholds. Theory suggests tropical lowland species, which are expected to be adapted to year-round stable environmental temperatures, may be particularly vulnerable to warming because of their limited capacity to acclimate (Cunningham & Read, 2002; Janzen, 1967), for example in terms of essential metabolic processes such as photosynthesis (Krause et al., 2010). Although species from tropical ecosystems are expected to be more vulnerable to climate change than species from high latitudes, there is little information regarding variation in species vulnerability within communities (Feeley et al., 2020). Determining how heat tolerance varies among plant communities in multiple habitats is essential to understand the vulnerability of plants to anthropogenic climate warming (Reyer et al., 2013).

Although plant thermotolerance is influenced by recent environmental conditions (Havaux, 1993; Havaux et al., 1991; Sastry & Barua, 2017), the role of phylogenetic conservatism in shaping plant thermal tolerances is seldom understood (Sastry & Barua, 2017). Phylogenetic conservatism of upper temperature limits is suggested to be similar among closely related terrestrial animals (Araújo et al., 2013). A recent study exploring macroecological patterns of thermal tolerance in plants showed that phylogeny, geography and local environment explain to some degree global variation in plant heat tolerance (Lancaster & Humphreys, 2020). However, in this global study, heat tolerance is better explained by geographical distance, likely reflecting the effect of colonization history, or maybe the effects of gene flow (Lancaster & Humphreys, 2020).

Previous studies suggest that the variation in heat tolerance among desert plants is associated with transpiration rates and water availability in different habitats (Curtis et al., 2016; Downton et al., 1984). Tropical forests exhibit considerable variation in thermal habitats. For example, plants growing along forest edges or gaps may experience much higher temperatures than those in shaded forests (Denslow, 1980; Fetcher et al., 1985; Nowakowski et al., 2017; Scheffers et al., 2014; Zellweger et al., 2020). Leaves exposed to full sunlight experience temperatures that can reach up to 40–45°C, resulting in a temperature range four times broader than those experienced by shaded leaves (GGH, personal observation; Krause et al., 2010; Pincebourde & Suppo, 2016). Higher heat tolerance of leaves exposed to direct sunlight compared to leaves in the shade was documented in two tree species (Slot et al., 2019). Many species are known to be specialized in forest gaps and other early successional habitats (Denslow, 1987; Rundel et al., 1998). The colonization success of such species may be influenced by their ability to tolerate higher temperatures.

Some evidence suggests that high heat tolerance promotes the geographical range expansion of invasive exotic species (French et al., 2017; Song et al., 2010). High stress tolerance contributes to the fact that exotic plants tolerate a wider range of temperatures along latitudinal gradients than native species (Dukes & Mooney, 1999). If this is true, such traits may confer some competitive advantage to exotic over native plants when invading new environments (Dukes & Mooney, 1999; Liu et al., 2017; Zhu et al., 2018). During extreme heat waves, invasive shrubs in Australia and China cope better with high temperatures relative to native shrubs (French et al., 2017; Song et al., 2010). This advantage becomes evident when invasive species can survive, or even grow at high temperatures, but the performance of native species is greatly reduced (French et al., 2017). Therefore, exotic species already adapted to withstand higher temperatures than native species have the potential to colonize niches previously occupied by native species (French et al., 2017; Song et al., 2010).

Many exotic herbaceous ornamental plants seem to be preadapted to disturbed habitats, which facilitates the colonization of early succession in tropical ecosystems (Binggeli, 2003; Clark et al., 2015; Svenning, 2002). The ornamental plant industry and botanical gardens frequently introduce plants to regions that match their temperature tolerance or to regions that will soon match their temperature tolerance due to climate warming (Dukes & Mooney, 1999). Some species in the order Zingiberales, which includes the bananas and gingers, are known to be invasive in tropical and subtropical forests in Hawaii, Brazil, Perú and South Africa

(Anderson & Gardner, 1999; Chiba de Castro et al., 2016; Denslow & DeWalt, 2008; Foxcroft et al., 2008; Ochoa & Andrade, 2003; Zenni & Ziller, 2011). At least four exotic Zingiberales have been introduced to the lowland Caribbean forests of Costa Rica as ornamentals (*H. coronarium*, *H. psittacorum*, *M.* velutina and *Z. spectabile*). Previous research on Zingiberales communities at La Selva demonstrated that native and exotic species are adapted to particular habitats with contrasting temperature and light regimes (Andersson, 1998a; Berry & Kress, 1991; Hammel et al., 2004; Horvitz, 1991; Horvitz & Le Corff, 1993; Rundel et al., 1998; Sun, 2011). This diversity in habi-tat use by a monophyletic group represents a unique opportunity to test potential associations between species' heat tolerance and temperatures in their habitats.

In this study, we measured heat tolerance of 39 species within six families of Zingiberales (32 native and 7 exotic). Using a phylogenetic framework, we tested which evolutionary and ecological factors affect photosynthetic heat tolerance among species present in contrasting habitats. This study focuses on the following questions: (a) Is heat tolerance constrained by evolutionary history? (b) Does heat tolerance vary among Zingiberales species from old growth, secondary forest and open areas? (c) Does heat tolerance of Zingiberales differ between native and exotic species? By determining patterns of heat tolerance in a monophyletic group of sympatric plants, this study aims to provide a better understanding of the effects of local plant habitat, shared evolutionary history and geographical origin on plant responses to global warming.

2 | MATERIALS AND METHODS

2.1 | Study site and study organisms

We conducted this research at La Selva Biological Station (hereafter La Selva), a tropical wet forest located in the Caribbean lowlands of Costa Rica (84°01′W, 10°43′N, 50 m a.s.l.). This area is characterized by mean and maximum annual temperatures of 23.9 and 31.6°C, respectively (Clark et al., 2015; McClearn et al., 2016). La Selva comprises a mosaic of different habitats displaying contrasting temperatures. Our study sites spanned three habitats: old growth forests, secondary forests (~19–37 years) and open areas (Table S2; Hammel et al., 2004; McDade et al., 1994; Taylor et al., 2019). The habitat categorized as 'open areas' includes recently abandoned pastures, gardens adjacent to the field station and any open area between the station buildings.

Old growth and secondary forests display similar average, minimum and maximum daily temperatures (Table 1). The mean daily temperature in open areas is 2°C higher than in old growth and secondary forests (Table 1). The maximum daily temperature in open areas can reach 8–10°C beyond maximum daily temperatures in the understorey (Table 1, Figure S1, *see* methods to estimate environmental temperatures in Supplement S1). Habitats also display differences in the percent of the canopy covered by leaves. The overstorey density in open areas, secondary forest and old growth forest range from 25.48%, 86.74% to 91.16%, respectively (*see* methods to estimate overstorey density in Supplement S2, Table S1).

TABLE 1 Air temperature of three habitats at la Selva Biological Station, Costa Rica. T_{MIN} is the mean daily minimum temperature, T_{MAX} is the mean daily maximum temperature and MT is the mean daily temperature. Mean temperature is followed by the standard deviation in parenthesis. Number of samples per habitat = 10. *See* methods to estimate air temperature in supplement S1

Habitat	T_{MIN} (°C)	MT (°C)	T_{MAX} (°C)
Open areas	22.08 (1.38)	26.19 (1.54)	38.15 (8.69)
Secondary forest	22.26 (1.21)	24.35 (0.65)	27.98 (1.97)
Old growth forest	22.40 (1.21)	24.67 (0.82)	30.08 (3.45)

We included in this study species from the following Zingiberales families: Musaceae, Heliconiaceae, Zingiberaceae, Costaceae, Cannaceae and Marantaceae (Figure 1, Table S2). The family Musaceae is native to Asia, Australia, the western Pacific and Africa (Andersson, 1998b). In our study site, *Musa velutina* was introduced from India and is currently naturalized in secondary forests (García-Robledo et al., 2017). The family Heliconiaceae is mostly from tropical America (Kress, 1984). At La Selva, in addition to eight native *Heliconia* species, one exotic species from northern South America, *H. psittacorum* is present in open areas (Table S2; García-Robledo et al., 2017). The family Zingiberaceae is pantropical, ranging from tropical Africa to Asia, and America (Kress, 1990). Three native and five exotic tropical Zingiberaceae species are present in secondary forests and open areas (Figure 1). The family Marantaceae is pantropical, with its highest diversity in America and Asia, and with few species in Africa (Andersson, 1998a). At La Selva, 21 native species of Marantaceae are present (Hammel et al., 2004). The pantropical family Costaceae is represented at La Selva by five species in the genus *Costus* (Larsen, 1998). The tropical America family Cannaceae is represented at La Selva by a single native species, *Canna tuerckheimii* (Table S2; Kubitzki, 1998). We refer to species 'origin' to indicate whether a species naturally occurs at La Selva (native) or was introduced from another location (exotic). Sistema Nacional de Áreas de Conservación granted us permission to conduct research in Costa Rica (SINAC-SE-CUS-PI-R-0141-2016 to SINAC-ACC-PI-R-047-2018, SINAC-ACC-PI-R-044-2019).

2.2 | Photosynthetic heat tolerance of Zingiberales species

To determine the heat tolerance of each plant species, we collected two to five undamaged, fully expanded mature leaves per individual. Leaves were collected from 7:00 AM to 10:00 AM, from June 17 to July 23 of 2017. Four extra individuals of *E. elatior* and *H. psittacorum* were collected on July 23 ad 24 of 2018. Leaves collected from open areas were previously exposed to full sun,

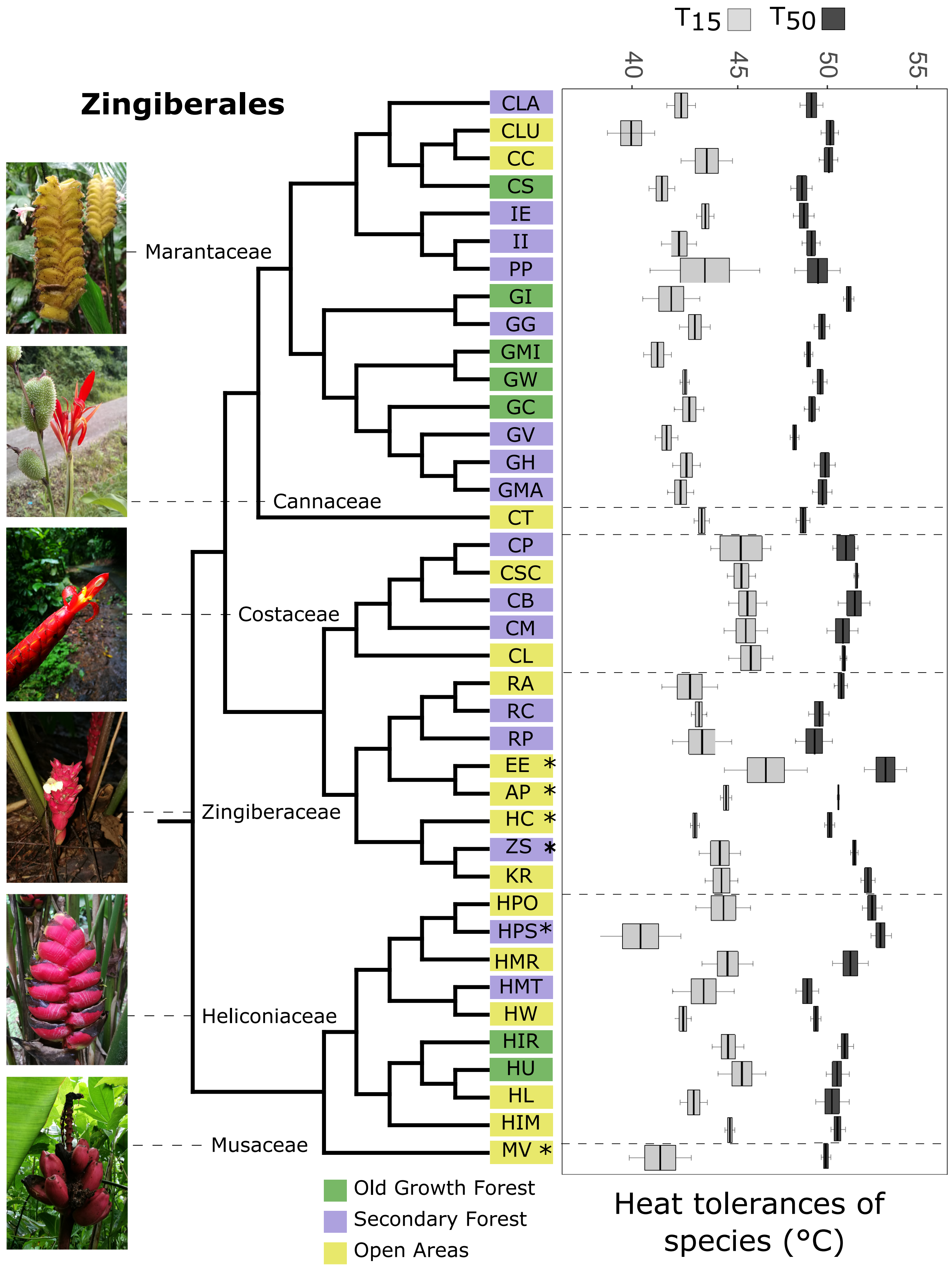
T15
T50
40
45
50
55
Zingiberales
Marantaceae
Cannaceae
Costaceae
Zingiberaceae
Heliconiaceae
Musaceae
CLA
CLU
CC
CS
IE
II
PP
GI
GG
GMI
GW
GC
GV
GH
GMA
CT
CP
CSC
CB
CM
CL
RA
RC
RP
EE *
AP *
HC *
ZS *
KR
HPO
HPS*
HMR
HMT
HW
HIR
HU
HL
HIM
MV *
Old Growth Forest
Secondary Forest
Open Areas
Heat tolerances of species (°C)

FIGURE 1 Heat tolerance (critical temperature, T_{15} and temperature at which fluorescence decreases 50%, T_{50}) in 39 Zingiberales at La Selva Biological Station, Costa Rica. Error bars indicate standard deviation, boxes indicate standard error and the central line represents the average for each species. Box colours indicate habitat use for each species: Old growth forest (OGF), secondary forest (SF) and open areas (OA). Asterisks indicate exotic species. Picture of *Canna tuerckheimii* was provided by JM Chaves-Fallas. Species abbreviations as in Table S2.

corresponding to their specific habitat. We cut six leaf disks per treatment of 1.9 cm in diameter, which were assigned to each temperature treatment at random. We used three leaf disks for the few species with small leaves. For all species in each habitat, we collected four to a maximum of six individuals per species, for a total of 198 individuals. The only exception was *Costus pulverulentus* for which only two individuals were sampled (see Table S2 for sample size by species).

To prevent anaerobiosis during the heat tolerance experiments, leaf disks were placed in Miracloth® (EMD Millipore Corp) (Krause et al., 2010). During heat treatments, the Miracloth® blocked some of the artificial light in the laboratory. Leaf disks were subsequently placed inside a waterproof Whirl-Pak® bag (Nasco) and immersed in one of several circulating hot water baths for 15 min (ANOVA Sous Vide Precision Cooker A2.2-120V-US 2014). The water bath has a temperature accuracy of ±0.1°C. The water bath has a temperature accuracy of ±0.1°C. We constantly checked the temperature with an infrared thermometer (accuracy: ±1.5°C). Water baths were programmed to reach the following temperatures: 23°C (representing our control), 38, 42, 44, 46, 48, 50, 52, 54 and 60°C. We removed leaf disks from the water baths and placed them in petri dishes lined with moist paper towels for 24 h. During heat treatments and when the leaves were placed in petri dishes, leaves were kept under dim light. We dark adapted each leaf disk for at least 20 min and then measured F_v/F_m (Model OS-30P; OptiSciences). At the beginning of the experiment, we selected six leaf disks per individual and measure F_v/F_m to confirm leaves had values high enough to be used in the experiment and to avoid stressed leaves.

Photosynthetic heat tolerance was measured using the maximum quantum yield (F_v/F_m) of the photosystem II (PSII). F_v/F_m was calculated as $(F_m - F_o)/F_m$, where F_m and F_o are the maximum and basal fluorescence yield, respectively. The maximum quantum yield is a well-established method for assessing heat tolerance that corresponds to damage to the photosynthetic apparatus and is not prone to error associated with changes in leaf optical properties during stress treatments such as heating (Baker, 2008; Baker & Rosenqvist, 2004; Maxwell & Johnson, 2000). We heated leaf samples to only one temperature each and quantified damage to PSII using F_v/F_m at each temperature. These values were used to calculate the heat tolerance for each of our study species (Table S2).

We modelled the response of F_v/F_m to determine two metrics of heat tolerance: T_{15} and T_{50}. The parameter T_{15} represents the temperature at which damage to PSII can first be detected with F_v/F_m; we calculated this value by finding the temperature where the line representing the slope of the F_v/F_m versus temperature relationship declined 15% from its highest F_v/F_m value. T_{50} was defined as the temperature that causes a 50% reduction in F_v/F_m compared to our control treatment. We calculated each metric of heat tolerance using a logistic decay model: $y = \frac{\theta_a}{1 + e^{-(\theta_b + \theta_c T)}}$, where T is the heat treatment temperature, θ_a is the asymptote of the heat treatment-response variable relationship, θ_b is a constant and θ_c is the decay parameter. Quantifying these two parameters is useful to determine temperatures that cause different levels of damage to PSII. Model parameters were fitted using the 'nls' function in r's 'stats' package (R Core Development Team, 2021). We generated bootstrapped confidence intervals per species for T_{15} and T_{50} by randomly resampling data. We fitted a new model for each individual 100 times.

2.3 | Community phylogenetics and evolutionary history effects on plant heat tolerance

To determine how phylogenetic relationships among species of Zingiberales affect heat tolerance, we assembled a community phylogeny of all 39 Zingiberales species present at La Selva. The topology was inferred from previously published molecular phylogenies by W. J. Kress, and represents the most up-to-date phylogenetic hypothesis for this group of plants (Carlsen et al., 2018; Kress, 1990; Kress et al., 2001; Kress & Specht, 2005, 2006).

2.4 | Phylogenetic signal of heat tolerance

To test for phylogenetic constraints of heat tolerance for the cladogram summarizing all known phylogenetic relationships among Zingiberales at La Selva (Figure 1), we estimated the phylogenetic signal for T_{15} and T_{50} using Pagel's λ (Pagel, 1999). The parameter λ is the result of transformations of the phylogeny, fitting each trait to a Brownian motion model of evolution (Münkemüller et al., 2012; Pagel, 1999).

Pagel's λ values can vary from 0 to 1; values close to 0 indicate an absence of phylogenetic signal, meaning the trait has evolved independent of phylogeny and as a result, traits of close relatives are similar to those of distant relatives (Molina-Venegas & Rodríguez, 2017). Pagel's λ was calculated using the package ' ' (Revell, 2012). We are using Pagel's λ because it is a robust estimate when phylogenies lack branch length and to avoid overestimation of the phylogenetic signal (Molina-Venegas & Rodríguez, 2017). In addition to the community phylogeny of all 39 species at La Selva, we wanted to compare the results of this inferred topology to a molecular tree including a subset of the community (see Supplement S3, Figure S2). We used Blomberg's K on this molecular phylogeny including 27 of the 39 Zingiberales species present at La Selva (see Supplement S3, Figure S2).

2.5 | Differences in heat tolerance among species from different plant families, habitats and origin

To test a potential correlation between our response variables (T_{15} and T_{50}), we performed a Pearson's correlation. To determine differences in heat tolerance among plant families, species within habitats or plants with different origin (native vs exotic), we performed phylogenetic generalized least squares (PGLS) analyses. These analyses test for differences among treatments, with phylogenetic relationships among species incorporated in the error term (Mundry, 2014). We first verified if the dataset met the assumptions of PGLS models. In our model, we included plant family, habitat and origin as independent fixed factors. We included as response variables T_{15} and T_{50}. All analyses were performed using Program R, version 4.0.4 (R Core Development Team, 2021).

In this study, the natural distributions of some families or exotic species are limited to particular habitats. We want to emphasize that this study includes most of the species of Zingiberales in our study area; therefore, it was not possible to implement a more balanced experimental design. We excluded from our analyses all rare species from the different families that we were unable to find more than one or two known individuals in our study site. Because of the unbalanced nature of the study, our analyses focused on the main effects in the larger model, and the specific effects of each factor (habitat, origin and family) on heat tolerance. In addition, we tested independent models (Table S2) excluding experimental levels containing one or no species (i.e. the old growth forest level in the categorical predictor 'habitat', which contains no exotic plants, and the families Cannaceae and Musaceae, which are represented by a single plant species). This is to ensure that our results are not biased by sample sizes of a particular experimental level.

3 | RESULTS

3.1 | Photosynthetic heat tolerance of a community of Zingiberales

We determined T_{15} and T_{50} for all Zingiberales species present at La Selva (Figure 1). Mean of T_{15} for this community was 43.9°C (SD = 1.8), and ranged from 39.9 to 47.4°C. The mean of T_{50} was 50.0°C (SD = 1.1) and ranged from 48.0 to 52.7°C. We detected a positive correlation between T_{15} and T_{50} (Pearson's $r = 0.5$, $p = 0.003$ df = 37; Figure S3).

3.2 | Phylogenetic signal and differences in heat tolerance among plant families, habitat and origin

Comparative phylogenetic analyses using Pagel's λ show that T_{15} and T_{50} have a strong phylogenetic signal. Closely related Zingiberales species have more similar heat tolerance than expected by scaling the phylogeny by a factor in which every species evolves independently (Figure 1, Phylogenetic signal for T_{15}: $\lambda = 0.6$, likelihood = −73.6, $p < 0.01$; T_{50}: $\lambda = 0.9$, likelihood = −54.4, $p < 0.001$). We did not detect differences in T_{15} or T_{50} among Zingiberales families (Table 2, Figure 2). Differences among families were also not detected when performing statistical analyses after removing plant families represented by a single species (Table S3). Each of the models includes all data (Table 2) except for those where we remove a factor, either a family or habitat to the analysis (Table S3). There is no significant difference in T_{15} or T_{50} among communities in each habitat (Table 2, Figure 3). We detected differences in T_{15} between native and exotic Zingiberales (Table 2, Figure 4a). Exotic Zingiberales displayed higher heat tolerance than native species when exposed to increasing temperatures (Table 2, Figure 4a). T_{15} values for exotic species are 44.0 (SD = 2.4) and 43.9 (SD = 1.6) for native species. Native and exotic Zingiberales displayed similar T_{50} values of 49.7°C (SD = 1.0) and 51.1°C (SD = 1.2), respectively.

4 | DISCUSSION

We evaluated the role of evolutionary history and ecological filtering on heat tolerance in the entire community of Zingiberales at La Selva, Costa Rica. Photosynthetic systems of the Zingiberales at La Selva displayed a relatively narrow range of heat tolerance compared to subtropical and temperate species (Lancaster & Humphreys, 2020; O'Sullivan et al., 2017). Our results suggest that heat tolerance is constrained by evolutionary history. The range of T_{50} for Zingiberales species from La Selva (48.05–52.72°C) is similar to ranges reported for other tropical tree and shrub species (Krause et al., 2010; Perez & Feeley, 2020b; Slot et al., 2019, 2021).

This study represents the first comprehensive phylogenetic analysis of heat tolerance in a single clade of co-occurring plant species. Previous studies on heat tolerance in tropical species have concluded that phylogeny is a weak predictor of photosynthetic heat tolerance (Lancaster & Humphreys, 2020; Perez & Feeley, 2020a; Slot et al., 2021). It is possible that the lack of phylogenetic signal

TABLE 2 Phylogenetic generalized least square models for T_{15} and T_{50} across 39 Zingiberales species at La Selva Biological Station, Costa Rica. Habitat types: Open areas (OA), secondary forest (SF) and old growth forest (OGF). Origin indicates whether species are native or exotic to La Selva

	df	F	p	r^2
Phylogenetic generalized least square for T_{15}				
Habitat	2	0.15	0.86	−0.05
Origin	1	8.07	0.01*	0.16
Family	2	1.17	0.34	0.02
Phylogenetic generalized least square for T_{50}				
Habitat	2	1.16	0.32	0.01
Origin	1	2.95	0.09	0.05
Family	2	0.62	0.68	−0.05

*$p < 0.05$.

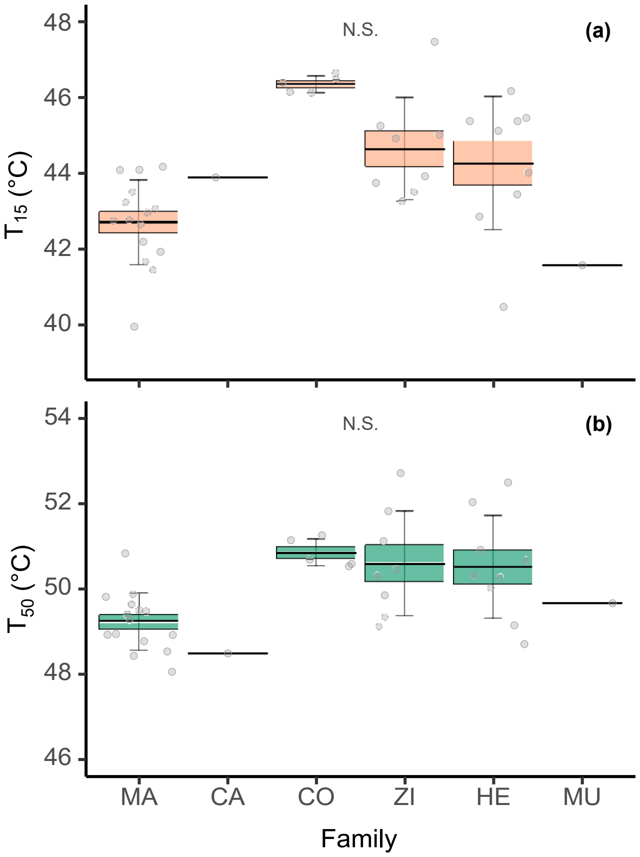

FIGURE 2 Heat tolerance of Zingiberales families at La Selva Biological Station, Costa Rica. (a) Critical temperature (T_{15}). (b) Temperature at which fluorescence decreases 50% (T_{50}). Plant families: Musaceae (MU), Heliconaceae (HE), Zingiberaceae (ZI), Costaceae (CO), Cannaceae (CA) and Marantaceae (MA). Error bars indicate standard deviation, boxes indicate standard error and the central line represents the average for each plant family. N.S., no significant differences.

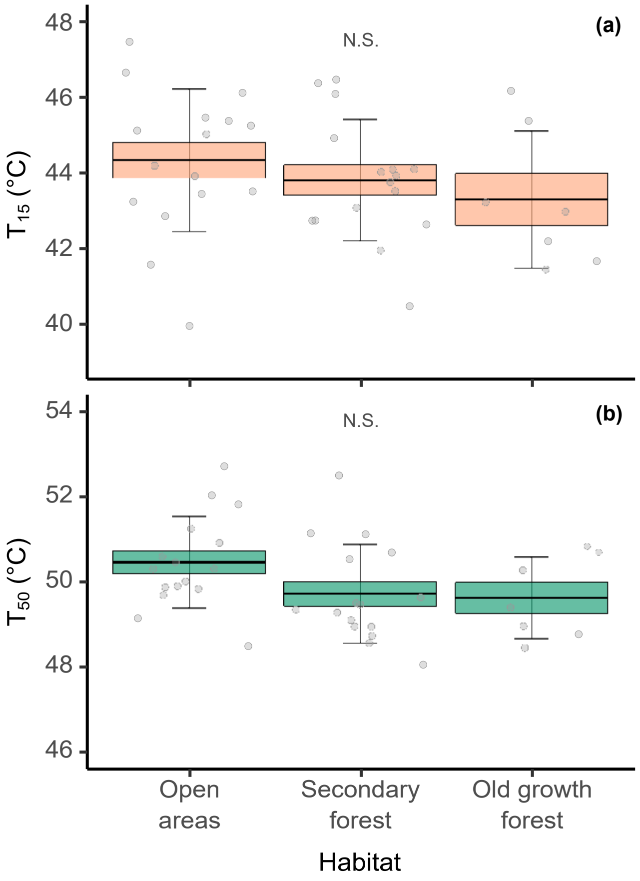

FIGURE 3 Heat tolerance of Zingiberales in open areas, secondary and old growth forest. (a) Critical temperature (T_{15}). (b) Temperature at which fluorescence decreases 50% (T_{50}). Error bars indicate standard deviation, boxes indicate standard error and the central line represents the average for each habitat. N.S., no significant differences.

reported in previous studies is the result of including paraphyletic plant groups or assessing heat tolerance on species from the same geographical origin (Cavender-Bares et al., 2006). Another possibility is that the phylogenetic conservatism detected in our study is due to a relatively large representation of sympatric species within a few genera and families. This contrasts with previous analyses, which included a few species from multiple orders (Perez & Feeley, 2020a; Slot et al., 2021) and sampling at larger geographical scales (Lancaster & Humphreys, 2020).

We did not find support for our original hypothesis of an association between heat tolerance (T_{15} and T_{50}) and habitat use by different Zingiberales species at La Selva. This suggests that local adaptation to microclimates is not the major factor constraining species distribution in this plant order. Evolutionary history, not local adaptation, is the most important factor associated with heat tolerance.

In tropical forests, temperatures change dramatically throughout the landscape (Canham et al., 1990; Zellweger et al., 2020). While secondary and old growth forests in our study area have similar maximum daily temperatures (27 and 30°C, respectively), open areas have a maximum daily temperature of 38°C. We expected that this variation would result in a greater difference in heat tolerance between habitats due to local acclimation or adaptation. Leaves in the deep understorey are rarely expected to experience temperatures higher than 33°C because they are seldom exposed to direct sunlight (Rey-Sánchez et al., 2016). However, intense direct solar radiation can cause leaves in open areas to rise to temperatures above 40°C (GGH, personal observation; Krause et al., 2010). Leaves exposed to direct sunlight can reach temperatures 5–18°C above air temperature (Fauset et al., 2019; Miller et al., 2021; Rey-Sánchez et al., 2016). Despite the striking differences between air temperature and the temperature of leaf surfaces, habitat was not a good predictor of plant responses to temperature. A recent study determined that an increase in leaf temperature can be the result of water stress, due to limited cooling through transpiration (Cook et al., 2021). However, heat tolerance is higher in species with limited cooling (Cook et al., 2021). It has been suggested that heat tolerance is potentially an adaptation to extreme leaf temperature (Perez & Feeley, 2020b). Hence, heat tolerance might be the result of a combination of changes in leaf temperature, water availability and morphological traits, and other factors not included in this study.

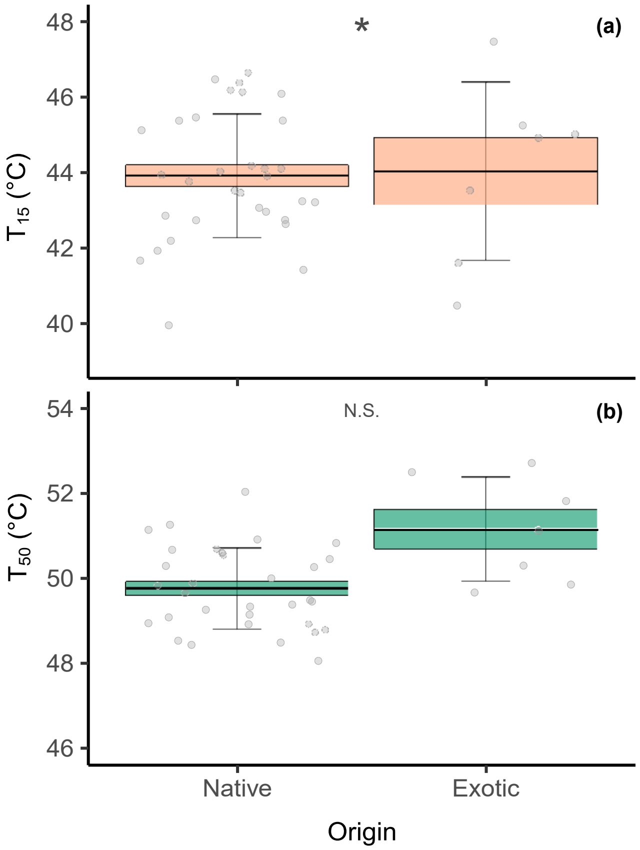

FIGURE 4 Heat tolerance of native and exotic Zingiberales at La Selva Biological Station, Costa Rica. (a) Critical temperature (T_{15}). (b) Temperature at which fluorescence decreases 50% (T_{50}). Error bars indicate standard deviation, boxes indicate standard error and the central line is the average for native or exotic species. $^*p<0.05$. N.S., no significant differences.

Some leaf traits other than heat tolerance may explain the distributions of species across forest habitats at La Selva. For example, most plants from the Marantaceae family have low PSII heat tolerance and are present in old growth forest and secondary forest where temperatures and solar radiation are lower than in open areas. However, this does not necessarily preclude them from colonizing environments characterized by high temperatures and solar radiation. *Calathea lutea* (Marantaceae) has the lowest T_{15} among members of this family. However, *C. lutea* colonizes open areas, where air temperatures can reach 45°C. A leaf trait other than heat tolerance, changes in the turgor of the pulvinus, allows *C. lutea* to move its leaves during the day (Herbert & Larsen, 1985). Members of the family Marantaceae use their pulvinus to alter the position of their leaves through the day to regulate their leaf temperatures (Herbert & Larsen, 1985), improve rates of carbon assimilation and minimize photoinhibition (Gamon & Pearcy, 1989). This type of leaf movement may be used by other Marantaceae and potentially explain their ability to colonize hot environments despite having such low heat tolerance.

Plant physiological responses to temperature are often associated with the temperatures of their environment of origin (Berry & Bjorkman, 1980). Heat tolerance of PSII is known to be highly plastic in temperate species, but less plastic in species from tropical climates (Knight & Ackerly, 2002). Tropical plants may have evolved limited acclimation to novel temperatures as the result of low climatic variability in the tropical regions throughout the year (Perez et al., 2016). Our results suggest that tropical plant heat tolerance is not correlated with temperatures prevalent in their microhabitat. Similar results were reported by other studies also accounting for phylogenetic non-independence (Perez & Feeley, 2020a).

Our results suggest that exotic Zingiberales tolerate marginally higher initial damage of PSII (T_{15}) than native species. In contrast, T_{50} was not different between exotic and native species. Although this study includes most species of Zingiberales in our study area, our results may be affected by the unbalanced representation of species and families in each habitat. Most exotic species belong to a single plant family (Zingiberaceae). At La Selva, there are no exotic Zingiberales colonizing old growth forest, and the family Musaceae is represented by a single species. When performing additional analyses excluding the family Musaceae, or old growth forest, we also detected marginal differences between native and exotic species only for T_{15}. It is important to note that because the experimental design is unbalanced, further research is required to determine if these results are biologically significant, or generalizable to exotic species beyond this community of Zingiberales.

Previous studies showed that high heat tolerance in exotic species may have facilitated their current establishment, and increased the probability of future invasions (French et al., 2017; Song et al., 2010). If high heat tolerance of exotic Zingiberales is associated with an increase in fitness in novel environments, this trait may be favoured by selection in future climates. Heat tolerance of invasive tree species in Mediterranean plants exhibited higher heat tolerance than native species (Godoy et al., 2011). However, these differences were only evident when plants experienced water stress (Godoy et al., 2011). This increased heat tolerance in invasive plants was reported in other ecosystems, such as coastal plants and humid subtropical forests (French et al., 2017; Song et al., 2010). Mounting evidence suggests that exotic species with high heat tolerances have the potential to outperform native species in a warming world (Foxcroft et al., 2008). Four out of the seven exotic species we sampled are already expanding their distribution at La Selva and adjacent forests (*H. coronarium*, *H. psittacorum*, *Z. spectabile* and *M. velutina*). These four species tend to have T_{50} values above average, but T_{15} values below the community average. These results suggest that these four exotic species tend to be more susceptible to initial temperature damage, but in the long term, can tolerate higher temperatures than most native species.

Evolutionary history will constrain photosynthetic responses of Zingiberales on a warming planet. The phylogenetic patterns of heat tolerances may also influence the risk of reducing phylogenetic diversity because the risk of extinction is not randomly distributed across the phylogenetic tree. At least at the geographical scale of this study, heat tolerance is a conserved trait that was not influenced by local adaptation to particular habitats. Exotic Zingiberales seem to have a marginal photosynthetic advantage over native species when experiencing warmer temperatures. The consequences of such differences on survival and fitness are unknown but might determine which species will tolerate future temperatures in a warming world.

AUTHOR CONTRIBUTIONS

Georgia G. Hernández and Carlos García-Robledo conceived the ideas, Georgia G. Hernández planned and designed the research with contribution from Timothy M. Perez, Ramón Molina-Bravo, Roberto A. Cordero and Jeffrey R. Seemann. Georgia G. Hernández collected the data; Oscar M. Vargas performed the molecular phylogeny; W. John Kress provided the community phylogeny; Georgia G. Hernández analysed the data, Georgia G. Hernández wrote the manuscript with help of Carlos García-Robledo and Timothy M. Perez. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.q573n5tmz (Hernández et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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