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ORIGINAL ARTICLE

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Diversity in habit expands the environmental niche of *Ziziphus* (Rhamnaceae)

Jess Rickenback[1,2] | R. Toby Pennington[2,3] | Caroline E. R. Lehmann[1,2]

[1]School of Geosciences, University of Edinburgh, Edinburgh, UK

[2]Tropical Diversity, Royal Botanic Garden Edinburgh, Edinburgh, UK

[3]College of Life and Environmental Sciences, University of Exeter, Exeter, UK

Correspondence
Jess Rickenback, School of Geosciences, University of Edinburgh, Edinburgh EH9 3FF, UK.
Email: jess_rickenback@yahoo.co.uk

Associate Editor: Ferry Slik

Handling Editor: Robert Bagchi

Abstract

Ziziphus (Rhamnaceae) is a widely distributed genus across the Australasian and African tropics with unusual diversity in habit, and many species of significance to people. Here, we quantify the environmental limits of *Ziziphus* species and examine inter-specific relationships among functional traits, environment, biome, and range size. We developed a curated geolocation database for *Ziziphus* and used it to examine the environmental limits of the genus relative to temperature, rainfall, and seasonality. To assess the relationship between biome and habit, permutational analysis of variance was used, while hierarchical clustering was used to determine whether habit, leaves, and fruit traits were related to biome. For 40 species with adequate geolocation data, range size was calculated to assess its relationship with habit, biomes, and cultivation. Finally, niche identity tests were used to determine niche equivalency among cultivated and non-cultivated species. Liana species are restricted to closed forests and the geoxylic habit is found only in open grasslands. Further, habit is significantly associated with range size, with trees having on average larger range sizes than shrubs, lianas, and geoxyles, but biome was not correlated with range size. Cultivated species have ranges ~10 times that of non-cultivated tree species and with significantly different and broader environmental niches. The unusually wide distribution of *Ziziphus* can be explained by its diversity of habits associated with different biomes spanning continents. This, along with the usage of many *Ziziphus* species by people for their fruits, expands the range and environmental occupation of the genus.

KEYWORDS
biomes, cultivation, functional traits, growth form, range size, tropics

1 | INTRODUCTION

Functional traits are a way to infer processes from pattern, and as such are used to disentangle the macroecology and biogeography of plant families (e.g., Onstein et al., 2019; Xue et al., 2020) and biomes (e.g., Gomes et al., 2020; Solofondranohatra et al., 2018), but only infrequently plant genera (although see Proches et al., 2012; Pezzini et al., 2021). As morpho-physio-phenological characters, functional traits relate to the life history strategies of plants that embody growth, reproduction, and survival (Violle et al., 2007) and indicate how species relate to the environment. Fruit traits have been used to interpret the fossil record and infer genus-level paleo-distribution

(Burge & Manchester, 2008). Habit can have a strong association with biome, with shifts into the rainforest, savanna, and temperate biomes associated with shifts in growth form (e.g., Gagnon et al., 2019). Suites of traits have been linked to the prediction of future ranges and successful establishment of invasive plants (Gallagher et al., 2015). We used a combination of functional traits, species ranges, and biome affinities to quantify the relationship of species of *Ziziphus* (Rhamnaceae) with environment to understand how that relates to biome and habit. *Ziziphus* is a model genus to investigate the associations between traits and biomes because it has species in all major lowland tropical biomes so can help us develop insights into the interactions between environmental pressures and functional responses.

Open tropical biomes span over a fifth of global landcover, comprising ecosystems where the climate is wet and warm enough to support forests but instead supports grasslands, shrublands, open woodlands, and savannas (Bond, 2019). By contrast, closed biomes, which receive substantially more academic attention (Bond & Parr, 2010), comprise the forested ecosystems of the world. These varied biomes represent distinct functional environments. Tropical rainforest, a key closed biome, is tall, multi-layered and has a closed canopy and an understory dominated by shrubs and young saplings (Dexter et al., 2018) and receives year-round precipitation. Tropical savanna, a characteristic open biome, is a disturbance-prone ecosystem characterized by a continuous C4 grassy layer, low soil nutrients, and an open to relatively open canopy (Sankaran et al., 2005). Savannas are maintained by stress and disturbance including herbivory, frost, edaphic properties, and fire (Archibald & Hempson, 2016; Finckh et al., 2021; Mbanze et al., 2019; Ratnam et al., 2011) which in the absence of disturbance such as fire can switch state to closed biomes such as rainforest or seasonally dry tropical forest (SDTF) (Staver et al., 2011). SDTF and savanna are both shaped by long dry periods, but SDTF differs by lacking fire and is characterized by plants that are intolerant to fire and share traits such as succulence (Gagnon et al., 2019). As water becomes increasingly limited, dry forests and savannas ebb into deserts (Pennington et al., 2018). In the Neotropics, fire adaptations have been easy to evolve leading to the frequent independent evolution of lineages into savanna from surrounding biomes, especially the rainforest (Simon et al., 2009). Neotropical savanna trees are deep-rooted to access ground-water year-round, but adaptations such as succulence and deciduousness needed to survive in SDTF and desert may represent a greater evolutionary barrier, explaining the lesser number of evolutionary transitions and high phylogenetic biome conservatism found in these biomes (Hughes et al., 2013).

Communities of species that occupy the same biomes often share suites of traits. Savanna-specific adaptations can include fire-resistant underground storage organs and bark characteristics (Dantas & Pausas, 2013; Simon & Pennington, 2012). Rainforest adaptations can include drip tips and buttress roots (Pennington et al., 2009). Since it may be "easier to move than evolve" (Donoghue, 2008), pre-existing traits may enable biome shifts rather than developing in response to them, such as storage organs

that facilitate fire resistance but may have developed as a drought response (Griffiths & Males, 2017). Understanding how traits and suites of traits evolved and interacted with the historical assembly of species comprising biomes through time can lead to a greater understanding of biome history (Couvreur et al., 2015). Different *Ziziphus* species have distinct life forms including trees, lianas, and dwarf shrubs with massive underground woody structures and limited aerial parts hereafter referred to as geoxyles (Gomes et al., 2020).

Both the evolutionary history of a species, and the environmental conditions of an area through time are likely to influence range sizes through colonization, speciation, and extinction (Brown et al., 1996). Range size is significant ecologically because it affects climate change resilience (Mace et al., 2008; Morueta-Holme et al., 2013), and is fundamental for conservation planning (Xu et al., 2017) and invasion prediction (Gallagher et al., 2015). At all scales, tolerance of a variety of environmental conditions enables occupation of a larger area (Slatyer et al., 2013), while range-restricted species tend to be habitat specialists (Cardillo et al., 2018). Species that inhabit biomes covering larger areas tend to have larger range sizes than species that occupy biomes that cover smaller areas (Sheth et al., 2020). Closed biomes of rainforest and SDTF occupy a smaller area than open biomes of savanna and grassland in the regions where *Ziziphus* occurs, so it is likely that the smallest ranges in the genus are occupied by closed biome species. It has been suggested that habit may be linked to range sizes, for example, taller trees which can disperse their fruit further are likely to have larger ranges (Thomson et al., 2011), so differences may exist between small-statured and large-statured species' range sizes. For *Ziziphus*, shrubs and geoxyles have the lowest stature and are likely to have the smallest ranges. Cultivated species are likely to have the largest ranges in the genus, as human use enables species to fulfill their potential ranges (Flower et al., 2021).

Ziziphus is a monophyletic, woody genus, comprising c. 53 species with a predominantly tropical distribution across Africa, Australia, and Asia, with Asia suggested as its likely origin (Liu & Cheng, 1995). Its age is disputed with estimates ranging from around 20 my (Richardson et al., 2004) to 66 my (Hauenschild et al., 2018). *Ziziphus* occupies multiple biomes, although its biome of origin is unknown. Even within the context of closely related genera in the Rhamnaceae, *Ziziphus* has an unusually broad distribution. In the tribe Paliurae, sister genus *Paliurus* has a narrower distribution in East Asia and the Mediterranean (Chen et al., 2017), while *Hovenia* is restricted to East Asia (Kyun-Hyun et al., 2010). *Ziziphus*' occupation of diverse biomes across continents is further noteworthy because similar biomes on different continents tend to be floristically dissimilar in that they share few genera (Dexter et al., 2015) and biomes on different continents are phylogenetically distinct (Echeverria-Londono et al., 2018). This suggests that *Ziziphus* has been successful at dispersing among continents and evolving into different biomes, perhaps repeatedly. Few genera occupy such wide distribution both geographically and ecologically; examples include *Diospyros* (Ebenaceae, 500 species, Duangjai et al., 2009), *Terminalia* (Combretaceae, 250 species, Das et al., 2020), *Maytenus*

(Celastraceae, ~300 species, Zhang et al., 2020), and *Syzygium* (Myrtaceae, 1200 species, Yuniarni et al., 2021), all significantly larger than *Ziziphus*.

Ziziphus species are commonly used by people, with two species—*Ziziphus mauritiana* and *Ziziphus jujuba*—widely cultivated for their edible fruit. *Z. jujuba* is economically significant, with exports from China totaling $5 million annually (Gao et al., 2013). Many *Ziziphus* species have medicinal uses; *Ziziphus spina-christi* has been used to treat bilharzia (Almeer et al., 2018), and the leaf and bark of *Ziziphus timoriensis* are used to treat malaria (Taek et al., 2019). The wood of *Ziziphus nummularia* and *Ziziphus rivularis* are used for building materials or forage (Bhandari & Bhansali, 2000; Constant & Tshisikhawe, 2018).

We investigate whether functional traits enabled *Ziziphus* to establish across a diversity of biomes and range sizes. We hypothesized that (1) species will display specific traits or suites of traits in different biomes. Trait patterns we anticipate include a prevalence of larger leaves in closed biomes to maximize light interception in warm wet environments that do not freeze (Wright et al., 2017). In contrast, hairy leaves will likely be prevalent in open biomes where herbivore defenses and mechanisms to minimize water loss are crucial. (2) Range size will vary among life forms with trees having the largest ranges due to their tall stature and ability to disperse seeds further. (3) Range sizes will vary among biomes with the smallest ranges in the genus occupied by closed forest species due to available habitat area being smaller. (4) Cultivated species will cover a broader environmental niche than non-cultivated species and there will be significant range size differences between cultivated and non-cultivated species because cultivation removes abiotic and biotic barriers to the expansion of the native range.

2 | METHODS

2.1 | Occurrence and environmental data

We curated species occurrence records that resulted in a taxonomically verified database of 1847 unique records for 50 species. We primarily used the BIEN package v1.2.4 (downloaded 9 December 2020) which integrates global botanical observation data from sources such as plot data, herbaria, and specimen records and where data have undergone additional taxonomic and spatial verification to that supplied by GBIF (The Global Biodiversity Information Facility, 2021) (Maitner et al., 2017). Following Meyer et al. (2017), where species had <10 geolocations, records were added from a combination of georeferenced herbarium specimens and from additional GBIF data (Table S1). For three species (*Ziziphus apetala*, *Ziziphus hoaensis*, and *Ziziphus linnaei*) no geographic information was available, possibly due to a combination of factors; the tropics are under collected (Prance et al., 2000), the availability of digitized herbarium specimens varies greatly, and digitized resources often suffer from a lack of maintenance and updating (Lughadha et al., 2018). Records without latitude and

longitude were excluded as were specimens for the same occurrences, and the remaining spatially georeferenced records were cleaned by removing occurrences outside of the known distribution of the genus. Taxonomy was checked using the Taxonomic Name Resolution Service, Plants of the World Online, GBIF, and floras. This taxonomy check resulted, for example, in occurrences of *Ziziphus pubescens* and *Ziziphus robertsonia* being excluded; genetic analysis by Islam and Simmons (2006) and Hauenschild et al. (2016) indicated both species as being more closely affiliated with the ampeloziziphoid group than with *Ziziphus*, and morphologically indistinct from *Bathiorhamnus*.

2.2 | Environmental variables

To examine the environmental limits of *Ziziphus* we used four bioclimatic variables related to growth and productivity. Initially, 19 bioclimatic variables were compiled for each species using the *Ziziphus* geolocation data and WorldClim 2.1 at 2.5 min resolution (Fick & Hijmans, 2017). For all bioclimatic variables, the skewness of data was calculated using the package "moments" (Komsta & Novomestky, 2015). Data with moderate skew (bio4, bio12, bio13, and bio16) were transformed using sqrt; where skewness >2 (bio14, bio17, and bio19) data were log10 transformed. We performed principal components analysis (PCA) with "prcomp" in R v3.6.2 (R Core Team, 2021) and visualized it with "factoextra" v1.0.7 (Kassambara & Mundt, 2016). Where variables had a correlation >0.8 we performed an additional and progressive elimination of collinear variables based on their variance inflation factor (VIF) in "usdm" (Naimi et al., 2014) and informed by our knowledge of their ecological relevance. Variables with a value above 4 were removed in order of greatest value first and VIF rerun. After this process the analysis incorporated four bioclimatic variables: bio1 Annual Mean Temperature, bio4 Temperature Seasonality, bio13 Precipitation of the Wettest Month, and bio14 Precipitation of the Driest Month. These variables directly influence how and where plants grow; annual mean temperature approximates the total energy inputs for an ecosystem. Temperature seasonality reflects the temperature change over the course of a year and can be characteristic of certain ecosystems—rainforests for example have very low seasonality (Keith et al., 2020). Precipitation of the wettest and driest months is significant if extreme precipitation conditions during the year influence species distribution, and are reflective of seasonality or the lack thereof in tropical environments (O'Donnell & Ignizio, 2012). Since fire maintains many open biomes and influences plant traits related to fire resilience (Archibald et al., 2019; Pausas, 2019), the mean yearly burned area was included as a variable, with data calculated over the period 2003–2016 and log-transformed. The mean yearly burned area is a reflection of the average amount of fire present in a given area and is used to indicate fire frequency (as in Phelps et al., 2022). Fire data were derived from the MODIS dataset MCD64A1 version 6 (Giglio et al., 2018). After this process the final analysis explained >70% of the variation in the data.

2.3 | Range size

Of the 50 species for which there were geo-location data, 44 had three or more unique records, the minimum number of records required to calculate range size. These species represented all biomes and habits (Table S2). The extent of occurrence (EOO) was calculated with alpha hull using "conR" v1.3.0 (Dauby et al., 2017). EOO is the smallest contiguous boundary measured by a minimum convex polygon which encompasses all the occurrences of a taxon (Dauby et al., 2017). Alpha hull is a modified minimum convex polygon that provides a more conservative estimate of range size than the minimum convex polygon. This method has been shown to be most appropriate for herbarium records and other such occurrence data collected non-systematically (Gallagher, 2016). After plotting multiple hulls with different alpha values, we chose alpha hull = 1, because it provided the most realistic distribution estimates when taking into account unsuitable habitats and dispersal limitations (Meyer et al., 2017). Additionally, our sensitivity analysis showed that alpha hulls 1 to 5 returned similar results (Table S3).

2.4 | Attribution of biome, functional traits, and human use

Species of *Ziziphus* were assigned to biomes based on data from floras, peer-reviewed articles, gray literature such as doctoral dissertations, United Nation Development Programme (UNDP) reports, herbarium labels, and expert knowledge from Dr. Gopal Rawat (personal correspondence) (Table S4). Biomes were categorized as "open," "closed," and "desertic." Following the typology of Earth's ecosystems by Keith et al. (2020) that groups ecosystems into biomes for the purpose of enabling comparative work, in the analyses here, closed biomes are analogous to T1 "tropical and subtropical forests" that include lowland rainforests, tropical montane forests, tropical dry forests, and tropical heath forests. Desertic biomes are analogous to T5 "deserts and semi-deserts," which include semi-desert steppes, thorny deserts and semi-deserts, sclerophyll hot deserts and semi-deserts, cool deserts and semi-deserts, and hyper-arid deserts. Open biomes are analogous to T3 "shrublands and shrubby woodlands" and T4 "savannas and grasslands" following Bond (2019) as both ecosystems are mediated by similar processes (Keith et al., 2020). These include seasonally dry tropical shrublands, seasonally dry temperate heaths and shrublands, cool temperate heathlands, rocky pavements, screes and lava flows, trophic savannas, pyric tussock savannas, hummock savannas, temperate woodlands, and temperate subhumid grasslands.

There is little to no previous work on the functional traits of *Ziziphus* despite its wide distribution and cultural and economic significance. Traits such as height, seed mass, and fruit weight are severely under-recorded and had to be excluded from analyses due to data deficiency. Trait data were primarily acquired from floras and where no flora accounts were available, trait data were compiled from varied gray literature sources such as worldagroforestry.org (Orwa et al., 2009) (Table S4) and assessment of type specimens (Table S4). Traits considered functionally informative were compiled and comprised: habit, spinescence, bark roughness (corkiness), bark or branch hairiness, leaf area, leaf hairiness, fruit color, fruit hairiness, and fruit fleshiness (Table 1).

Cultivated species and primary human uses were identified from peer-reviewed articles, floras, and gray literature such as the United States Department of Agriculture Handbook (Table S4). Following Flower et al. (2021), we distinguished between species with no use or unknown uses, species which are widely used but not cultivated (harvested in situ), and species that are deliberately cultivated. Uses for non-cultivated species included spiritual, medicinal, edible, and wood for building or forage. Where multiple uses were listed for a species, the most common usage was selected.

2.5 | Analyses

2.5.1 | Environmental distribution of *Ziziphus* and interaction with habit

To clarify the limits and environmental distribution of *Ziziphus*, and whether habit affected environmental distribution, we performed PCA on extracted bioclimatic data. Only unique data were retained, and cultivated species records were removed leaving 1249 *Ziziphus* records. Permutational analysis of variance (PERMANOVA) in "vegan" v2.5–7 (Oksanen et al., 2020) was conducted to test for differences in bioclimatic space between non-cultivated species with biome as the dependent variable. We ran a second PERMANOVA in "vegan" v2.5–7 (Oksanen et al., 2020) with habit as the dependent variable to identify whether *Ziziphus* species with the same habit are more closely connected in bioclimatic space than those with different habits. Since all of our geoxyle records came from one species, *Ziziphus zeyheriana*, we ran our PERMANOVA a third time without these species records to account for the risk of pseudoreplication.

2.5.2 | Range size

Analysis of variance (ANOVA) (R Core Team, 2021) was used to test for differences in range size by habit between all non-cultivated species, and differences in range sizes between cultivated and non-cultivated species.

2.5.3 | Identifying shared trait syndromes

We aimed to identify species groupings with shared trait syndromes and assess the impact of trait combinations on species' occupations of different biomes. PCA was used to identify and select informative characters. Once species that were substantially data deficient in the remaining categories were excluded the trait database covered

TABLE 1 Trait data prioritized for collation and their significance to plant function

Trait	Data	Interpretation
Habit	Categorical: "geoxyle," "tree," "liana," "shrub."	A proxy for life history strategy that can also reflect traits including seed size (Foster & Janson, 1985), and the allocation of photosynthetic resources (Santiago & Wright, 2007). When species were not assigned to a distinct life form (i.e., "tree or shrub") allocations followed Gaillard et al., 2018 and where species were under 6 m tall and or multi-stemmed were assigned as "shrub."
Spinescence	Categorical: present/absent	Indicative of herbivory (Osborne et al., 2018) and anti-herbivory defenses both physical and biological (Halpern et al., 2007).
Bark roughness/ corkiness. Branch hair	Categorical: present/absent	Corkiness can be an adaptation to fire (Osborne et al., 2018). Hairiness in young branches may perform similar functions to hairiness in leaves; defense against herbivory and reduction of water loss.
Leaf hair	Categorical: present/absent	Hairiness in leaves functions as a defense against herbivory (Woodman & Fernandes, 1991) and reduces water loss (Ripley et al., 1999).
Leaf area	Continuous	Significant for leaf energy and water balance (Díaz et al., 2016) and informative in terms of allocation of resources. Leaf area was calculated following Li et al., 2020 as $2/3 \times$ length $\times$ width.
Fruit fleshiness	Categorical: "unknown," "not fleshy," "woody," "fleshy"	Fruit traits are relevant to dispersal and therefore species distribution, with Blendinger et al. (2016) finding that fruit pulpiness (fleshiness) was the main driver of selection by fruit-eating birds. Principal components analysis (PCA) was used to determine categories of fruit fleshiness.
Fruit color	Categorical: "unknown," "red-orange-yellow-brown," "green-yellow," "black," "gray"	Schmidt et al. (2004) have suggested that the global predominance of red and black fruit may be linked to conspicuousness for frugivores (but see Schaefer et al., 2007).
Fruit hair	Categorical: present/absent	Protects against water loss, UV radiation, heat gain (Hanley et al., 2007, and promotes propagule dispersal (Werker, 2000)

Note: A smaller set of traits used for analysis were selected by principal components analysis as described in the methods. A complete set of trait data is shown in Table S4.

47 species or 88.7% of the genus and included five traits; habit, leaf hair, bark hair, fruit hair, and spinescence (Table S5).

Due to the categorical nature of the data, functionally similar species were identified using multiple correspondence analysis (MCA). We performed hierarchical clustering of principal components on the five traits described above. Multiple correspondence analysis and clustering analyses used the FactoMineR package in R (v 2.4, Le et al., 2008) which uses the Ward method based on Euclidean distance. The clusters were visualized using "factoextra" v1.0.7 (Kassambara & Mundt, 2016). The number of clusters chosen is based on the sum of within-cluster inertia where the ultimate number of clusters aligns with the highest relative loss of inertia.

2.5.4 | Environmental niche of cultivated versus non-cultivated species

To test if cultivated and non-cultivated *Ziziphus* species occupy non-equivalent environmental niches, we used the enmtools.ecospat.id function of the ENMTOOLS R package (Warren et al., 2021) with nreps = 100 because this is sufficient to reject the null hypothesis with high confidence (Warren et al., 2008). The test uses kernel

density smoothing to estimate the density of a species' environmental niche space (Myers et al., 2020). Models are built for each species using the empirical data and overlap is measured between them. Repeated randomizing of each data point is used to create a null distribution, keeping the sample size for each group consistent with the empirical data, and overlap is measured between the randomized models. The distribution of these overlaps represents the expected similarity between groups if their environmental distributions represent repeated draws from the same underlying distribution (Warren et al., 2021). Niche overlap is measured using Schoener's D (Schoener, 1968) and the I statistic (Warren et al., 2008). Both I and D range from 0 (species that have completely discordant environmental niche models (ENMs)) to 1 (species that have identical ENMs). Two species in *Ziziphus* are widely cultivated: *Z. jujuba* and *Z. mauritiana*. For each of these cultivated species, we chose a non-cultivated species for comparison which shared biome, location, and life form. Only species with a minimum of five occurrence records could be included in this analysis. Testing used the uncorrelated bioclimatic variables described above.

To explore whether usage by people affected environmental distribution we performed PCA on unique extracted bioclimatic data comprising 1472 *Ziziphus* records for two cultivated species and 33

species where use had been identified. PERMANOVA in "vegan" v2.5–7 (Oksanen et al., 2020) was run to ascertain whether *Ziziphus* species with the same uses are more closely connected in bioclimatic space than those with different uses.

3 | RESULTS

3.1 | Geography and ecology of *Ziziphus*

The distribution data for 50 *Ziziphus* species based on 1847 occurrences showed that of the non-cultivated species 12 are found in open biomes, 31 in closed biomes, and 5 in desertic biomes (Table S4). Within the study area, species associated with open biomes dominate in Africa, species associated with closed biomes are mainly restricted to Southeast Asia, and desertic species are mainly found in Africa and the Arabian Peninsula (Figure 1a). Of the 50 species, 19 are lianas, 16 trees, 14 shrubs, and one geoxyle.

3.2 | Biome-specific traits

The closed biomes occupied by *Ziziphus* species were typified by an average temperature of 25°C and annual precipitation of 2277mm. The open biomes experience average temperatures of 20°C and annual precipitation of 911mm. The desertic biomes were typified by average temperatures of 23°C and annual precipitation of 318mm (Figure 1b–e).

Principal components analysis (Figure S1) indicates that species' environmental distribution is predominantly driven by precipitation and temperature, with species tolerating temperature seasonality distinct from those which occupy wet environments (axis one). Species which tolerate increasing fire frequency are distinct from those found in drier environments (Figure S1, axis two). PERMANOVA showed significant differences in bioclimatic space between species groupings by biome (*pseudo F* = 406.01, *p* <.001, R^2 =0.39).

Multiple correspondence analysis explained 43.6% of the variance in the data (Figure S2). Hierarchical clustering identified five functional groups of species. Biome and trait data are plotted onto the cluster dendrogram in Figure 2.

The trait dendrogram representing species with similar suites of traits based on combinations of fruit hair, leaf hair, branch hair, habit, and spinescence shows a strong biome signal (Figure 2). Group one features species from open and closed biomes in mixed clusters such as *Ziziphus mucronata*, *Ziziphus mairei*, and *Z. hoaensis*, but all species in group one share the trait of hairless leaves and all of them are trees. Group two is also mixed, with species from open, closed, and desertic biomes in clusters. All group two species are spiny and have hairless branches, and 4/5 of them are shrubs. Group three comprises one species, the geoxyle *Z. zeyheriana*, found only in open biomes. It is a spiny species, with hairy leaves and bark. Most of the lianas are found in the closed biomes trait group (group 4). All

group four species are spiny with hairy fruit. Some species found in closed biomes form trait clusters in group five; *Ziziphus montana*, *Ziziphus xylopyrus* and *Ziziphus rugosa*, and *Z. apetala*, *Ziziphus elegans*, *Ziziphus cuspidata*, and *Ziziphus funiculosa*. All species in group five are spiny, and 21 out of 24 have hairy bark.

Principal components analysis shows distinct environments occupied by lianas and geoxyles, with liana distribution driven by high rainfall and geoxyle distribution driven by temperature seasonality. The environmental distribution of trees and shrubs somewhat overlaps, with shrub distribution dominating where the annual mean temperature is higher (Figure 3). PERMANOVA showed significant differences in bioclimatic space between species groupings by habit (*pseudo F* = 226.64, *p* <.001, R^2 =0.35) even when *Z. zeyheriana* is excluded (pseudo F = 224.37, *p* <.001, R^2 =0.29).

3.3 | Effects of habit and biome on range sizes

There is a broad spread of geographic range sizes among non-cultivated species that differed by a factor of 100, with the smallest range 1013km² (*Ziziphus xiangchengensis*) and the largest 684,533km² (*Z. mucronata*). Open biome species occupied geographic ranges from 1013 to 684,533km² with a median extent of 11,492km². *Ziziphus* species that characterized closed biomes had ranges from 3113km² (*Ziziphus affinis*) to 130,748km² (*Ziziphus oenopolia*) and median range size of 21,164km². Finally, desertic *Ziziphus* species were found to have geographic range extents from 3252km² (*Ziziphus hamur*) to 28,801km² (*Z. spina-christi*) with a median of 5046km².

Range sizes varied significantly between habits (*F* = 5.6, *p* <.01). There was a significant difference in range sizes between trees and shrubs (Figure 3b). Trees had the largest range sizes (median = 28,801km²) and shrubs the smallest (median = 3565km²). We found no evidence that biome affects range sizes in *Ziziphus* species (*F* = 0.1, *p* >.5).

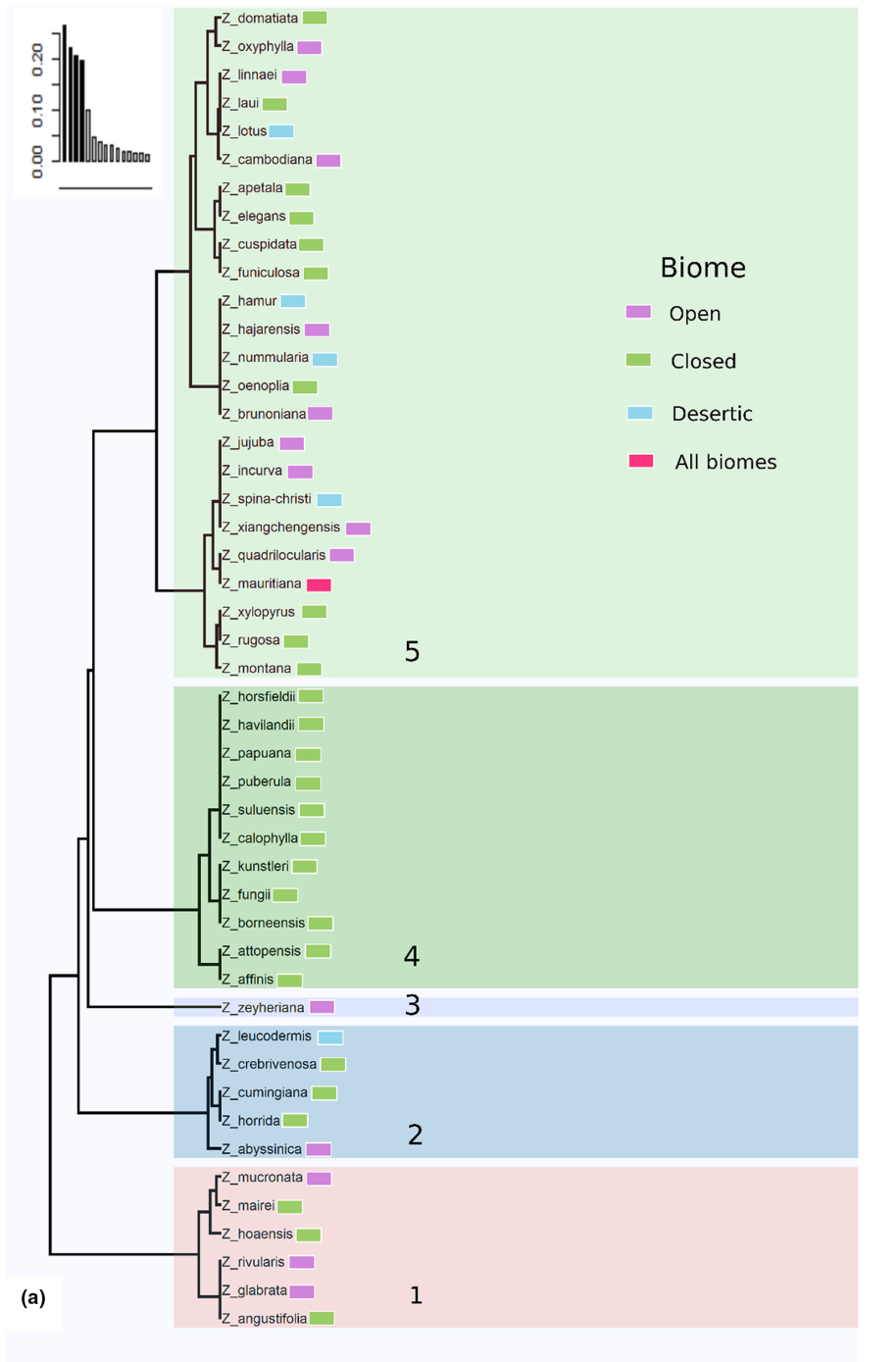## 3.4 | The environmental niche, range sizes, and traits of cultivated species

For 18 species no human use was found. Two species—*Z. mauritiana* and *Z. jujuba*—are widely cultivated for their edible fruits. Other species of *Ziziphus* are edible (21 species), medicinal (8 species), useful for their wood products (2 species), or have spiritual significance (2 species). PERMANOVA showed significant differences in bioclimatic space between species groupings by use (*pseudo F* = 82.03, *p* <.001, R^2 =0.18).

The two cultivated species—both trees—had range sizes of 284,684km² (*Z. jujuba*) and 161,221km² (*Z. mauritiana*), almost 10 times larger than the median of the range sizes of non-cultivated tree species; 29,890km² but the differences in range size between cultivated and non-cultivated tree species was not significant (*F* = 2.876, *p* >.1). However, we also used ANOVA to test for range
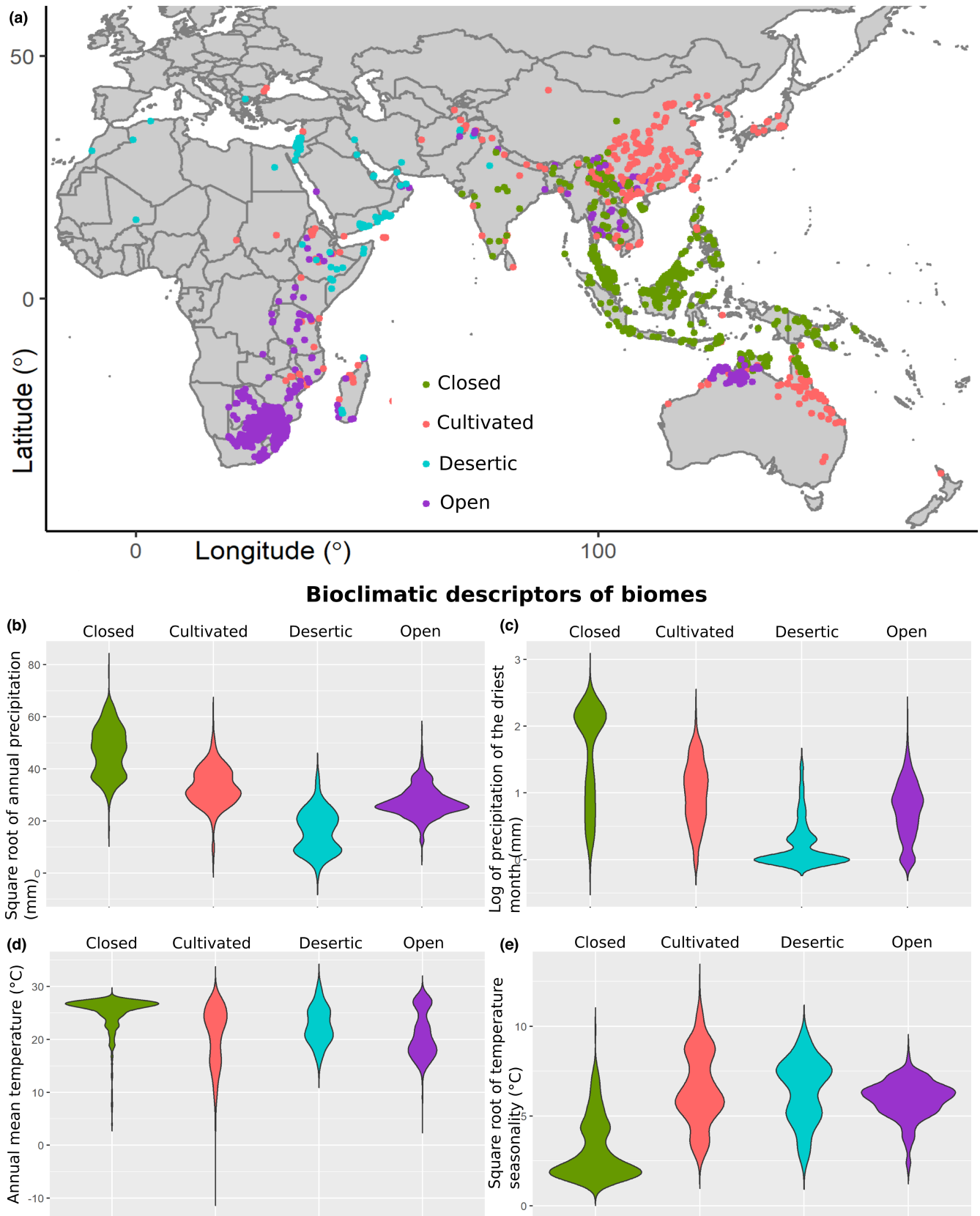
FIGURE 1 Geographic limits and environmental limits of *Ziziphus*. (a) Geolocation of 50 *Ziziphus* species and associated biomes. Descriptions of how biomes were attributed can be found in the methods and Table S4. Geolocation data were curated from a combination of sources and are described in the methods and Table S1. (b–e) Descriptors of the environmental limits of the biomes used in the study, clockwise from top left; (b) annual precipitation, (c) precipitation of the driest month, (d) annual mean temperature, and (e) temperature seasonality. Bioclimatic data were extracted using *Ziziphus* geolocation records from WorldClim 2.1 at a 2.5 min resolution (Fick & Hijmans, 2017).

FIGURE 2 Functional traits and ecology of *Ziziphus*. (a) Hierarchical cluster dendrogram based on multiple correspondence analysis of five traits for 47 species; habit, spinescence, hairiness of leaf, fruit, and bark. Descriptions of how trait data were collated and chosen can be found in the methods and Table S4. Biome attributions are described in the methods and Table S4. (b) A summary of the trait data used and how it relates to the groups numbered in (a).

size differences between cultivated and non-cultivated *Ziziphus* species of all habits, not limited to trees, and found that when different habits are included, cultivation correlates with range size ($F = 5.87$, $p < .05$).

For cultivated and non-cultivated species of the same growth form occupying similar locations and biomes, we found that the niche for *Z. mauritiana* (cultivated) and *Z. spina-christi* (non-cultivated) was significantly different (D statistic = 0.12, p value = .01, I statistic = 0.26, p value = .01) as was the niche for *Z. jujuba* (cultivated) and *Ziziphus incurva* (non-cultivated) (D statistic = 0.07, p value = .01, I statistic = 0.25, p value = .01). Fruit traits between the pairs were similar when known; both *Z. mauritiana* and *Z. spina-christi* have hairless yellow-red edible fruit. *Z. incurva* and *Z. jujuba* have similar-sized red edible fruit. The key trait difference between the pairs is that in both cases, the cultivated species is described as "succulent" or "juicy," and not solely "fleshy."

4 | DISCUSSION

Ziziphus species with different habits occupy different biomes, and distinct, albeit somewhat overlapping, environmental spaces. Diversity of habit effectively broadens the environmental range over which *Ziziphus* species can establish. Habit significantly relates to range sizes, and the cultivated species have wider ranges than non-cultivated species.

4.1 | Biome-specific traits

Lianas and the single geoxylic species are associated with different biomes, with clear significant differences in groupings of species by habit in environmental space (Figure 3a). The association of liana with closed biomes and geoxyle with open biomes suggests either the pressures of a novel biome prompted adaptive habit evolution or that these habits evolved beforehand and then enabled novel biome occupation. Studies in different groups have shown concordance between growth forms and biomes (i.e., in the succulent biome Gagnon et al., 2019; in SDTF Dexter et al., 2018; in the campos rupestres Alcantara et al., 2018). For insights into the evolutionary history of these associations in *Ziziphus*, phylogenetic work is required. While trees and shrubs occupied a wide range of environmental conditions and even occasionally overlapped in environmental space (Figure 3a), a clear distinction was seen between lianas and geoxyles. Lianas occupy the wettest climatic space, extending the environment occupied by *Ziziphus* (Figure 3a). The geoxylic habit is nested within the environmental space occupied by trees (Figure 3a) which may be because, beyond habit, geoxylic traits do not consistently differ substantially from their tree congeners (Gomes et al., 2019; Meerts, 2017). Environmental factors which drive the geoxylic habit are often related to frost (Finckh et al., 2016) and fire (Lamont et al., 2017; Maurin et al., 2014) or both in combination with herbivory (Meller et al., 2021). For *Ziziphus*, fire frequency aligns with shrub and tree forms whereas the one species of *Ziziphus*

with a geoxylic habit is associated with seasonality of temperature (Figure 3a). This association is replicated in other geoxylic species (Meller et al., 2021) in genera such as *Protea* (Lamont et al., 2017) and *Parinari* (Gomes et al., 2019).

Habit itself is an integrative trait, combining, for example, height, woodiness, multi-stemmed, or single-stemmed, which may clarify why assessed alone it can be used to differentiate groups of species in environmental space. To identify clusters of shared trait syndromes we used five traits—habit, spinescence, leaf hair, fruit hair, and bark hair. However, traits characteristic of different biomes, for example, seed size (in tropical rainforest; Eiserhardt et al., 2017), were not included in our analysis due to a lack of data. Given the significant role habit plays in the occupation of biomes by *Ziziphus*, it is likely that with a fuller set of trait data, a biome signal would emerge in the hierarchical clustering. Clustering analysis based on trait data showed that much of the variation in the data is unexplained, leading to an occasionally unclear signal of habit and biome in Figure 2. This suggests that trait variation in *Ziziphus* is driven by factors not explored in the MCA. Leaf area was not informative and was removed from analyses. While the leaf economic spectrum is a widely used framework for the positioning of traits in global trait space, some traits are likely to be independent of the resource acquisition/conservatism axis and these may well reflect regional or ecological adaptations to disturbance (Díaz et al., 2004; Wigley et al., 2020) or dispersal strategies. More studies are needed that examine how traits relate to plant performance across different environments (Funk et al., 2017), particularly in relation to dispersals across biomes. Leaf traits such as leaf nitrogen content per unit mass might provide a future pathway to unpicking some of the trait variations between species and its correlation with biomes. Nitrogen content in leaves varies by biome (Reich et al., 1999) and bark thickness has been shown to vary between trees from open and closed biomes (Charles-Dominique et al., 2017). While many *Ziziphus* species have edible fruits, only two are cultivated. Since softer fruit and a change in flavor are commonly observed trait changes in the domestication of crops (Meyer & Purugganan, 2013), for *Ziziphus*, data on wet and dry fruit mass and sugar content would likely start to separate species along a spectrum of cultivation traits.

4.2 | Effects of habit and biome on range sizes

Range size varied between habits with trees having a larger range than shrubs (Figure 3b). There are likely to be climatic and physiological reasons for this; trees dominate over shrubs when water supply is not limiting (e.g., in the United Kingdom; Kelly, 1996). Shrubs are better adapted to harsh conditions, dominating over trees in areas affected by drought or fire (Gaillard et al., 2018). Trees are taller than shrubs and tall species disperse further than short ones where the dispersal syndrome is shared (Thomson et al., 2011). Where height and range size data were both available, there was a positive, non-significant relationship (Figure S4).

In *Ziziphus*, lianas and trees did not have significantly different range sizes (Figure 3b). *Ziziphus* lianas are restricted to closed forests
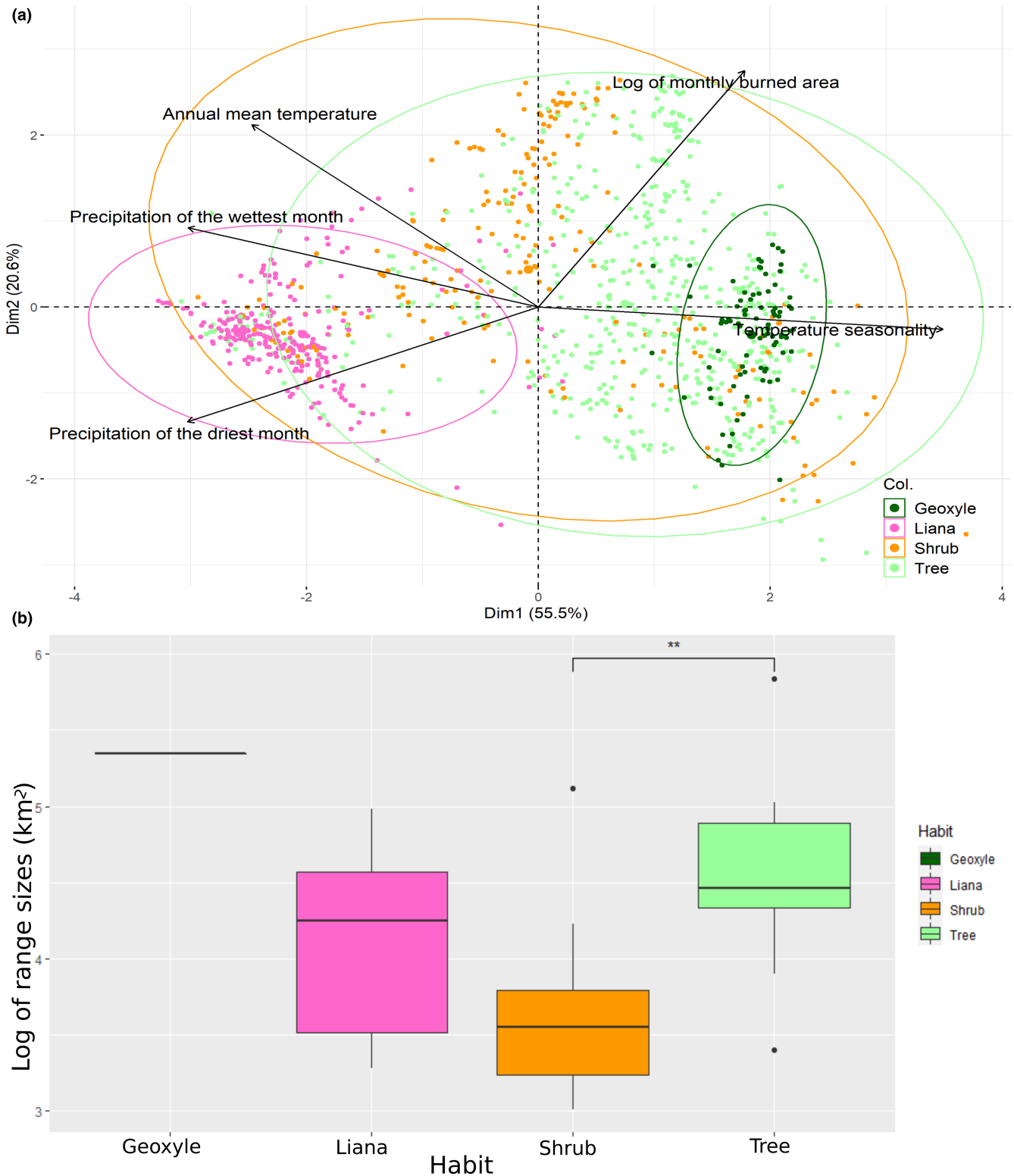
FIGURE 3 The effects of habit on environmental distribution and range size in non-cultivated *Ziziphus* species. (a) Principal components analysis biplot showing the environmental limits of 48 non-cultivated *Ziziphus* species and their associated habits. Ellipses indicate a 0.95 confidence interval. Habit attribution is described in the methods. Data on habits were curated from a combination of sources and are described in the methods and Table S4. Fire data were derived from the MODIS dataset MCD64A1 version 6 (Giglio et al., 2018) as described in the methods. Bioclimatic data were extracted using *Ziziphus* geolocation records from WorldClim 2.1 at 2.5 min resolution (Fick & Hijmans, 2017) and reduced to four variables as described in the methods. Variables utilized in the PCA are bio1 annual mean temperature, bio4 temperature seasonality, bio13 precipitation of the wettest month, and bio14 precipitation of the driest month. (b) Range size of non-cultivated *Ziziphus* species. Range sizes were ascertained for 44 species as described in the methods. Asterisks indicate $p < .01$.

where they are reliant on trees for support (Figure 2). Large-scale forest disturbance and tree-falls benefit liana abundance, but they also promote clonal reproduction. Unlike seed dispersal in trees, clonal ramets develop—and sometimes remain—attached to their parent plant (Ledo & Schnitzer, 2014). While this could restrict range size, Yorke et al. (2013) identified increasing liana abundance due to long-distance clonal dispersal. Further, lianas suffer less water stress than competitors in periods of seasonal drought due to their efficient vascular system and deep roots (Schnitzer, 2005). Although trees cover a greater environmental range than lianas (Figure 3a), lianas can densely occupy areas (Ledo & Schnitzer, 2014) which may lead to essentially equivalent range sizes under EOO where alpha hull = 1. Under less conservative alpha hulls, range sizes differed significantly between lianas and trees ($p < .05$) (Figure S5).

We hypothesized that range size would differ by biome, with the smallest range sizes in the closed ecosystem. We expected this because biome boundaries are barriers to the establishment of propagules and limit the geographic space available to species (Sheth et al., 2020). Closed forests in Southeast Asia are already highly fragmented due to logging and oil palm plantations (Waddell et al., 2020), increasing the number of establishment barriers and decreasing the amount of available habitat. Our finding that range size did not differ by biome strongly suggests that ultimately functional traits are more important for controlling range size than biome, because of their direct effects on dispersal, establishment, and survival. It is also likely that under-collection in open biomes leads to underprediction of range sizes.

4.3 | The environmental niche, range sizes, and traits of cultivated species

We found that in *Ziziphus* human use has expanded the climatic space occupied by *Z. jujuba* and *Z. mauritiana* (Figure S3). Beyond these two cultivated, edible species, the utilization of species differs bioclimatically. Wood use seems to be driven by temperature seasonality. Firewood and forage, the main uses for *Ziziphus* wood, are most likely to be required in drier regions where seasonal temperature fluctuations affect the availability of food and warmth (Figure S3). Edible species cover the broadest bioclimatic range (Figure S3), reflecting the fact that almost three times as many *Ziziphus* species' primary use is for edible fruit than for medicine. This may be a result of effective dispersal since species with tastier fruits are most likely to be dispersed by frugivores (Hladik, 1993). Further, although only *Z. mauritiana* and *Z. jujuba* are actively cultivated, many other species are harvested in situ, with some species such as *Ziziphus abyssinica* edible but eaten under famine conditions (Ruffo et al., 2002). Both wild harvesting and deliberate propagation of plants for food significantly increase plants' distribution (Flower et al., 2021). We also found that cultivated species occupied significantly different environmental niches than a non-cultivated comparator. This likely reflects the expansion of the environmental niche through cultivation. Human niche construction and ecosystem engineering have

been a feature of human society since the Late Pleistocene (Boivin et al., 2016) with the transplanting of fruit-bearing trees to settlements dated as far back as 11,000 years ago (Kislev et al., 2006).

While cultivation did not increase range sizes significantly, this is likely to be because of the small sample number—only two species in *Ziziphus* are cultivated. The range sizes of these two species are almost 10 times larger than the median of the range sizes of non-cultivated tree species. This relationship may well be reciprocal; the species selected for widespread cultivation are likely able to thrive in a variety of conditions as well as being useful (i.e., *Z. mauritiana*; a tree found abundantly in arid/semi-arid places; Singh et al., 2021; Singh & Meghwal, 2020; and also in humid forests; eFloras, 2008) and species used by humans fill more of their potential ranges than unused species (Flower et al., 2021). Flower et al. (2021) found that unused plant species filled significantly less of their range compared to species used for food, but that the difference was less clear when comparing food plants with species used for other purposes (i.e., medicinally). In *Ziziphus*, species were predominantly used, and species without known uses were excluded from our analysis. It is likely that the most striking range differences would be between cultivated and these unused/unknown species.

While we identified biome as a crucial component of the wide distribution and habit of *Ziziphus*, it is possible that geographic location may have a confounding effect. Within our study area, closed forest species are mainly restricted to Southeast Asia, and open biome species dominate in Africa (Figure 1a). It has been suggested that *Ziziphus* originates in Asia (Liu & Cheng, 1995) and the most recent phylogenetic work suggested a stem age for Ziziphus of 66my (Hauenschild et al., 2018). Given the relative youth of open biomes (~3–15my) in comparison to closed biomes (~66my) (Davies et al., 2020; Eiserhardt et al., 2017) it is likely that *Ziziphus* evolved out of the closed biome and the habits associated with it. Phylogenetic work is needed to investigate whether the age of *Ziziphus* species and habits is linked to biome and/or location.

5 | CONCLUSION

Diversity in habits and the utility of the *Ziziphus* species have compounded to expand the range and environmental occupation of the genus over evolutionary and human timescales. Liana species are restricted to closed biomes and the geoxylic habit is found only in open biomes, replicating broader geoxylic patterns (Maurin et al., 2014; Meller et al., 2021). Further, habit is significantly associated with range size, with trees having on average larger range sizes than shrubs, lianas, and geoxyles. We found that biome was not correlated with range size, however, this is likely to be an artifact of systematic under-collection in open biomes. Human use strongly affects species with cultivated species having ranges ~10 times that of non-cultivated tree species, and occupying significantly different and broader environmental niches.

Whether different habits in *Ziziphus* evolved in response to evolution into novel biomes and their specific biotic and abiotic

pressures, or whether diversity of habits facilitated this spread should be unpicked through future phylogenetic work. We can develop a greater understanding of biome evolution by investigating how traits interacted with biome diversification over time (Couvreur et al., 2015). Future work assessing the drivers of functional traits will be fundamental to understanding the dynamic processes which promote spread and diversification within the genus.

AUTHOR CONTRIBUTIONS

JR and CL designed the research and methodology. JR collected, curated, and analyzed data with inputs from CL and TP. JR wrote the first manuscript draft. All authors reviewed and edited the manuscript.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.34tmpg4p0 (Rickenback et al., 2022).

ORCID

Jess Rickenback https://orcid.org/0000-0001-5803-7728
Caroline E. R. Lehmann https://orcid.org/0000-0002-6825-124X

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SUPPORTING INFORMATION

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