RESEARCH PAPER

Diversification is decoupled from biome fidelity: *Acacia* – a case study

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Abstract

Aim: To investigate species and clade biome occupancy patterns of Australian *Acacia* to test for within-biome diversification, which indicate biome conservatism.

Location: Australia.

Taxon: *Acacia* (Fabaceae).

Methods: Species distributions were predicted for 481 Australian *Acacia* using the Thornley Transport Resistance Species Distribution Model and mapped across four biome typologies. Within *Acacia* 19 clades were identified. The number of biomes occupied and niche size was quantified for every species and clade using the range area projected by the distribution model. Relationships between clade species richness, niche size and biomes occupied were tested using phylogenetic least squares regression models.

Results: Only 9% of the *Acacia* 481 species and no clades were biome specialists. There were most specialist taxa in the Crisp Biome classification (8.7%), followed by WWF Biomes (6.2%), González–Orozco Biomes (5.0%) then Functional Biomes (1.2%). On average *Acacia* species occupied four WWF Biomes, seven Functional Biomes, three Crisp Biomes and three González–Orozco Biomes (out of 7, 13, 5 or 6 biomes respectively). Clades were also distributed across multiple biomes (2–13) with a significant positive relationship between clade species richness and the number of biomes occupied for all biome typologies. Species richness had positive linear relationships with biome area for all biome concepts except the González–Orozco Biomes. Larger clades had larger niche sizes.

Main conclusions: *Acacia* diversification occurred across biome boundaries and was not associated with biome specialization. Species and clades mainly occurred in multiple biomes, and there were typically few biome specialists. Diversification in *Acacia* appears to be decoupled from biome conservatism, associated with expanding niche size across biome boundaries. Major ecological–environmental units such as biomes may constrain adaptive radiation processes via biome conservatism in many groups, but this study leads us to hypothesize that for some lineages biome boundaries are permeable.

KEYWORDS

Acacia, biome, biome conservatism, diversification, evolutionary ecology, functional biomes, niche conservatism, species distribution modelling

1 | INTRODUCTION

Niche conservatism is the preservation of niche-related traits through time and is often considered a strong influence that shapes ecological and evolutionary interactions to determine patterns of biodiversity across a range of spatial scales (Wiens et al., 2010). Regional hotspots of biodiversity are often attributed to the accumulation of species with conserved environmental niches (Skeels & Cardillo, 2017) while the latitudinal gradient of species diversity is thought to reflect older, stable, tropical biomes having had more time to accumulate species (Wiens & Donoghue, 2004). Community assembly may also be influenced by niche conservatism if traits are filtered by local environmental factors (Ackerly, 2004). Niche conservatism may therefore restrict groups to specific habitats or biomes and thereby limit diversification opportunities.

Previous work indicates biome conservatism, in which species and lineages tend to diversify primarily within biomes, is common (Crisp et al., 2009; Crisp, Burrows, Cook, Thornhill, & Bowman, 2011; Cruz et al., 2017). Speciation events associated with biome shifts are apparently rare, but when they occur it tends to be between similar biomes (Crisp et al., 2009). The rarity of biome shifts suggests that biome boundaries are difficult for species and lineages to cross and may represent adaptive limits for evolutionary processes within groups. It is thought to be easier for species to disperse, sometimes intercontinentally to similar biomes, rather than occupy less similar but geographically adjacent biomes (Crisp et al., 2009; Donoghue & Edwards, 2014). Frequent biome shifts have been inferred in some lineages, but the species within such lineages are still typically restricted to one or a small number of biomes (Cardillo et al., 2017; Gamisch, Fischer, & Comes, 2016; Simon et al., 2009).

Biome conservatism is important to understand because it may have a fundamental influence on lineage diversification and constrain the ability of certain groups to adapt to global climate change and novel biomes in the future. Biomes are a conceptual typology that help us to understand how vegetation and ecosystem functioning is structured globally (Higgins, Buitenwerf, & Moncrieff, 2016a). Many terrestrial biomes are descriptive constructs developed by experts based on species distributions and broad patterns of climate and soil (Moncrieff, Bond, & Higgins, 2016). However, biome concepts do not generally consider disturbance or biotic processes which are known to influence species distributions (Moncrieff et al., 2016), and therefore may represent incomplete descriptors of the niches of species. There are many biome classifications defined in a variety of ways (Mucina, 2018), our approach is to use a range of biome classifications that differ strongly in their underlying assumptions.

Previous studies of biome conservatism have typically used descriptive and relatively simple biome concepts (e.g. Crisp et al., 2009; Simon et al., 2009). Many studies also assign species to a single biome or utilize analyses which can only accommodate one biome per species (e.g. Crisp et al., 2009; Crisp et al., 2011; Crisp, Cook, & Steane, 2004; Holstein & Renner, 2011), which is problematic because it assumes intraspecific biome conservatism. Assuming biome conservatism when species are actually occupying multiple biomes introduces bias by reducing the capacity to detect biome

shifts within a lineage. This is because shifts can only be detected when there is change in the modal biome between two sister taxa. In fact, studies that allow species to occur in multiple biomes appear to detect a higher frequency of biome shifts (e.g. Cardillo et al., 2017; Gamisch et al., 2016; Simon et al., 2009).

The emergence of new functional biome models and methods for predicting species distributions provides new opportunities for investigating biome conservatism and the evolutionary diversification within lineages. We aimed to investigate the role of biome conservatism in the diversification of a hyper-diverse group on a single continent to address our hypotheses:

1. Biome conservatism ensures that species are generally biome specialists, restricted to one or a small number of similar biomes.
2. Clades have clear biome preferences due to ancestral biome affinities and subsequent within-biome diversification driven by biome conservatism.
3. Highest richness clades are those that occupy few, similar, biomes due to biome conservatism favouring diversification of clades within a single biome or across several similar biomes.
4. Diversification in lineages is driven by within-biome specialization and niche packing, due to biome conservatism favouring partitioning of the ancestral niche, rather than niche expansion into different biomes.

We will also consider area effects and specialization to soil as possible alternatives to the within-biome specialization expected under biome conservatism.

In this study, we use four different biome classifications, defined using contrasting methods and are either global or continental in scope, with a process-based species distribution model (SDM) to determine occupancy of species in biomes. We selected Australian *Acacia* as a focal group to address these hypotheses because of the group's species richness (1,063 taxa; Maslin, 2015), and availability of phylogenetic, distributional and environmental information. *Acacia* is a characteristic group in the Australian flora and is hyper-diverse, to the extent that it is one of the most diverse vascular plant genera globally (Frodin, 2004). Hyper-diverse genera such as *Acacia* represent extreme examples of diversification. Even though such groups provide excellent opportunities for testing how biomes effect macroevolutionary dynamics, they have seldom been studied in this context.

2 | MATERIALS AND METHODS

2.1 | Biome concepts

We selected four biome concepts, two global and two limited to Australia. The aim was to compare inter- and intra-clade diversification in these four biome concepts, representing different typological methods. World Wildlife Fund (WWF) Ecoregions (Figure 1a, Olson et al., 2001, https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world), herein referred to as 'WWF Biomes' are global and based on climate, soils, existing vegetation maps and expert knowledge. There

WWF Biomes

Functional Biomes

Crisp Biomes

Gonzalez−Orozco Biomes
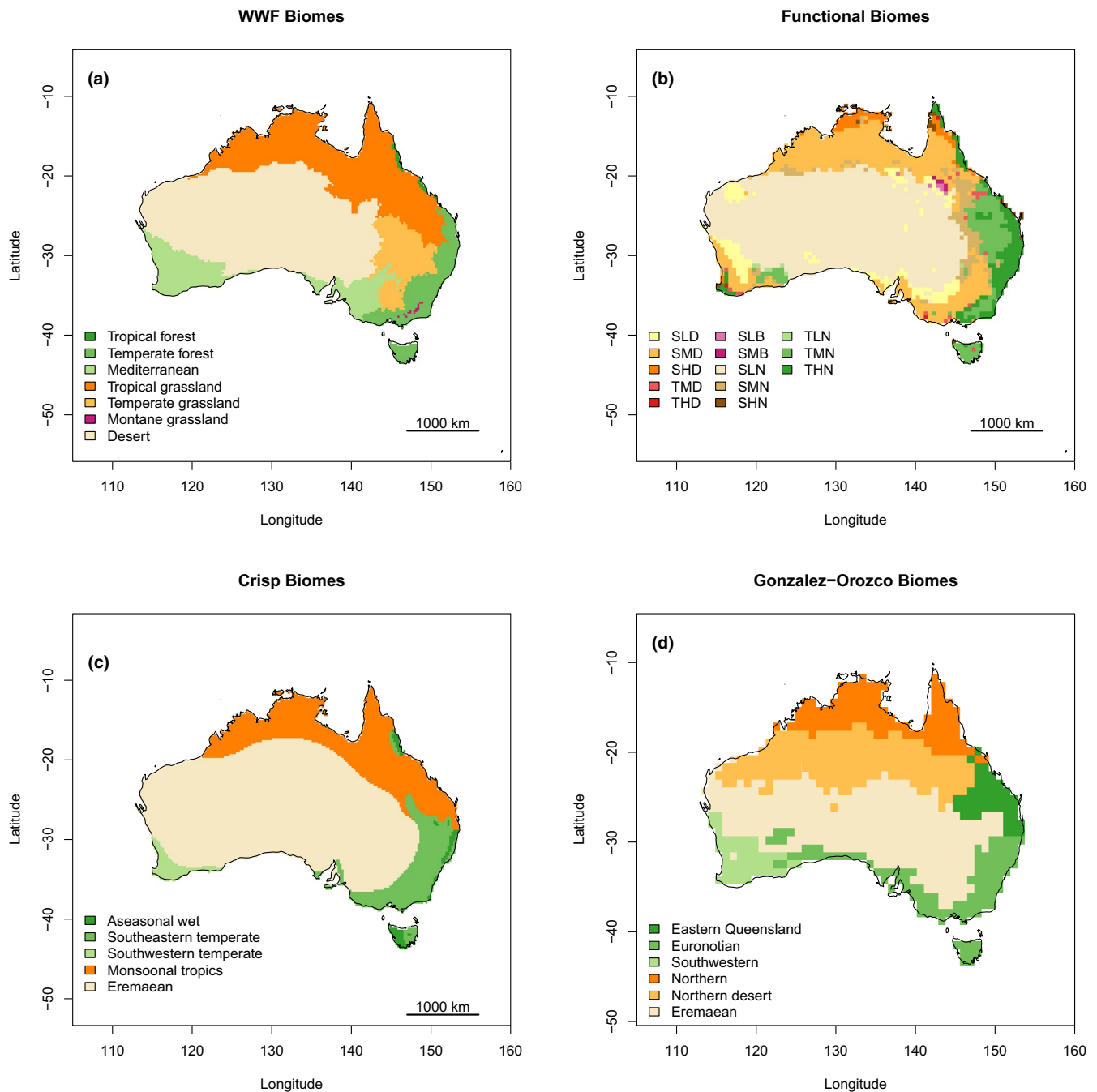
FIGURE 1 Biomes of Australia showing (a) WWF Biomes (Olson et al., 2001), (b) Functional Biomes (Higgins et al., 2016a), (c) Crisp Biomes (Crisp et al., 2004), and (d) González-Orozco Biomes (González-Orozco et al., 2014). The names of the Functional Biomes are a combination of vegetation height (S - Short or T - Tall); vegetation productivity index (L - Low, M - Medium or H - High); and how temperature and soil moisture limit growth seasonally (D - Dry, B - both cold and dry or N - non-seasonal). Projection is Mollweide and cell resolution is 0.25° (WWF Biomes, Crisp Biomes), 0.5° (Functional Biomes), and 0.9° (González-Orozco Biomes)

are seven WWF biomes that occur in Australia. We have shortened the WWF Biome names for brevity, with the original WWF names indicated within brackets: Tropical forest (Tropical and Subtropical Moist Broadleaf Forests), Temperate forest (Temperate Broadleaf and Mixed Forests), Mediterranean (Mediterranean Forests, Woodlands and Scrub), Tropical grassland (Tropical and Subtropical Grasslands, Savannas & Shrublands), Temperate grassland (Temperate Grasslands, Savannas and Shrublands), Montane grassland (Montane Grasslands and Shrublands), and Desert

(Deserts and Xeric Shrublands). Functional Biomes (Figure 1b, Higgins et al., 2016a; Higgins, Buitenwerf, & Moncrieff, 2016b) are also global and based on vegetation attributes quantifiable from satellite imagery: vegetation height (Short or Tall), vegetation productivity index (High, Medium or Low) and seasonality of growth (moisture limited, Dry; cold limited, Cold; moisture and cold limited, Both; or non-seasonal, Non-seasonal). Each of the 24 different Functional Biomes represents a different combination of these three vegetation attributes, and 13 of these Functional

Biomes occur in Australia: SLD (Short Low Dry), SMD (Short Medium Dry), SHD, (Short High Dry), TMD (Tall Medium Dry), THD (Tall High Dry), SLB (Short Low Both), SMB (Short Medium Both), SLN (Short Low Non-seasonal), SMN (Short Medium Non-seasonal), SHN (Short High Non-seasonal), TLN (Tall Low Non-seasonal), TMN (Tall Medium Non-seasonal) and THN (Tall High Non-seasonal). Crisp Biomes (Figure 1c, Crisp et al., 2004) are Australian biomes based on expert maps which consider climate, endemism and vegetation structure. There are five Crisp Biomes: Aseasonal wet, Southeastern temperate, Southwestern temperate, Monsoonal tropics and Eremaean. González–Orozco phyto-geographical regions (Figure 1d, González-Orozco et al., 2014), herein referred to as 'González-Orozco Biomes', are Australian biomes which are based on spatial turnover in species composition of nine major Australian vegetation groups: *Acacia*, Asteraceae, eucalypts, ferns, hornworts, liverworts, *Melaleuca*, mosses and orchids; determined from herbarium records on a 100 km^2 grid. There are six González-Orozco biomes: Eastern Queensland, Euronotian, South-western (hereafter 'Southwestern'), Northern, Northern desert and Eremaean.

2.2 | Phylogeny

Williams, Miller, Small, Nevill, and Boykin (2016) constructed a non-ultrametric phylogeny of Australian *Acacia* using a combination of genomic and amplicon sequences. For 65 *Acacia* taxa, sequences from the entire chloroplast genome and two nuclear ribosomal loci were used, and for 508 *Acacia* taxa, amplicon sequences of four chloroplast loci and two nuclear ribosomal loci were used (Mishler et al., 2014). This phylogeny has relatively even coverage across the entire lineage, including a range of species from six recognized major clades. We utilize this phylogeny, which includes 481 described *Acacia* species (45%) and is not time calibrated, but made ultrametric by scaling the root to 1 using the *chronos* function in the 'ape' package.

2.3 | Clade selection

We used the 481 described *Acacia* species included in the phylogeny of Williams et al. (2016) and selected 19 clades within this phylogeny with at least five species (5–22) and bootstrapped node support of at least 0.7 (Figure 2). Clades covered a total of 147 species (31% of species in the phylogeny).

2.4 | Modelling species distributions

Spatial data for all *Acacia* species were downloaded from the Australian Virtual Herbarium (AVH, http://avh.ala.org.au/) on 18th September 2015 (Data S1). All *Acacia* records within Australia, including Tasmania, were filtered using the filters in the AVH system to exclude 'cultivated', 'presumably cultivated', 'possibly cultivated',

0.05
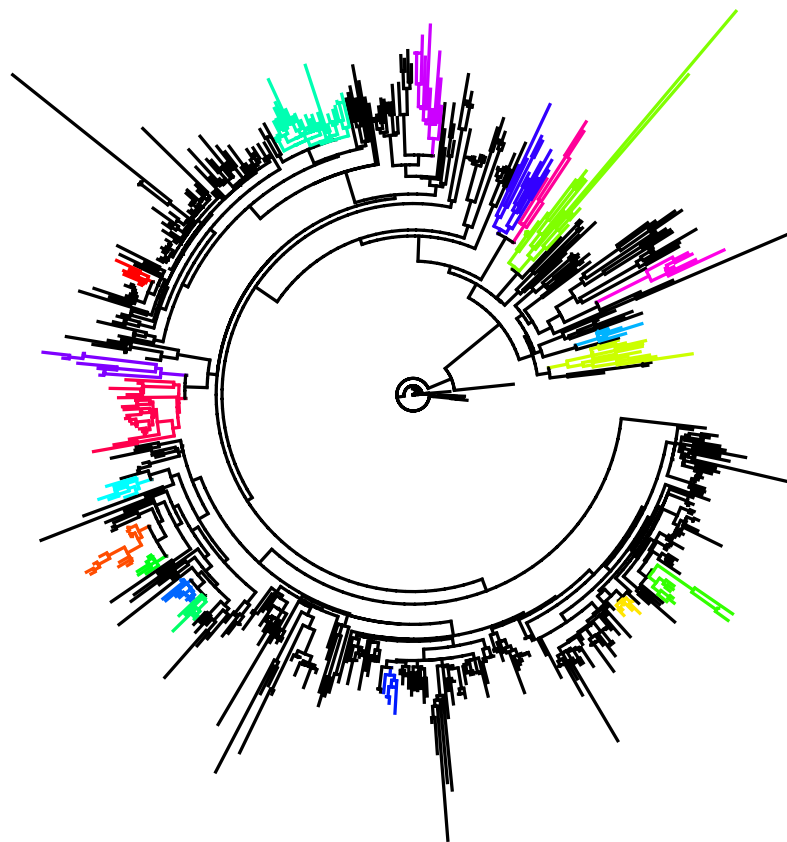
FIGURE 2 Phylogeny of Australian *Acacia* constructed by Williams et al. (2016) coloured to show the clades selected in this study. Scale is substitutions per site. An ultrametric version of this phylogeny was used for relevant analyses

'assumed to be cultivated' and any points that were not 'spatially valid'. Points are flagged as not 'spatially valid' in the AVH system if the coordinates are out of range, transposed, in the centre of the country of state, do not match the supplied state, are in the wrong hemisphere, have an uncertainty that is unspecified or <1, or have been flagged by a user as a suspected outlier. All hybrids and records not identified to species level were removed and any taxonomic classifications below species level (e.g. var. or subsp.) were combined with other records of that species. Two species present in Williams et al. (2016) phylogeny (*Acacia diphylla, A. bartleana*), were not represented in the spatial data so were excluded from this study.

To ensure that the species names in the phylogeny and distribution data matched, scientific names were checked using the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/) with the International Legume Database and Information Service (ILDIS) as the highest-ranked source. Only accepted names within *Acacia* were used. For Species Distribution Modelling we randomly sampled a maximum of 2000 AVH occurrence records to be used as the presence point of each species. If fewer than 2000 occurrence records were available, we used all data points as presence points. Because absence data are not available we generated pseudo-absence points by randomly sampling an equivalent number of points from Australia, but excluded points within 0.1° of the occurrence records of the target species. Use of pseudo-absences is widely practiced in species distribution modelling (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012).

Potential species distributions were modelled for 481 *Acacia* species in the Williams et al. (2016) phylogeny using the 'TTR.SDM' R package which utilizes the Thornley Transport Resistance (TTR) model (Higgins et al., 2012). The TTR-SDM defines the physiological niches of vascular plant species by using distribution data to calibrate a process-based physiological model derived from the Thornley Transport Resistance (TTR) model (Thornley, 1972, 1998). It considers pools of carbon, nitrogen and biomass in the roots and shoots of plants and how physiological processes of resource assimilation, resource allocation, growth and respiration interact to determine these pools. Each physiological process in the model is constrained by environmental factors on a monthly time step. For example, shoot growth is limited by temperature, whereas nitrogen uptake is co-limited by temperature, soil moisture and soil nitrogen levels. The parameters which describe these environmental constraints are estimated by inferring the parameter combinations which best explain the observed distribution of each target species. These ecologically informative output parameters we hereafter refer to as 'niche traits'. As is typical for species distribution models, our predicted distribution reflect the potential niche of species. This does not consider dispersal limitation or biotic interactions which are likely to limit actual distribution of species to a subset of their potential niche. Other assumptions of the model are addressed in detail in Higgins et al. (2012). Environmental data layers used in the model were World Clim mean monthly temperature, maximum monthly temperature and minimum monthly temperature (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005); GSDE soils total *N* (Shangguan, Dai, Duan, Liu, & Yuan, 2014), CGIAR's monthly solar radiation and soil water content (Trabucco & Zomer, 2010). All environmental layers were at a resolution of 1 km, except GSDE soil total N, which was available in 0.5' resolution, and data were extracted from all these layers for each presence and pseudo-absence point.

The model fits were assessed using the confusion matrix of true positives, true negatives, false positives and false negatives, with particular emphasis being given to the rate of false negatives (see Table S1 in Data S2). The model fits were good for all species. For 95% of species the false negative rate was <0.018, and across all species it was never worse than 0.064.

2.5 | Biome occupancy

Biome occupancy for each focal species and *Acacia* clade was determined by identifying which WWF Biomes (using a 0.25° resolution raster), Functional Biomes (using a 0.5° resolution raster), Crisp Biomes (using a 0.25° resolution raster) and González–Orozco Biomes (using a 0.9° resolution raster) each cell of the predicted species distribution occurred in.

Biome areas ranged in size over a similar magnitude for three of the biome concepts. WWF Biome sizes ranged from 0.14% (Montane grassland) to 46.6% (Desert) of the surface of Australia, Functional Biomes ranged between 0.1% (THD) to 50.7% (SLN) of the surface of Australia and Crisp Biomes ranged between 1.4% (Aseasonal wet) and 64.0% (Eremaean) of the surface of Australia. The González–Orozco Biomes had less variation in biome sizes compared to the other biome concepts, with biomes ranging in size from 4.9% (Eastern Queensland) to 36% (Eremaean).

2.6 | Hypothesis testing

2.6.1 | Species and clade biome specialization

We tested for within-biome diversification by quantifying phylogenetic signal in the number of WWF, Functional, Crisp and González–Orozco Biomes occupied by species and clades using the *K* statistic (Blomberg, Garland, & Ives, 2003) and Pagel's (1999) λ, calculated using the *phylosig* function in the 'phytools' package (Revell, 2012). Significant phylogenetic signal would demonstrate clustering of biome specialization across the *Acacia* phylogeny. The *K* and λ statistics quantify the observed variance in number of biomes occupied in relation to expected variance with evolution of the phylogenetic tree under Brownian motion. Values of *K* or λ < 1 indicate that the relatives are less similar than expected under Brownian motion evolution along the phylogeny, while *K* and in some cases λ > 1 imply relatives are more similar than expected. We generated a null distribution for *K* and λ by randomly shuffling the tips of the phylogeny 1,000 times using the *tipShuffle* function in the 'picante' package (Kembel et al., 2010) and calculating the *K* and λ for each shuffled phylogeny. Phylogenetic signal was considered significant if the observed *K* or λ was greater than null *K* or λ more than 95% of the time.

2.6.2 | Diversification in relation to biomes

We investigated the significance of the relationships between number of species in a clade and number of biomes occupied using a phylogenetically corrected least squares (PGLS) achieved with the R package 'caper' (Orme et al., 2013). The lambda parameter was estimated using the maximum likelihood function. This allowed us to test our hypothesis of highest species richness in clades that occupy few, similar biomes due to biome conservatism.

To allow for the effect of differences in biome area for niche size calculations, we stratified sampling of the cells in Australia, for all resolution rasters, to include an equal number of cells from each biome. We excluded biomes that covered less than 1% of Australia, then identified the remaining biome with the smallest number of cells in each biome typology and used this number of cells as the sample size for stratified sampling of cells within each biome. This resulted in a random sample of cells from across Australia with an equal number of cells from each biome. We identified whether each *Acacia* species and clade was predicted to occur in each cell based on our TTR-SDM predicted distributions. We refer to these as the 'area corrected' predicted distributions. We determined species and clade niche size, to test for niche packing within biomes, by quantifying the proportion of the total available area covered by the area corrected predicted distribution of each species and each clade.

We used a PGLS model to model clade niche size by number of species and number of biomes occupied to test the hypothesis of diversification driven by within-biome specialization and niche packing due to biome conservatism. The model was implemented using the 'caper' package with the lambda parameter and was estimated using a maximum likelihood function.

2.6.3 | Area effects

To provide an alternative model of diversity patterns in relation to biomes to expectations under biome conservatism, we tested the relationship between biome area and *Acacia* species richness, clade richness and phylogenetic diversity using a linear regression model. For these regressions, we tested model assumptions by constructing residuals versus fitted values plots and using normal Q-Q plots.

We quantified phylogenetic diversity of *Acacia* within each biome by calculating mean pairwise distance on the original, non-ultrametric, phylogeny of all the species occupying each biome using the *mpd* function in the R package 'picante' (Kembel et al., 2010).

2.6.4 | Specialization to soil

To test for specialization to soil within *Acacia*, as a potential alternative driver of diversification to within-biome specialization, we quantified

trait dissimilarity between species for climate and soil traits. Climate traits were the 22 climate-based TTR-SDM traits (Higgins et al., 2012) from this study. Soil traits were the two soil nitrogen TTR-SDM traits from this study and median soil nutrient preferences of Australian *Acacia* species quantified by Bui, González-Orozco, and Miller (2014). Soil nutrient traits from Bui et al. (2014) were aluminium, calcium, magnesium, sodium, phosphorus, pH and electrical conductivity. These soil traits were sampled at 0–10 cm (Al, Ca, Mg, Na, P, pH and EC) and 60–80 cm (Al.B, Ca.B, Mg.B, Na.B, P.B, pH.B and EC.B). To determine trait dissimilarity between species we rescaled each variable from 0–1 then calculated the mean Euclidean distance in values of each trait for species within each clade.

2.7 | Examining sampling bias

To determine how our cell-based approach for determining biome affinity was influencing biome occupancy trends, we quantified biome affinity of each *Acacia* species and clade with a range of cell thresholds from 1 to 10 cells. Cell thresholds were the minimum number of cells of a biome that a species or clade had to occur in for that species or clade to be considered as occurring in that biome. The frequency distribution of biomes per species was qualitatively equivalent for each cell threshold of 1–10 cells (Figure S1 in Data S2). Ten cells equate to 5% or more of the biome area for two of the seven WWF biomes, 11 of the 14 Functional Biomes, one of the five Crisp Biomes, and two of the six González–Orozco Biomes; representing a reasonable area that is not so large that smaller biomes have insufficient cells for species to cross the threshold for biome occupancy. Based on this cell threshold test, presence of a species or clade in a single cell of a biome was used to determine the biome membership throughout the study. Because we have used a single cell as the threshold for affiliation with a biome, we will refer to biome membership as 'biome occupancy' throughout.

We also determined biome occupancy for each species based on the AVH occurrence records to check whether biomes were evenly sampled in herbaria. Relative sample size of presence points were quantified for every species in this study by $\log_{10}$ transforming the number of presence points in each biome then dividing it by the area of the biome. Expected sample size was calculated as the mean number of presence points per species divided by the area of Australia. To test whether sampling was even across biomes we compared the median relative sample size for each biome to the expected sample size. A median relative sample size less than the expected sample size would indicate under-sampling of that biome.

3 | RESULTS

3.1 | Species biome specialization

We found that few species (6.2% for WWF Biomes, 1.2% for Functional Biomes, 8.7% for Crisp Biomes and 5.0% for González–Orozco Biomes;
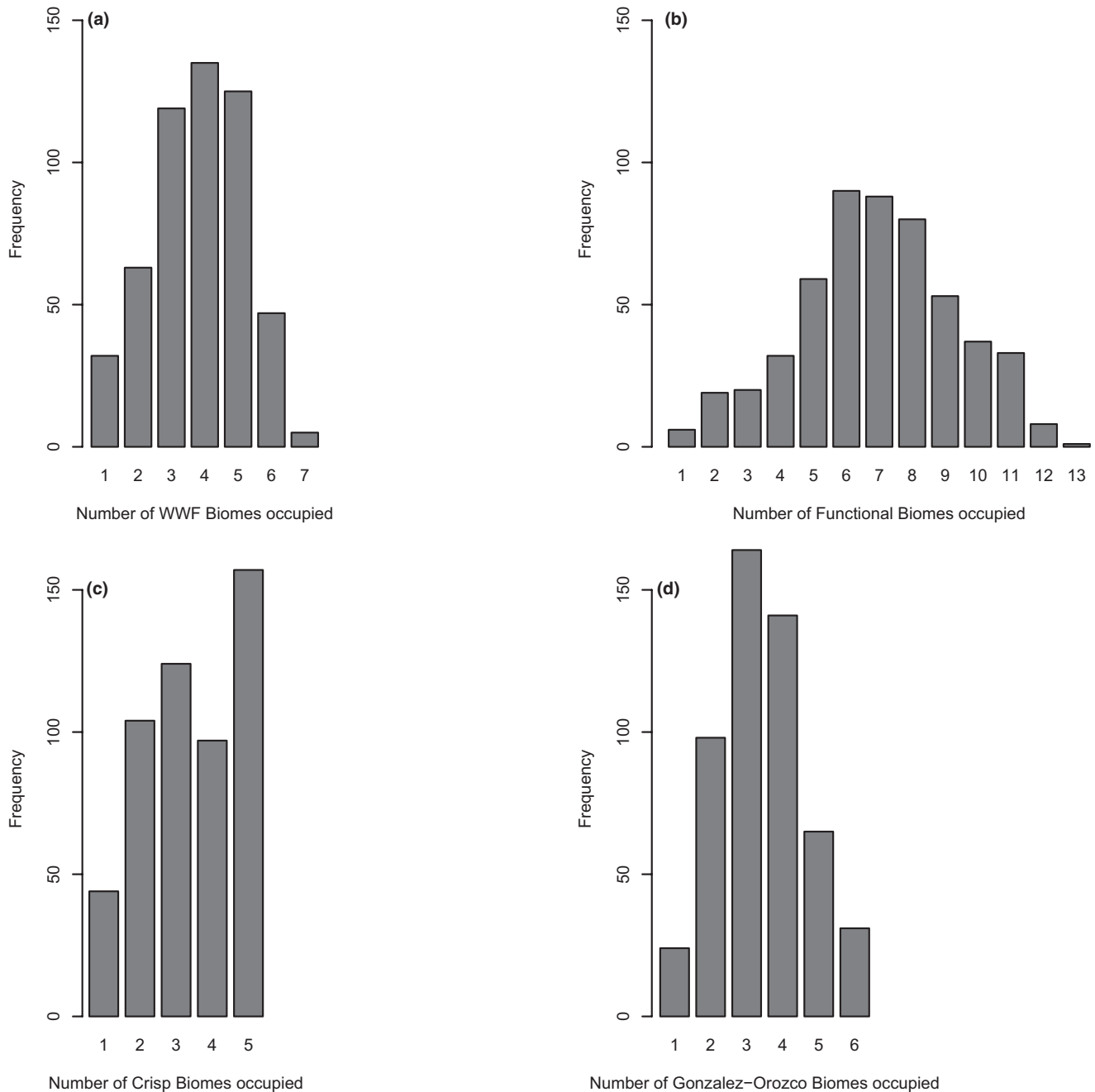
FIGURE 3 Number of biomes (a) WWF Biomes, (b) Functional Biomes, (c) Crisp Biomes, and (d) González-Orozco occupied by *Acacia* species in Australia derived from predicted species distributions

Figure 3) were restricted to a single biome. Few species were predicted to occur in all biomes for three biome typologies: four (0.8%) for WWF Biomes, one (0.2%) for Functional Biomes and 27 (5.61%) for González–Orozco Biomes. The majority of species in these three biome typologies were distributed across an intermediate number (2–6 for WWF Biomes, 2–11 for Functional Biomes and 2–5 for González–Orozco Biomes) of biomes. The Crisp Biomes contrasted to this with 143 species (29.7%) occurring in all five biomes. Only 30 species were in a single WWF Biome, the greatest number were in Tropical grassland (17), followed by Mediterranean (6), Temperate forest (4) and Desert (3). Restricted biome distributions were much less frequent for Functional Biomes, with THN

(4) and SLN (2) the only biomes with species exclusively in one biome. There were 42 species that occurred in a single Crisp biome, the most occurred in the Eremaean (32) and the rest in the Monsoonal tropics (10). The González–Orozco Biomes has 24 species occurring in a single biome, half of which were restricted to the Northern biome (12), with Eremaean (4), Euronotian (3), Southwestern (3) and Eastern Queensland (2) as the next most frequent biomes occupied. These results were qualitatively similar irrespective of the threshold used (1–10 cells) to define biome membership (Figure S1 in Data S2). The K and λ statistics generally indicated low resemblance among relatives in the degree of biome specialization. Phylogenetic signal in the number of WWF Biomes, Crisp

Biomes and González–Orozco Biomes occupied by species were not significant for the K statistic (WWF Biomes observed K < 0.0001 <95% of null distribution, Crisp Biomes observed K < 0.0001 <95% of null distribution, González–Orozco Biomes observed K < 0.0001 <95% of null distribution), but were significant for Pagel's λ (WWF observed λ = 0.99 >95% of null distribution, Crisp observed λ = 0.94 >0.95% of null distribution, González–Orozco observed λ = 0.27 >0.95% of null distribution), though they were less than one indicating low resemblance among relatives. In contrast, Functional Biomes had significant phylogenetic signal in number of biomes occupied for both metrics (observed K < 0.0001 >95% of null distribution, observed λ = 0.93 >0.95% of null distribution). Despite exhibiting significantly higher phylogenetic signal than the null K or λ distributions, the value of the K statistic was close to zero (8.15 x 10^{-4}), and Paygel's λ was less than one (0.93), indicating that the number of Functional Biomes occupied has low resemblance among relatives.

3.2 | Clade biome specialization

No clades occupied a single biome in any classification typology. All clades were distributed across at least two WWF Biomes, five Functional Biomes, three Crisp Biomes, or four González–Orozco Biomes (Figure 4). There was no phylogenetic clustering of clades based on number of biomes occupied (Figure 4a) for WWF Biomes (observed K = 0.03 <95% of null distribution, observed λ < 0.001 <95% of null distribution), Functional

Biomes (observed K = 0.11 <95% of null distribution, observed λ < 0.001 <95% of null distribution), Crisp Biomes (observed K = 0.04 <95% of null distribution, observed λ < 0.001 <95% of null distribution) or the González–Orozco Biomes (observed K = 0.03 <95% of null distribution, observed λ < 0.001 <95% of null distribution).

3.3 | Diversification in relation to biomes

We detected a significant relationship between species richness of a clade and the number of biomes occupied for all biome concepts (Figure 5).

There was a significant positive relationship between clade niche size and species richness for all biome typologies (Figure 6), suggesting that diversification is associated with niche expansion rather than niche partitioning. The number of biomes occupied for all biome typologies was a non-significant variable in the models (Figure 6), indicating that diversification is occurring independently of biomes.

3.4 | Area effects

Larger biomes had greater species richness. There was a significant positive linear relationship between biome area and species richness
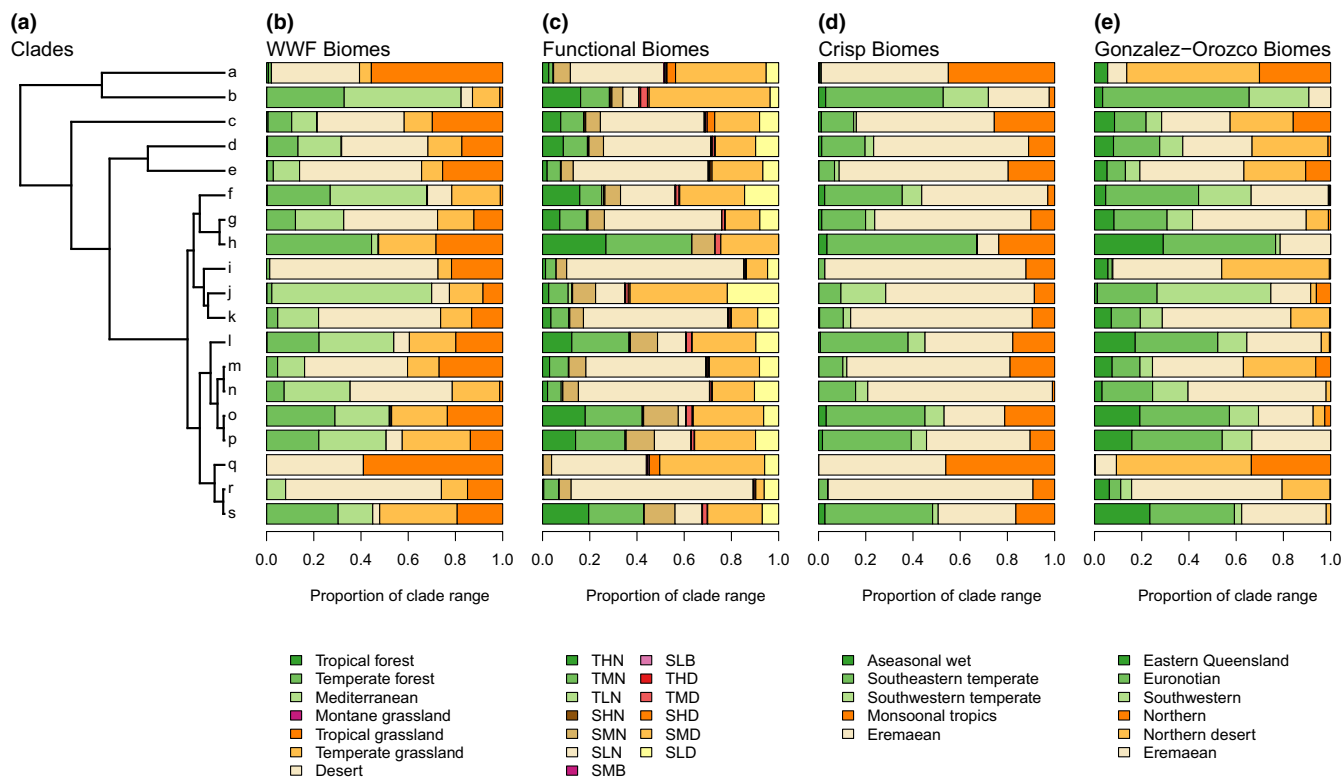
FIGURE 4 (a) Phylogeny of clades of Australian *Acacia* with biome occupancy in (b) WWF Biomes, (c) Functional Biomes, (d) Crisp Biomes, and (e) González-Orozco Biomes calculated using distributions predicted using Thornley Transport Resistance Species Distribution Model. Colours indicate different biomes

FIGURE 5 Species richness of Australian *Acacia* clades in relation to number of (a) WWF Biomes, (b) Functional Biomes, (c) Crisp Biomes, and (d) González-Orozco Biomes occupied using area-corrected predicted distributions generated using the Thornley Transport Resistance Species Distribution Model. *p*-values and lines indicate phylogenetic Poisson regression models fitting predicting species richness of clades by the number of biomes occupied by each clade
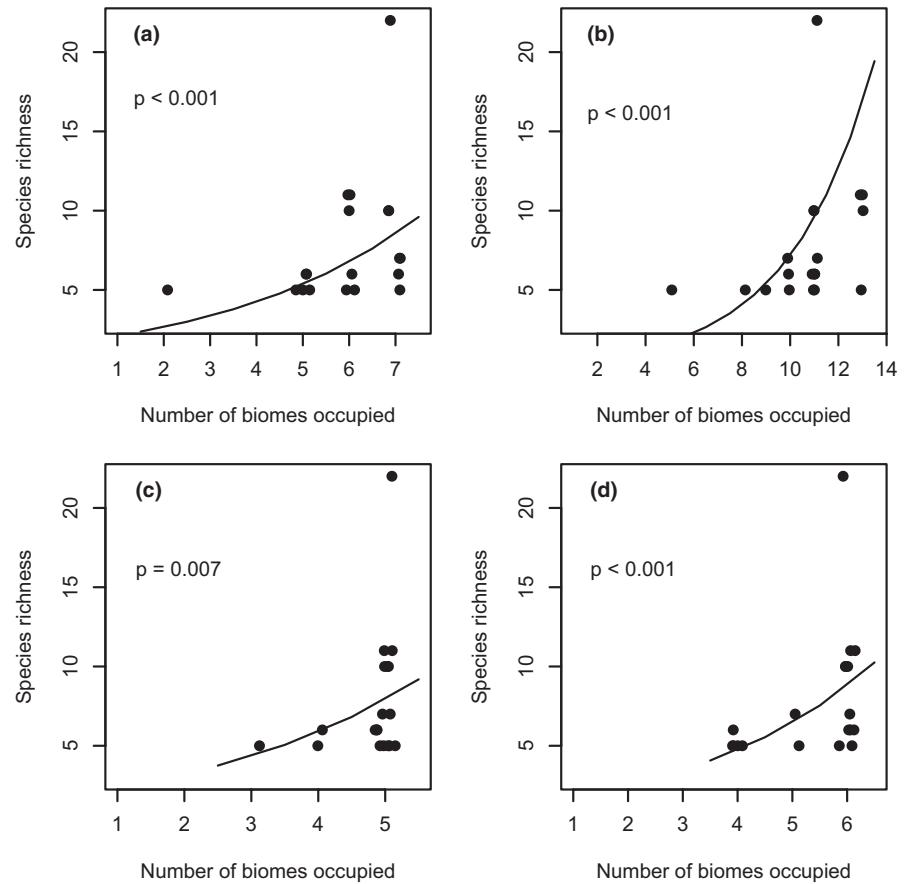
for WWF Biomes, Functional Biomes and Crisp Biomes, but not González–Orozco Biomes (Figure 7). Biome area was also positively associated with the number of clades present in a biome for WWF Biomes and Functional Biomes (Figure 7). There was no significant relationship between biome area and phylogenetic diversity of a biome for any of the biome typologies (Figure 7).

3.5 | Specialization to soil

We found no evidence of specialization to soil type. Dissimilarity between species in relation to the nutrient status of soils were equal to or lower than the trait dissimilarity between species of the TTR-SDM climate traits (Figure S2a,b in Data S2). This was a consistent trend in trait dissimilarity across all 481 species and within each clade. This indicates specialization to soil is not a convincing alternative to biome specialization as a driver of diversification in *Acacia*.

3.6 | Examining sampling bias

There was a greater degree of biome specialization (12%–35% biome specialist species) detected when using the observed species data records (Figure S3 in Data S2) rather than the distributions predicted using SDM. However, when assessing sampling bias, we found three WWF Biomes (Tropical grassland, Temperate grassland, and Desert),

four Functional Biomes (SMD, SLN, SMN, and TMN), one Crisp Biome (Eremaean) and two González–Orozco Biomes (Eremaean and Northern Desert) had median relative sample sizes lower than expected (Figure S4 in Data S2), which is indicative of under-sampling.

4 | DISCUSSION

4.1 | Species and clade biome specialization

For Australian *Acacia* we found few biome specialists, at both the species and clade level. This contrasts with our hypothesis that biome conservatism leads to biome specialization in species and in clades, resulting in a pattern of within-biome diversification. We did not detect any evidence for biome conservatism within clades, species, or across the phylogeny. Our results show that the majority (>80% for WWF Biomes, >95% for Functional Biomes, 71% for Crisp Biomes and 75% for González–Orozco Biomes) of *Acacia* species occupy a broad range (3 or more) biomes. This generalist biome strategy and the absence similar biome preferences across clades contrasts to the previous work indicating that biome shifts are infrequent (Crisp et al., 2009; Cruz et al., 2017; Holstein & Renner, 2011). The multitude of *Acacia* species occupying a range of biomes was unexpected, considering the environmental disparity between biomes commonly occupied by single species, for example Temperate forest and Desert (WWF Biomes) or TMN (tall, medium productivity, non-seasonal) and
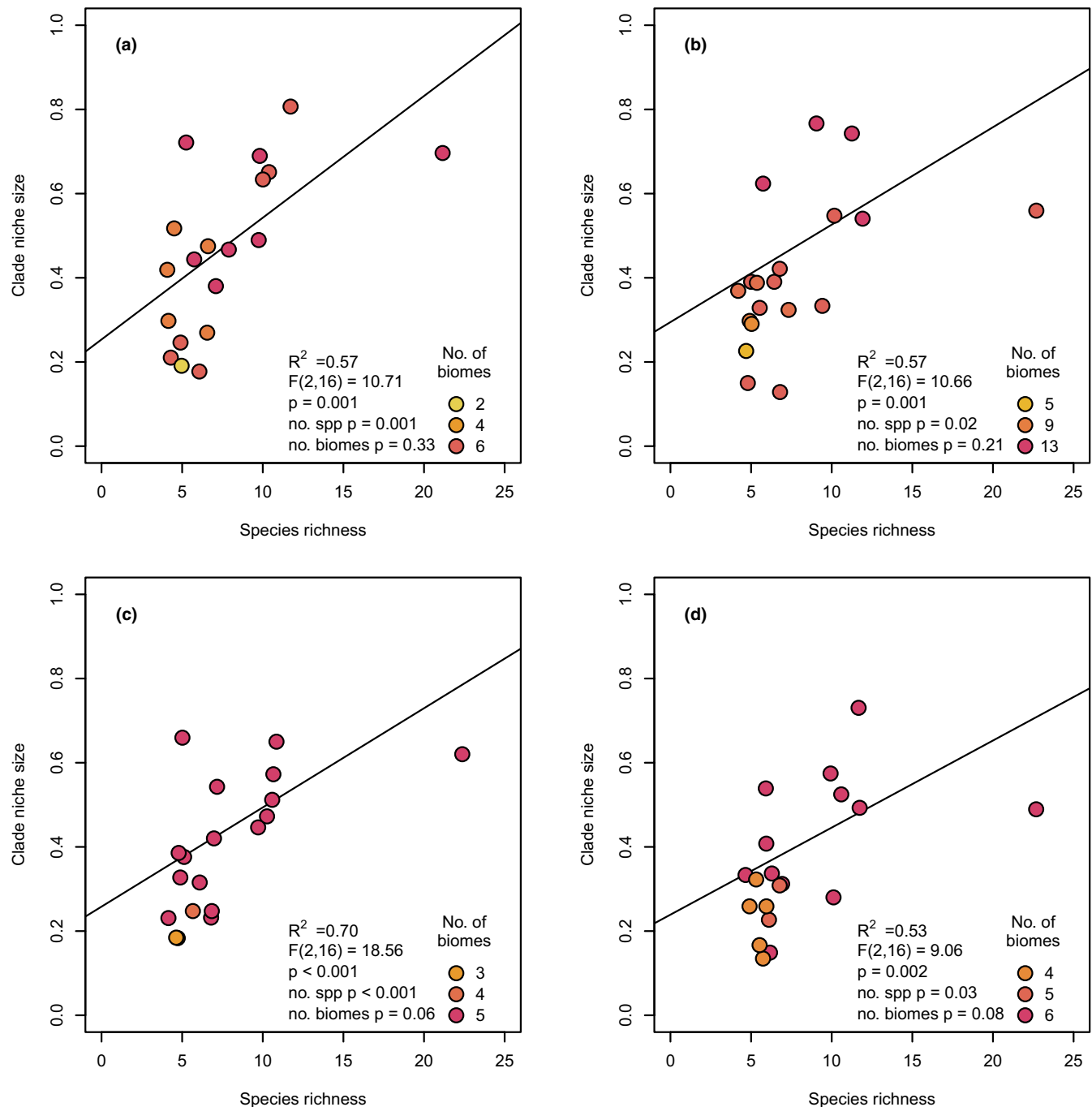
FIGURE 6 Effect of species richness and number of biomes occupied on niche size for 19 Australian *Acacia* clades based on predicted distributions derived from the Thornley Transport Resistance Species Distribution Model, in (a) WWF Biomes, (b) Functional Biomes, (c) Crisp Biomes, and (d) González-Orozco Biomes. Clade niche size is as a proportion of total available niche size. Model information is for best fitting phylogenetic least squares models between niche size, number of species and number of biomes occupied. Lines indicate the relationship between niche size and number of species because the number of biomes occupied was not a significant model predictor

SLD (short, low productivity, moisture limited; Functional Biomes). It was also surprising given the time available for species specialization and accumulation in these particular environments. *Acacia* has been present in Australia since at least the Late Oligocene–Early Miocene (Macphail & Hill, 2001). Arid biomes developed in Australia in the Mid-Miocene (Crisp & Cook, 2013), and at that time the ancestor to *Acacia* is thought to have inhabited everwet or sclerophyll

biomes (Crisp & Cook, 2013), equivalent to the WWF Biomes of Tropical forest, Temperate forest and Mediterranean; TLN, TMN and THN for Functional Biomes, Aseasonal wet and Southeastern temperate for Crisp Biomes, and Eastern Queensland and Euronotian for González–Orozco Biomes. This early occurrence provides opportunity for *Acacia* to capitalize on the formation and expansion of arid biomes, such as Desert and Temperate grassland (WWF Biomes), SLN
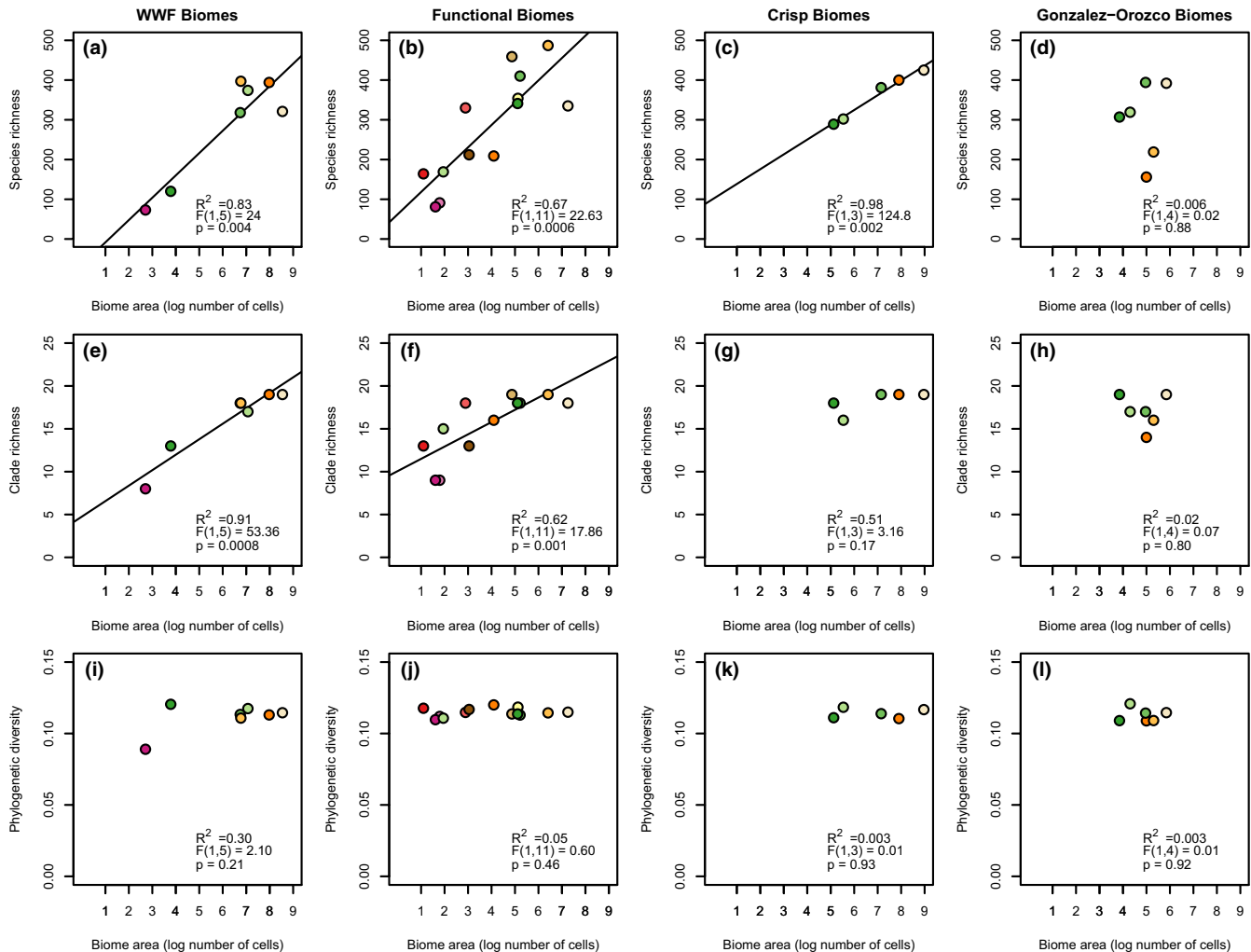
FIGURE 7 Species richness, clade richness, and phylogenetic diversity of Australian *Acacia* within each biome in relation to biome area. Species richness for each biome of (a) WWF Biomes, (b) Functional Biomes, (c) Crisp Biomes, and (d) González-Orozco Biomes. Clade richness for each biome of (e) WWF Biomes, (f) Functional Biomes, (g) Crisp Biomes, and (h) González-Orozco Biomes. Phylogenetic diversity for each biome of (i) WWF Biomes, (j) Functional Biomes, (k) Crisp Biomes, and (l) González-Orozco Biomes. Phylogenetic diversity is mean phylogenetic pairwise distance. Area calculations based on predicted species distributions. Cell resolution is 0.25° (WWF Biomes, Crisp Biomes), 0.5° (Functional Biomes), and 0.9° (González-Orozco Biomes). Lines show significant, best fitting linear regression models

and SLD (Functional Biomes), Eremaean (Crisp Biomes) or Eremaean and Northern desert (González–Orozco Biomes). The development of these arid biomes in central Australia during the Miocene, coincided with major diversification in *Acacia* (Miller, Murphy, Ho, Cantrill, & Seigler, 2013), however, our results suggest that this diversification was not associated with biome specialization.

4.2 | Diversification in relation to biomes

We hypothesized that biome conservatism would favour within-biome diversification and predicted that clades with the highest species richness would occupy few biomes. But in fact we found the opposite pattern. We observed a positive relationship between the species richness of a clade and the number of biomes occupied for all biome typologies. This relationship contrasts with the expectation

under biome conservatism of diversification predominantly happening within biomes, resulting in species-rich clades that occupy few biomes. Because of the degree of diversification involved in a hyper-diverse lineage like *Acacia*, we may expect to see different patterns and drivers of diversification than in less diverse lineages. It is possible that the lack of biome conservatism is a prerequisite for such prolific and unusual diversification. González-Orozco, Laffan, Knerr, & Miller et al. (2013) identified five bioregions of *Acacia* using a cluster analysis of species turnover patterns. These *Acacia* bioregions conform to similar boundaries as the biomes used by Crisp et al. (2004) and González-Orozco et al. (2014) for the entire Australian flora, indicating consistent environmental drivers of diversification for *Acacia* as for the entire Australian flora. Our findings linking higher species richness to occupying multiple biomes, indicate that diversification occurred across biome boundaries rather than via specialization within biomes.

We hypothesized that lineage diversification would be linked to within-biome specialization and niche packing, reflecting the constraints of the ancestral niche. Niche packing within biomes would therefore limit niche size, which would be independent of species richness. Results for *Acacia* show that total niche size of clades increased with the species richness of the clade, but was independent of the number of biomes occupied. This niche size–richness relationship highlights the importance of niche expansion across biomes boundaries in *Acacia*.

4.3 | Area effects

We observed a positive relationship between the area of a biome and its species richness, and, to a lesser degree, clade richness. This biome species richness–area relationship indicates that geographic space is important in the diversification process and subsequent community assembly (Vamosi & Vamosi, 2010), which together shape current spatial patterns in species richness. Although we detected no relationship between biome area and phylogenetic diversity, the consistency of the positive biome area and richness association across clades and species makes us confident that area is important at a range of diversity levels. Geographic space likely promotes diversification through greater topographic variability (Kisel, McInnes, Toomey, & Orme, 2011), which presents more opportunities for specialization to microclimate and provides refugia (Speziale & Ezcurra, 2015), which elevates potential for allopatric speciation (Kisel et al., 2011) and lowers extinction rates (Payne & Finnegan, 2007). Microclimate specialization can be seen in isolated communities of *Acacia*-dominated species away from the climate zone they typically inhabit, resulting from retreat of favourable habitat with changing climate that leaves refugia surrounded by unsuitable habitat (Johnson & Burrows, 1994). Large areas also decrease extinction risk by providing greater total resources, which can provision more individuals, than an equivalent smaller area.

4.4 | Specialization to soil

Our findings show diversification in *Acacia* is not characterized by specialization to biomes, and is therefore independent of broad scale climate patterns. It has previously been suggested that *Acacia* diversification is linked to edaphic heterogeneity (Bui et al., 2014). If diversification in *Acacia* is driven by specialization to different soil types, rather than climate, we would expect to see greater variation across the phylogeny, or within clades, in soil preferences compared to climate occupancy. However, we found lower variability in *Acacia* soil nutrient traits across the phylogeny, for both those derived using the TTR-SDM and those measured by Bui et al. (2014), compared to climate-based TTR-SDM parameters. The similarity of soil traits suggest soil overall is unlikely to be a key selective pressure in driving reproductive isolation and *Acacia* diversification. However, the presence and diversification of *Acacia* in oligotrophic and arid environments during the

Miocene (Crisp & Cook, 2013) may have been facilitated by the development of nitrogen fixation, that is, a gateway trait sensu (Donoghue & Edwards, 2014).

Our findings of species and clades typically occupying multiple biomes, diversification across biome boundaries and a lack of support for biome conservatism contrast to several previous studies. Crisp et al. (2009) revealed strong phylogenetic biome conservatism across 45 southern hemisphere phylogenies and seven biomes, noting that the majority of sister-pairs (94%) occupied the same biome. However, the outcome of their analysis may have been influenced by a conservative biome assignment strategy and the subjectivity of biome differentiation. Mishler et al. (2014) who utilized phylogenetic measures (diversity, endemism) to identify geographic patterns in the age of endemism in Australian *Acacia*, found areas with taxa representing a combination of paleo and neo-endemics were much more common than centres of either primarily paleo or neo endemics. This supports our conclusion of ongoing diversification across all biomes, rather than diversification occurring primarily within specific biomes. Hopper and Maslin (1978) suggested that local *Acacia* diversity in Western Australia was the result of the interaction between Pleistocene climate fluctuations, topographic variation and local climate gradients creating high temporal and spatial heterogeneity for the migration, extinction and isolation of populations. If this combination of conditions is consistent at the continental scale and is driving *Acacia* diversification, our results suggest they are appear to occur across all biomes occupied by *Acacia*.

Our findings of few biome specialist species contrasts to previous work in which within-species biome specialization is typical, even in lineages where biome shifts are common, as these shifts are often deep in the phylogeny. For example, the proportion of species occupying a single biome was 87% for *Bulbophyllum* orchids in Gamisch et al. (2016) and 75% in Cardillo et al. (2017). Work by Cardillo et al. (2017) on *Hakea*, also using WWF Biomes in Australia, found frequent biome shifts which demonstrated evolutionary transitions between contrasting biomes occurs often and, like our findings, challenge the prevailing view of biome conservatism as a standard pattern in lineage evolution. In contrast to the widespread generalist biome strategy we found in *Acacia*, Cardillo et al. (2017) observed a high degree (75%) of biome specialization at the species level. Perhaps this difference in biome specialization between these lineages is due to a fundamental niche difference, because *Hakea* is dominated by species specialized to the Mediterranean biome. Cardillo et al. (2017) used occupancy in biomes based on AVH occurrences to identify biome fidelity; it is possible that this method is more likely to identify biome specialization than our approach which uses species distribution models to interpolate between observations – we explore this further in the sampling bias section below.

4.5 | Effect of biome typology

Our study used four qualitatively different biome classifications, yet none of these biome constructs appeared to influence *Acacia* diversification. We had expected species ranges to perhaps conform to

Functional Biome or González–Orozco Biome boundaries most, because primary limiting growth factors or geospatial species turnover are used to define these biomes. Alternatively, the WWF or Crisp Biome classifications also gave us reason to expect species might conform to biome boundaries because they are based on expert knowledge of species distributional limits. One minor point of difference in observed trends between the biome typologies was the difference in phylogenetic signal in the number of biomes occupied by species for Functional Biomes (significant) and the other biome typologies (non-significant). This difference suggests that Functional Biomes may represent relevant environmental factors linked to speciation slightly better than the other biome typologies. Alternatively, there are fewer Crisp Biomes (5), González–Orozco Biomes (6), and WWF Biomes (7) than Functional Biomes in Australia (13), which provides less scope for variation in biome occupancy among clades, so the likelihood of detecting a relationship involving clade size with these simpler biome typologies is probably lower than for Functional Biomes. It is also possible that all biome maps might be missing a key attribute that defines biomes from an *Acacia* perspective.

4.6 | Sampling bias

There are a few caveats to our approach. The TTR-SDM, like most species distribution models, does not directly consider biotic interactions, disturbance or dispersal. *Acacia* has a suite of biotic relationships which may influence distribution, including herbivores such as gallthrips (McLeish, Crespi, Chapman, & Schwarz, 2007), pollinating insects (Stone, Raine, Prescott, & Willmer, 2003) and seed-dispersing birds and ants (O'Dowd & Gill, 1986). This means the predicted distributions are a closer reflection of fundamental niche rather than the realized niche.

One advantage of using predicted distributions to determine biome occupancy rather than using herbarium records alone is that it is less affected by sampling bias. We observed under-sampling of three WWF Biomes, four Functional Biomes, one Crisp Biome and two González–Orozco Biomes (Figure S4) in the occurrence data. This was much less of an issue for the TTR-SDM predicted distributions because predicted distributions have presences and absences over the entire continent, unlike occurrence data which are highly influenced by patterns in human sampling effort. Uneven sampling of species occurrences by biome is problematic when examining biome occupancy, particularly when several biomes are incompletely sampled as it is likely to cause overestimation of biome specialization in lineages. Our observation of under-sampled biomes in the AVH *Acacia* records is consistent with previous work on spatial bias. Haque, Nipperess, Gallagher, and Beaumont (2017) observed the Gibson Desert, Nullarbor and Great Sandy Desert, and therefore the Desert or Eremaean biomes, as the least sampled areas in Australia. Using predicted distributions for species minimizes the effect of this type of bias.

Species with ranges that only have a slight presence in another biome due to geocoding errors, such as a raster resolution that is too coarse, may be introducing bias towards occupancy in more biomes. However, our sensitivity analysis of cell thresholds for determining biome occupancy demonstrated that a higher cell threshold of up to ten cells, was qualitatively equivalent to the single cell threshold we used, so this source of bias likely has a minimal effect.

Another potential source of sampling bias is in the species included in the phylogeny, if many of the species not included in our study had strong biome affinities, this could confound our results. Our analysis only included approximately 45% of the 1,063 species of *Acacia* in Australia, because we were limited to the species included in the Williams et al. (2016) phylogeny with adequate AVH distributional data. However, we compared biome occupancy in all 1,037 species represented in the AVH data (Figure S3a,c,e,g in Data S2) against the 481 used in the main text (Figure S3b,d,f,h in Data S2), and they displayed comparable trends in the number of biomes occupied, suggesting there is unlikely to be a strong bias associated with species sampling.

5 | CONCLUSION

Our work indicates that biome conservatism has been of minor importance during the diversification of Australian *Acacia*, with species and clades typically occurring in multiple, and often contrasting, biomes. Future changes in biome boundaries and the relative extent of biome areas with climate change are expected. Such biome changes are predicted to cause substantial biodiversity loss (Huntley et al., 2016). Our findings indicate that *Acacia*, both at the species and clade level, is remarkably adaptable in natural heterogeneous environments where the rate of change is commensurate with evolutionary processes. Although *Acacia* seems to be resilient to biome changes, our findings show that greater diversity is supported in larger areas so a large conservation estate is crucial for safeguarding the evolutionary potential of hyper-diverse lineages like *Acacia*.

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DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available in the supplementary material of this article.

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BIOSKETCH

Esther Dale is a plant ecologist interested in lineage diversification. This forms a part of her work examining the role of biome shifts in lineage evolution.

Author contributions: initial idea from SIH, conceptualized by EED, SIH and WGL; analyses completed by EED with assistance from SIH and MJL; written by EED with input from WGL, SIH and MJL.

SUPPORTING INFORMATION

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