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Macroecology, life histories, and diversity of Australian birds

Makroekologie, životní strategie a diverzita ptáků Austrálie

Ph.D. thesis

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Supervisor: doc. Mgr. Vladimír Remeš, Ph.D.

Frankfurt am Main 2019

‘reading an academic paper: i mean it's alright but it's no tgcf’

– kirbymp3

I declare that this thesis is my original work under the supervision of doc. Mgr. Vladimír Remeš, Ph.D. and has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My contribution to each of the appendices comprising this work is expressed through the authorship order of the included appendices and has been declared in the Application for recognition of publishing activities, approved prior to the submitting of the thesis.

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Abstract

Macroecology seeks to study relationships between organisms and their environment on large spatial, temporal, and taxonomical scales. Environment can affect the evolution of traits important for reproduction and survival, so-called life history traits. Among these traits belongs for example clutch size, i.e. number of eggs per one breeding attempt. Many theories were proposed to explain variability and evolution of clutch size, focusing for instance on the productivity of environment, predation, or nestling development. One of the life history traits is also beak size, which is thought to be driven mainly by diet, but can also be tied to thermoregulation and climate. Life history traits can affect species' diversity patterns. Diversity can be affected by evolutionary processes, history, or abiotic and biotic conditions. Effects can be direct or indirect and can differ across spatial scales. In this thesis I applied macroecological approaches to study variability and evolution of life history traits and diversity of Australian avifauna. I found that (i) clutch size of Australian songbirds was probably influenced by different factors than in Northern Hemisphere species, as it showed no relation to environmental productivity or nest predation, but instead was related to the nestling development. (ii) Beak size of Australasian honeyeaters and allies was shaped by winter, not summer temperatures. It thus appears that while diet affects beak shape, its size is driven by thermoregulation. (iii) While the gradient in species richness in Australian birds was driven by water availability both directly (physiology) an indirectly (vegetation complexity and niche availability), phylogenetic and functional diversity appeared to be more strongly related to the age of biomes and evolutionary history. (iv) Species richness and specialization were closely related across several ecological traits and spatial scales. However, abiotic factors, not interspecific interactions, were probably major drivers shaping assemblage composition of Australian songbirds. Thus, the evolution of avian life history traits appears to be under the influence of different factors in Australia than in other regions of the world. The diversity patterns and assemblage composition are mostly driven by the historic effects rather than by current ecological conditions.

Key words: Australia, beak size, birds, climate, clutch size, diversity, evolution, macroecology, life history

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Abstrakt

Makroekologie studuje vztahy mezi organismy a jejich prostředím na velkých prostorových, časových a taxonomických škálách. Prostředí může ovlivnit evoluci znaků důležitých pro reprodukci a rozmnožování, tzv. life-history (životní historie) znaků. Mezi tyto znaky patří třeba velikost snůšky, tedy počet vajec snesených v jednom reprodukčním pokusu. Byl navrhnut nespočet teorií snažících se vysvětlit variabilitu a evoluci velikosti snůšky, které se soustředily třeba na produktivitu prostředí, predaci nebo gradient ve vývoji mláďat. Jedním z life-history znaků je také velikost zobáků, která je údajně závislá na potravě, ale může být také svázána s termoregulací a klimatem. Life-history znaky mohou také ovlivnit patrnosti v druhové diverzitě. Diverzita může být ovlivněna evolučními procesy, historií nebo abiotickými a biotickými podmínkami. Vlivy mohou být přímé nebo nepřímé a mohou se lišit napříč prostorovými škálami. V této práci jsem aplikovala makroekologické přístupy na studium variability a evoluce patrností v life-history znacích a diverzitě australské avifauny. Zjistila jsem, že (i) velikost snůšky australských pěvců je pravděpodobně ovlivněna jinými faktory, než jak je tomu u druhů ze severní polokoule, neboť neukázala žádný vztah k produktivitě prostředí či hnízdní predaci, ale k vývinu mláďat. (ii) Velikost zobáku australských medosavek je řízena zimními, a ne letními teplotami. Zdá se proto, že zatímco potrava ovlivňuje tvar zobáku, jeho velikost je řízena termoregulací. (iii) Zatímco je gradient v druhové bohatosti australských ptáků řízen dostupností vody, a to jak přímo (fyziologicky), tak nepřímo (komplexnost vegetace a dostupnost nik), fylogenetická a funkční diverzita se zdá být spíše spjata se stářím biomů a evoluční historii. (iv) Druhová bohatost a specializace jsou úzce spjaté s množstvím ekologických znaků a napříč prostorovými škálami. Nicméně, abiotické faktory, a ne mezidruhové interakce zřejmě hrají prim v utváření složení společenstev australských pěvců. Evoluce ptačích life history znaků se tedy zdá býti v Austrálii ovlivněna rozdílnými podmínkami, než je tomu v jiných oblastech světa. Diverzita a složení společenstev jsou řízeny především historickými vlivy spíše než současnými ekologickými podmínkami.

Klíčová slova: Austrálie, diverzita, evoluce, klima, makroekologie, ptáci, velikost snůšky, velikost zobáku, životní historie

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The list of used abbreviations

AIC	Akaike information criterion
ENSO	El Niño Southern Oscillations
FD	functional diversity
GLS	generalized least squares
HANZAB	Handbook of Australian, New Zealand and Antarctic birds
Mya	millions years ago
NDVI	normalized difference vegetation index
PCoA	principal coordinates analysis
PD	phylogenetic diversity
PET	potential evapotranspiration
SAR	simultaneous autoregressive model
SEM	structural equation modelling
SES	standardized effect sizes
SR	species richness

1 Introduction

1.1 Macroecology

Macroecology is a rather new scientific field that investigates relationships between organisms and their environment on large spatial, temporal, and taxonomical scales (Brown 1995, McGill 2019). Although studies with similar focus existed for a long time (e.g. works of Wallace, Darwin, or Humboldt), the term ‘macroecology’ was first coined by Brown and Maurer at the end of 20th century (Brown & Maurer 1989). Since then, macroecology experienced a boom. Brown and Maurer drew attention to the fact that typical ecological studies are usually carried out on small spatial scales or populations of just one species. However, one cannot draw universal conclusions from local studies. Thus, macroecology rose to utilize results of many small-scale studies and integrate them into a single framework that is able to analyse large-scale patterns (Brown & Maurer 1989, Brown 1995, McGill 2019). Macroecology is interlinked with other scientific fields, such as evolutionary biology, community ecology, or most closely, biogeography. However, while biogeography studies the spatial patterns in biodiversity, macroecology seeks explanations of the observed patterns (Blackburn & Gaston 2002, Kent 2005, Jenkins & Ricklefs 2011, Keith et al. 2012). Still, a discussion on the exact definition of macroecology persists even in these days (McGill 2019).

Early macroecological studies focused mostly on latitudinal gradients of diversity and variability in species richness, species abundance, body size, and range size (Brown & Maurer 1989, Gaston & Blackburn 2000, Storch & Reif 2002). They also sought to help clarify ecogeographical rules (Gaston et al. 2008), such as Bergmann’s rule of increasing body size in colder climates (Blackburn et al. 1999), or Allen’s rule of downsizing of body appendices in colder environments (Nudds & Oswald 2007). Now, the focus has shifted towards, for example, effects of different spatial scales on diversity patterns (e.g. Lessard et al. 2012, Belmaker & Jetz 2013, Pärtel et al. 2016), responses of organisms to climate change (e.g. Khaliq et al. 2014, Distler et al. 2015, Diniz-Filho et al. 2019), integrating palaeontology (e.g. Diniz-Filho et al. 2013, Huang et al. 2017), studying biotic interaction networks (e.g. Trøjelsgaard & Olesen 2013, Staniczenko et al. 2017, Zanata et al. 2017), and life history traits (e.g. avian clutch size: Jetz et al. 2008; nest type: McEntee et al. 2018; juvenile survival: Remeš & Matysioková 2016; generating large data sets: e.g. Jones et al. 2009, Wilman et al. 2014, Storchová & Hořák 2018). Many of these works used birds in their research. Birds represent a very suitable group of organisms used in macroecological studies because they are quite well studied and large databases with their functional traits, phylogeny, and geographic distribution exist.

1.2 Life histories

Species show a great intra- and interspecific variability in their life history traits (Fig. 1). While some birds lay many eggs in one brood, others lay only one egg. Some species' life span is only a few years while others can live for decades. This variability is in the focus of the life history theory. Life history theory seeks to explain how the environment drives natural selection and shapes organisms so that they optimize their fitness via reproductive effort and survival (Stearns 2000). The optimization is based on trade-offs between the life history traits, i.e. traits that are tied to fitness. According to the theory, species should divide their energy into the optimal combination of traits leading to the highest fitness (Stearns 1989). However, the choice differs according to the environment or evolutionary history of species. For instance, it is thought that nest predation rates are lower in higher latitudes than in the tropics (Skutch 1949, Slagsvold 1982, Remeš et al. 2012a). With the higher risk of nests being destroyed, tropical birds should probably lay fewer eggs to minimize the loss and to save energy for eventual subsequent breeding attempts (Ghalambor & Martin 2001). Many of the life history traits were studied extensively in the past, for example body size, egg size, lengths of the incubation and fledging periods, or life span (Western & Ssemakula 1982). Here, I focus on two aspects of avian life histories discussed in this thesis – reproductive effort and morphology, particularly on clutch size and beak size.

First, one of the most studied aspects of life history traits in birds is clutch size. Birds show high interspecific variability in clutch sizes where some species lay only one egg, while others up to fourteen eggs. Clutch size appears to be related to latitude and species with largest clutches inhabit mostly temperate regions on the Northern Hemisphere (Moreau 1944, Cardillo 2002, Jetz et al. 2008). Many theories were suggested to explain interspecific variation in avian clutch size and its relationship to latitude. According to Lack (1947, 1948), birds are limited by available resources, specifically by the amount of food they can provide to their offspring, which is tied to the day length. Birds have more time for foraging in temperate regions with longer day periods during the breeding season than those in the tropics and thus could afford to have larger clutches and raise more offspring. Ashmole (1963) proposed that the seasonality in resources could drive clutch size via the variation in population densities and per-capita food availability. Higher

Figure 1. Examples of Australian avifauna and its diverse life history characteristics. (**a**) Megapodes (family Megapodiidae; pictured Australian Brush-turkey*, Alectura lathami*) are ground-dwelling birds that build large nests in the form of mounds made of raked leaves or sand, into which they bury eggs. Warm decaying vegetation or geothermal heat incubates the eggs while the male measures the temperature with its beak and adjusts it accordingly. Chicks are superprecocial and fully mobile after hatching. (**b**) Endemic lyrebirds (family Menuridae) represent a basal branch of songbirds (order Passeriformes). Superb Lyrebird (*Menura novaehollandiae*) is the largest songbird on the continent of Australia (and one of the largest worldwide). Lyrebirds are long-lived and lay only one egg that the female takes care of alone. They are also well known for their ornamental tail feathers, courtship displays of males, and voice imitation. (**c**) Two representatives of large and flightless paleognaths of order Casuariiformes can be found in Australia, specifically Southern Cassowary (*Casuarius casuarius*; pictured) and endemic Common Emu (*Dromaius novaehollandiae*). They are polygynous with the male taking care of offspring. (**d**) Australian birds show a high incidence of cooperative breeding when offspring from the previous nesting help parents raising their new clutch. White-winged Choughs (*Corcorax melanorhamhos*; pictured) even kidnap fledglings from other groups to use them as helpers. (**e**) Australia is occupied by many species of estrildid finches (family Estrildidae). Thick beaks and colourful plumage are specific for these small granivorous passerines. Zebra Finch (*Taeniopygia guttata*) is one of the most popular species of birds bred in captivity and used in scientific research. (**f**) Many Australian species feed on nectar and pollen, for example honeyeaters (family Meliphagidae; pictured Red Wattlebird, *Anthochaera carunculata*). Thus, they exhibit various forms of beak shapes adapted to feeding on flowering plants. (**g**) Interesting courtship displays can be found in some clades. Birds of paradise (family Paradisaeidae) are known for distinct plumage coloration and ornaments of males together with their courtship dances. Related bowerbirds (family Ptilonorhynchidae; pictured Great Bowerbird, *Chlamydera nuchalis*) are specific by the constructing bowers, structures made mostly out of sticks and other decorative material, for attracting females. (**h**) Many species of colourful parrots (order Psittaciformes) inhabit Australia, but of all the species worldwide, only two are migratory and both of them can be found there. They nest on Tasmania and winter in the south-eastern Australia – critically endangered Swift Parrot (*Lathamus discolor*) and Orange-bellied Parrot (*Neophema chrysogaster*; pictured). (**i**) High diversity of native fauna is also complemented by many introduced species. Acclimation companies transported there many European species of birds back in 19th century, one of them being Common Blackbird (*Turdus merula*). Pictures by L. Harmáčková (**a, c−g, i)**, J. Manger **(b)**, and J. J. Harrison **(h)**.

mortality during the winter months can be found in temperate regions, which could loosen the competition for resources in the following breeding period. This could increase per-capita food availability and more resources could then support larger clutches.

Skutch (1949) focused on the effect of predation and expected that in areas with high number of predators it is more effective to have smaller clutches. High number of offspring demands frequent feeding visits of parents and this can attract predators. Thus, it should be advantageous to have smaller clutches when there is higher risk of the nest being depredated. Similarly, when adults face higher risk of predation, it should be more advantageous to invest more energy into a large clutch (age-specific mortality theory; Stearns 1976, Martin 1995, Ghalambor & Martin 2001). Recently, Martin (2014, 2015) proposed a new theory that focuses on a gradient in nestling development and is tied to the nest predation rates. He assumes that higher nest predation risk drives offspring to leave the nest earlier with underdeveloped wings and body mass. This affects parents as they need to spend more energy per offspring after fledging and it is thus more favourable to have smaller clutches.

Many other hypotheses were proposed to explain variability and evolution of clutch size, for example the effect of body mass (clutch size increases with decreasing body mass; Averill 1933), nest type (species nesting in closed nest have larger clutches due to the lower predation risk than species nesting in open nests; Slagsvold 1982, Jetz et al. 2008), egg size (larger clutches consist of smaller eggs; Blackburn 1991, Figuerola & Green 2005), or the number of broods per year (short breeding season enables to raise only few large clutches, while species with long breeding seasons can allocate their resources into many smaller clutches; Cody 1966, Martin 1995).

The evidence for the diverse theories is mixed. While the effect of environmental productivity and its seasonality was found by many authors (e.g. Ricklefs 1980, Yom-Tov & Geffen 2002, Jetz et al. 2008, Griebeler et al. 2010, Hořák et al. 2015), often substantial residual variability remains (Ricklefs 1980, Jetz et al. 2008) and thus other factors might influence clutch size as well. Support for the nest predation as the driver of latitudinal gradient in clutch size has not been clarified. Predation rates are thought to decrease with latitude (Skutch 1949, Slagsvold 1982, Ghalambor & Martin 2001), but they seem to highly differ between the regions (Martin 1996, Martin et al. 2000, Remeš et al. 2012a). Moreover, the new Martin's (2014, 2015) hypothesis remains to be tested on more taxa from different parts of the world. Furthermore, most of the hypotheses were not tested simultaneously and the research on clutch size was mostly carried on Northern

Hemisphere species. This creates a bias as the highest number of species can be found in the tropics. Tropical and Southern Hemisphere species have considerably longer nesting periods, smaller clutches, and the latitudinal gradient in clutch size is not so pronounced in the Southern Hemisphere (Jetz et al. 2008). Thus, it is important to focus research effort on life history traits of tropical and Southern Hemisphere species.

Second, avian morphology plays an important role in life histories as well. For example, larger species inhabit colder climates (Olson et al. 2009), the shape of wings is vital for movement and migration (Mönkkönen 1995), and avian morphology is also related to species' ecology, habitat occupation, and foraging and diet preferences (Miles & Ricklefs 1984, Ricklefs 2012, Pigot et al. 2016). One of the most specific avian structures is beak. Beaks show a great range of shapes and sizes and have an important role in foraging. The most famous example represents the evolution of beak shapes in Darwin's finches (subfamily Geospizinae) related to specialization on different diet (Grant et al. 1976, Grant & Grant 2002). However, beaks probably have thermoregulatory functions as well and can affect the dissipation of body heat (Tattersall et al. 2009, Greenberg et al. 2012a). According to Allen's rule (Allen 1877), the length of body appendices should be shorter in colder climates due to thermoregulation. This appears to be true at least in shorebirds' tarsi (Cartar & Morrison 2005, Nudds & Oswald 2007), but studies concerning the relationship between beak size and thermoregulation are still scarce. For instance, beak surface in North American swamp sparrows shows positive relationship to summer temperatures (Greenberg et al. 2012b). Moreover, a comparative analysis across over two hundreds of bird species found positive relationship between their beak length and ambient temperature and thus showed a support for Allen's rule. However, it is still not clear whether thermal effects are really important and if so, whether hot temperatures which could drive the increase in beak sizes to dissipate heat, or cold temperatures driving smaller beaks because of the heat retention are more important.

1.3 Diversity

Environment can affect not only life history traits of species, but also interact with their ecological niche to affect diversity. Niche can be expressed by species' requirements, such as the environmental conditions they occur in (Grinnellian concept; Grinnell 1917, Devictor et al. 2010), or by their impact, i.e. biotic interactions, such as foraging or competition (Eltonian concept; Elton 1927, Devictor et al. 2010). However, the most often used definition in ecology is assumedly the Hutchinson's (1957) concept that considers niche as an n-dimensional hypervolume consisting of both biotic and abiotic properties (Devictor et al. 2010). Niche is thus seen as an ecological space available for species to divide it between them. Specialization on a limited range of resources can help partition the niche and thus enhance coexistence of species and promote diversity (Hutchinson 1959, MacArthur 1972, Eeley & Foley 1999, Mason et al. 2008, Pigot et al. 2016). However, evidence for this assumption is mixed (Belmaker et al. 2012, Pigot et al. 2016). Most of the studies focused on the specialization on habitat utilization and diet preferences, yet niche partitioning can take place also in foraging behaviour. For example, species in the mixed flocks of titmice (family Paridae) differ in their position on trees with larger-bodied species foraging closer to the trunk, while small species occupy outer branches (Lack 1971, Suhonen et al. 1994, Jablonski & Lee 1998). The packing of species in ecological space and their specialization can therefore play an important role in interspecific interactions, shaping community composition, as well as affecting diversity.

Countless number of definitions exists of what diversity is and how to express it (see Magurran 2004). Diversity usually refers to the variability in a set of characteristics, or differences within and among organisms (biodiversity; Swingland 2001). Diversity of assemblages can be expressed in many ways. The most simple is the number of species present (species richness, SR), where it is expected that assemblages with more species are more diverse, as species differ in their traits and life histories. However, SR is certainly not a complete determinant of diversity and of e.g. niche filling. It can be improved by taking species' abundances into account (Tokeshi & Schmid 2002), as species with low abundances might have smaller role in shaping community assembly than species that are abundant. Moreover, diversity metrics can be also improved by incorporating information on species characteristics, such as their phylogenetic relations or life history traits. Phylogenetic diversity (PD) increases the information value by including species' evolutionary history (Tucker et al. 2016), while functional diversity (FD) focuses on ecological differences between species and assemblages and employs functional traits (e.g. morphological or ecological characteristics, including life history traits; Petchey & Gaston 2006). Adding another dimension to the expression of diversity is helpful in more detailed analyses of assemblage composition and also in management and conservation.

Patterns of diversity are affected by the evolutionary processes, such as speciation and extinction, but also by the environment (Swenson 2011). Out of several climatic variables it appears that energy (e.g. environmental productivity, solar radiation) and water (e.g. rainfall, PET) are the major drivers of biodiversity worldwide (Hawkins et al.

2003). The effect of these variables can be either direct (physiological tolerances; Buckley et al. 2012) or indirect, e.g. environmental productivity can facilitate more complex vegetation and thus create 'larger' ecological space (Hurlbert 2004, Tews 2004). Moreover, past and current environment could differently affect SR, PD, and FD. Old and climatically stable regions show higher PD (Voskamp et al. 2017) and, for example, arid environments are expected to be inhabited by a small number of species, yet these species can specialize on the extreme conditions and thus show high FD (Miller et al. 2017). Patterns in SR of various groups of organisms in relation to environment were studied widely (e.g. Hawkins et al. 2003, Kissling et al. 2008, Jiménez-Alfaro et al. 2016), but less attention was paid to PD and FD (e.g. Graham et al. 2009, Schleuter et al. 2012, Lanier et al. 2013). Moreover, quantifications of direct and indirect effects of environment on gradients in diversity are still scarce (e.g. Vollstädt et al. 2017). The effect of environment on diversity is thought to be most prominent on large spatial scales (in terms of bioregions and larger), while on finer scales assemblage composition should be shaped more by interspecies interactions, such as competition for resources and niche partitioning (Whittaker et al. 2001, Belmaker & Jetz 2011, Ferger et al. 2014, Fergnani & Ruggiero 2017). Yet, most of the studies fail to incorporate various spatial scales to differentiate between these processes (Belmaker et al. 2012).

1.4 Australia

Australia represents a unique system for studying geographical patterns and evolution of diversity and variation in life history traits in local avifauna. Even in these times, studies performed on Northern Hemisphere temperate species still make a majority of scientific work and we still lack sufficient knowledge about variables shaping diversity and life histories of species on the Southern hemisphere and in the tropics. In comparison to species from other Southern hemisphere continents, Australian avifauna is quite well studied and therefore suitable for macroecological studies.

Since the split of Gondwana (around 80 Mya in the late Cretaceous period), Australia became isolated and started shifting northwards (50 Mya, Eocene), which naturally came with climatic changes. However, the most pronounced alterations started around 15 Mya (Miocene) and were represented by shifts in sea levels and the substantial increase of the Antarctic ice cap (Byrne et al. 2008). The continent was originally mesic and covered in dense forests. Fluctuations in glaciation then triggered an extensive aridification of the continent, which brought the fragmentation of original mesic environments and

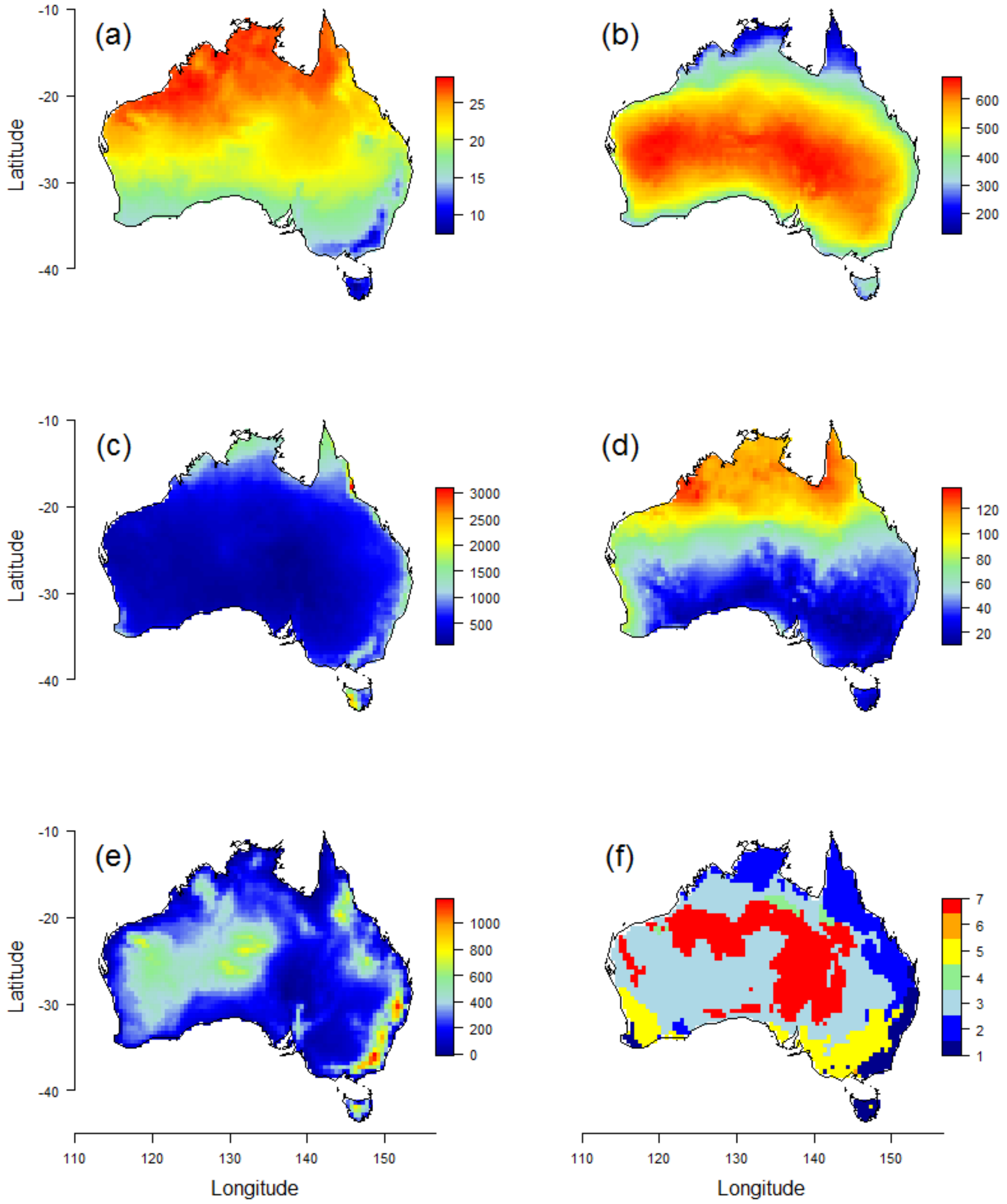


Figure 2. Spatial variation of climatic conditions in Australia and Tasmania. **(a)** Mean annual temperature (°C), **(b)** temperature seasonality (SD*100), **(c)** mean annual precipitation (mm), **(d)** precipitation seasonality (CV), **(e)** elevation (m), and **(f)** type of habitat (1 = evergreen trees, 2 = other trees, 3 = shrubs, 4 = herbs, 5 = fields, 6 = urban, 7 = barren). Data were obtained from WordClim.com **(a−d)** and EarthEnv.org **(e−f)** and re-scaled on a 0.5 x 0.5 (longitude x latitude) degree grid.

consequently led into the extinction of many components of the original biota (Byrne et al. 2011). The present belt of the dense forest occurring along the eastern coast of the continent is a remnant of the previous dense forestation that covered the whole continent more than 20 Mya and probably served as an origin for many clades of biota (majority of plants, birds, mammals, and reptiles; Byrne et al. 2011).

Currently, even though the climatic and environmental conditions, as well as fauna in Australia are highly diverse, most of the continent (around 70%; Byrne et al. 2008) is arid with the presence of several deserts in the central plateau. Remnants of the historic mesic environments can be found along the eastern coastline, which is covered by tropical and temperate rainforests with high and non-seasonal patterns in rainfall (Fig. 2). While in the north, a monsoon region with high temperatures and fluctuations in rainfall is present, south of the continent and the island of Tasmania fall to the temperate zone with variation in temperature, but not in rainfall (Fig. 2). Surface of the continent is overall flat (Fig. 2) and the lack of mountain ranges contributes to the low overall precipitation. Together with the El Niño Southern Oscillation (ENSO), these conditions contribute to long cycles of droughts (ca ten years; Orians & Milewski 2007). Most of the Australian environment therefore consists of arid and semi-arid habitats (Byrne et al. 2011), such as open forests, woodlands and shrublands.

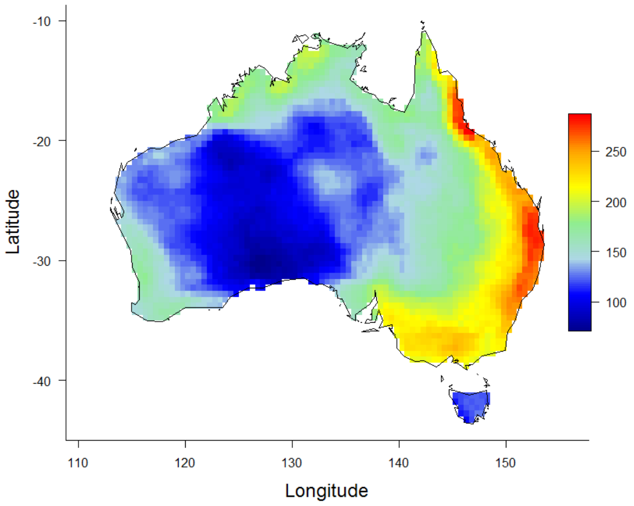


Figure 3. Spatial variation in species richness (number of species in an assemblage) in Australian birds. Data on 560 species were obtained from Bird Life International & Nature Serve (2014) and re-scaled on a 0.5 x 0.5 (longitude x latitude) degree grid.

In such arid environment, water availability is thus thought to play the most prominent role in shaping avian diversity in Australia (Hawkins et al. 2005). Nearly 900 species of birds are now recognized to reside in Australia and Tasmania, from which 45% are local endemics (Chapman 2009) and the majority of species comprises of songbirds (*Passeriformes*) and parrots (*Psittaciformes*), which are orders that probably originated in this area before the split of Gondwana (Ericson 2012). Distribution of SR is highly uneven, with the lowest number of species in central arid plains and the highest along the mesic eastern coast (Fig. 3). This does not agree with the usual north-south gradient in SR observed in the Northern Hemisphere (Hurlbert & Jetz 2007) yet is in accordance with the history of the continent and shows the highest avian diversity in remnants of the ancient forest cover (Hawkings et al. 2005). It also appears that Australian birds have low diversification rates (Jetz et al. 2012) and only few clades were able to invade newly arisen arid environments (Brooker et al. 1979), for example some lineages of honeyeaters (family *Meliphagidae*; Miller et al. 2013). This represents an interesting contrast to Australian lizards, whose radiation has conversely been highest in the deserts (Pianka 1973).

1.5 Thesis outline

Aims of this thesis are to apply macroecological approach to study patterns in diversity and life history traits of Australian birds. More specifically, **Chapter I** concerns interspecific variability in clutch size of Australian songbirds (order Passeriformes). We focused on three sets of hypotheses involving (i) resource availability, (ii) nest predation, and (iii) development of fledglings. For the first time we tested these hypotheses simultaneously while focusing on less explored Southern Hemisphere species.

Chapter II shifts the attention from clutch size to the evolution of beak size. The role of beak shape in foraging is well known, but the evolution of its size might have been caused by the need for thermoregulation; either to dissipate excess body heat or for heat retention in cold ambient temperatures. We tested this assumption on three families of Australian and New Guinean songbirds.

In **Chapter III** we tried to disentangle direct and indirect effects of environment on shaping diversity of Australian birds. Climate can affect patterns in diversity either directly via physiological tolerances of species, or indirectly via facilitation of vegetation complexity and resource availability. We computed several diversity indices based on the number of species, their phylogenetic relations and variability in functional traits, and quantified to which extent their spatial patterns were affected directly or indirectly by climate.

Finally, **Chapter IV** focuses in more detail on the coexistence of species and how foraging specialization enables partitioning of resources and increase in SR. It is to be expected that more species can coexist if they are specialized and thus the competition between them is relaxed, and that this relationship should be more pronounced on local spatial scales than on the large ones. We tested this concept on Australian songbirds while using detailed data on their habitat, diet and foraging preferences. We worked across three spatial scales ranging from small localities to bioregions.

2 Materials and methods

2.1 Data extraction

We used data from ornithological handbooks, primary literature, museum measurements, and public databases. In **Chapters I, III, and IV**, we collected data on clutch size, habitat and dietary preferences and other intrinsic traits from the Handbook of Australian, New Zealand and Antarctic birds (HANZAB; Higgins & Marchant 1990, 1993; Higgins & Davies 1996, Higgins 1999, Higgins et al. 2001, 2006; Higgins & Peter 2002). Still, some data were not possible to obtain from HANZAB, so we used data on daily nest predation rates that were published in a public digital repository and then searched recent primary literature to increase the number of studies included (**Chapter I**). Morphological data on various body measurements available in literature and public databases are usually not detailed enough. We thus measured our own data on beak length, depth, width and curvature on museum specimens (**Chapter II**). In terms of species distributions, we employed two types of observation data. First, in **Chapters I–IV** we used species distribution maps in the form of polygon shapefiles (BirdLife International & Nature Serve 2014). Second, in **Chapter IV** we used also observation data from the Australian Bird Count (Clarke 1999), which was a citizen science project carried out on small localities (ca 2–6 ha).

Extrinsic variables, such as climate, vegetation cover, or altitude were obtained from online databases. Geospatial data come in various resolutions and measured in different years and regions of the world. One of the most used databases for worldwide climatic data is Worldclim (Hijmans et al. 2005; **Chapter II**), which provides environmental conditions such as mean, maximum and minimum temperature, precipitation or solar radiation for various time scales. For analyses on local (not global) scale, more detailed data is usually provided by local agencies, such as daily measurements of climate and vegetation cover provided by Australian Government's Bureau of Meteorology (2015; **Chapter I**) or by The Atlas of living Australia (2018; **Chapters III and IV**).

For comparative (species-level) analyses, values of extrinsic variables can be assigned to each species by various methods. First, by overlapping the variable with species' range map, selecting of all the values falling in the species' range and computing their mean (**Chapter I**). Second possibility is to find a centroid of the range and use only a single value of the extrinsic variable that overlaps with the centroid. In analyses of assemblages, extrinsic variables were rescaled to fit the resolution of the studied assemblages (**Chapters II–IV**).

2.2 Assemblage composition

Assemblages, used as units in macroecological studies, are usually artificial communities with their extent defined by the researcher. Due to the fact that these studies are carried across large spatial scales, obtaining detailed field data on species presence in actual communities is difficult. Therefore, most macroecological studies depend on creating assemblages and estimating species' presence from information about their distribution, such as atlas data or range maps.

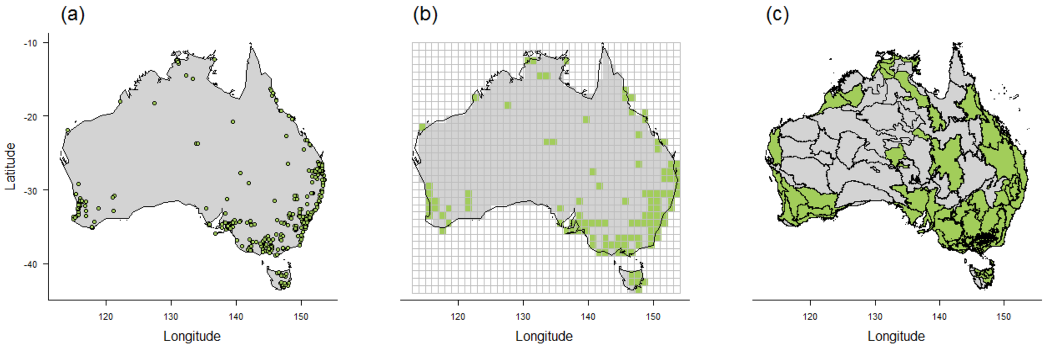
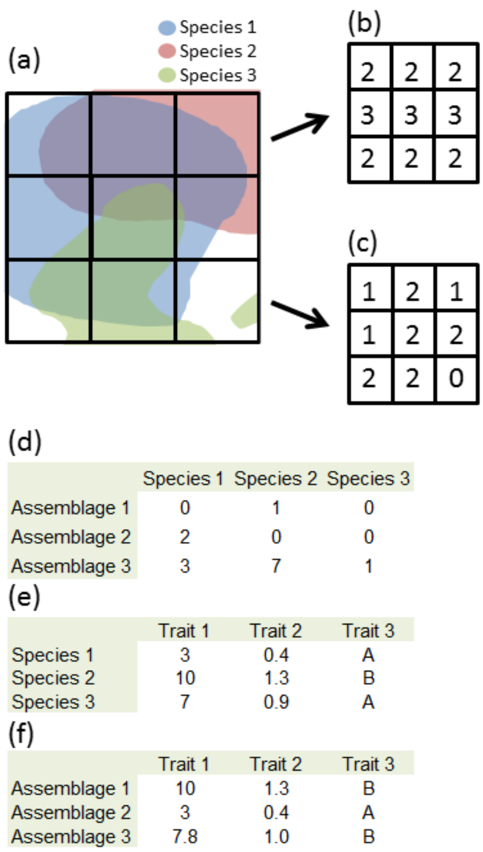


Figure 4. Examples of various spatial scales: **(a)** Localities of 2−6 ha size (n = 470), **(b)** a grid with 1 x 1 (longitude x latitude) degree cell size (n = 692), and **(c)** bioregions (n = 89). Grey colour represents the continent of Australia and Tasmania, while green colour highlights cells and bioregions that contain at least one locality. Adopted from **Chapter IV**.

The most common practice of creating assemblages is constructing a grid composed of cells with their size decided beforehand (e.g. cells of 1 x 1 longitude x latitude degree or 100 x 100 km size; Fig. 4). Cell size and scale can have a large impact on the study focus and results (Hurlbert & Jetz 2007). For instance, it is better to use larger cells to detect biodiversity hotspots on the scale of the world, but for studying assemblage composition and species interactions it is better to use small cells or even actual field observations. We created assemblages as grid cells with 1 x 1 (longitude x latitude) degree resolution in **Chapters I–IV**. Since we studied changes in species interactions on various spatial scales, we also included detailed field observation data, as well as whole bioregions in **Chapter IV**.

Species composition of assemblages can be extracted by overlapping assemblages with species' distribution maps to derive species richness as a number of species present in an assemblage (Fig. 5; **Chapter I–IV**). Based on this composition, trait values for each assemblage the can be computed. Trait values are generally computed as a mean of trait



(b)

2	2	2
3	3	3
2	2	2

(c)

1	2	1
1	2	2
2	2	0

(d)

	Species 1	Species 2	Species 3
Assemblage 1	0	1	0
Assemblage 2	2	0	0
Assemblage 3	3	7	1

(e)

	Trait 1	Trait 2	Trait 3
Species 1	3	0.4	A
Species 2	10	1.3	B
Species 3	7	0.9	A

(f)

	Trait 1	Trait 2	Trait 3
Assemblage 1	10	1.3	B
Assemblage 2	3	0.4	A
Assemblage 3	7.8	1.0	B

Figure 5. Examples of obtaining species' occurrences and trait values in assemblages. To obtain species' occurrences in grid cells with the use of range maps in the form of polygons, the first step is to overlap the grid with individual species' ranges (coloured polygons in **a**). A list of species per grid cell is then represented simply as all species' ranges that overlap given grid (number of species per grid cells, **b**). Sometimes it is desirable to count only ranges that overlap cells by more than e.g. 50% **(c)**. This process creates species' distribution matrix with assemblages (i.e. grid cells) as rows, species as columns, and values one/zero as species' presence/absence. In the species' distribution matrix in **(d)** values represent abundances (no. of individuals) of species in assemblages (note that abundances cannot be obtained by methods described in **a-c**, i.e. busing range maps, but instead can be retrieved by field observations). To obtain trait values for each assemblage, the trait matrix **(e)** with species identities as rows and traits as columns is needed as well. Trait values for assemblages are then computed by combining these two matrices **(d-e)** and computing e.g. a mean of trait values of all species present in an assemblage (traits 1 and 2), or (in case of categorical traits) establishing the most abundant category in an assemblage (trait 3). If species' abundances are available, mean weighted by abundances can be used. The resulting matrix **(f)** then has assemblages as rows and traits as columns.

values taken from all species present in an assemblage (Fig. 5; **Chapters I and II**). Diversity indices are more complicated to calculate, and their selection and computation depends on the study aims. The simplest diversity indices include only the number of species and their abundances (e.g. Simpson's and Shannon's diversity indices, or modified Levin's specialization index used in **Chapter IV** that uses trait data instead of abundances). However, even though including abundances in the indices increases their quality, data on species' abundances are hard to acquire and in fact cannot be obtained when using range maps. Other diversity indices can also include information on evolutionary history or functional traits (Fig. 6). As there exist many different indices and each of them focuses on a slightly different aspect of diversity, we computed several of them in **Chapter III** to study patterns and evolution of diversity in Australian birds.

We used four types of PD and three types of FD indices (**Chapter III**). The simplest computation of PD is to connect all species present in an assemblage on the phylogenetic tree and to sum their branch lengths (Faith 1992; **Chapter III**; Fig. 6). Other metrics can also utilize the distance between the species (measured as the length of branches connecting them) and we can compute the mean, minimum, or variation of pairwise distances between the species in an assemblage (Clarke & Warwick 2001, Webb et al. 2002; **Chapter III**). The selection of metrics depends on the studied question and can

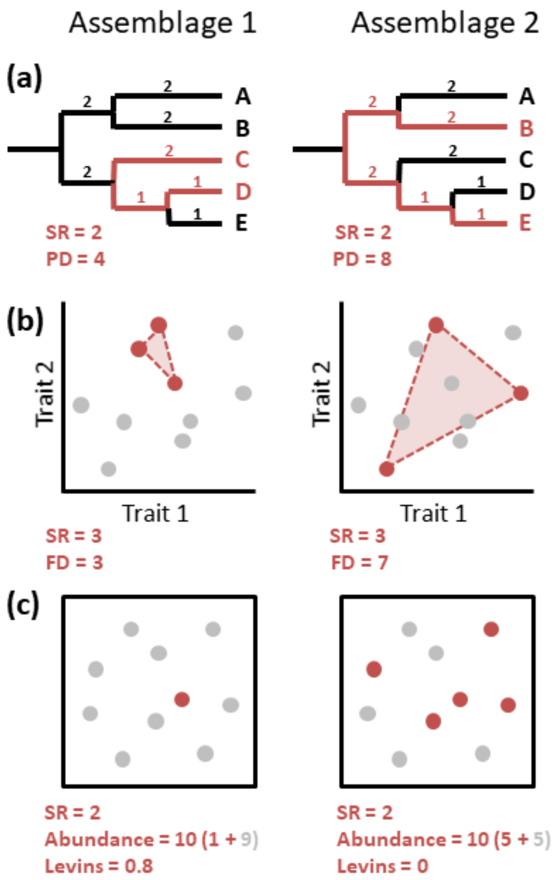


Figure 6. Examples of computations and differences between diversity indices. (a) From the five species (A−E) found in the whole study system, only two are present in Assemblage 1 and 2 and thus both assemblages share the same value of species richness (SR). However, assemblages differ in their phylogenetic diversity (PD). In Assemblage 1, present species (C and D) are closely related (red colour of branches on the phylogenetic tree) and PD (computed as Faith's index, i.e. the sum of branch lengths connecting all species present in an assemblage; Faith 1992) is low, while species in Assemblage 2 (B and E) are more distantly related and thus PD is higher. **(b)** Ten species are plotted in functional space presented here as a two-dimensional space. In both assemblages, three species are always present (red colour; SR = 3) and convex hull volume of functional space between the connected species (Villéger et al. 2008) can be computed by linking them and used as a measure of functional diversity (FD). Since in Assemblage 2 present species have higher variability in their traits and hull volume is larger, there is also higher FD. **(c)** There are ten individuals of two species (differentiated by grey and red colours) present in each assemblage, but species differ in their abundances (number of individuals). While SR and overall abundance in both assemblages are identical, abundance per species is uneven in Assemblage 1 (one vs nine individuals) and balanced in Assemblage 2 (both species are presented by five individuals). This unevenness can be captured e.g. by Levins' diversity index (modified by Belmaker et al. 2012).

focus on the overall evolutionary history accumulated in an assemblage, how even its distribution between species is, or how similar the species in an assemblage are (Tucker et al. 2016). FD indices are usually divided into three categories – functional richness, evenness, and divergence (Mason et al. 2005). Their computation is usually based on 'functional space' computed as a principal coordinates analysis (PCoA) based on a distance matrix between species (based on the similarity of their traits). Functional richness is the most basic FD metric that represents the overall amount of functional space filled by the species in an assemblage. It can be computed by many ways; as a sum of branches on a trait dendrogram (Petchey & Gaston 2002), a convex hull volume (Villéger et al. 2008; **Chapter III**; Fig. 6), or an *n*-dimensional hypervolume (Blonder et al. 2014, Blonder et al. 2017). Functional evenness then shows how evenly species are distributed in the functional space, while functional divergence focuses on species' dispersion in the functional space. Evenness is usually computed as the sum of branch lengths of a minimum spanning tree that links all species in the functional space of an assemblage (Villéger et al. 2008; **Chapter III**). Divergence is then a mean of species' distances from a centre of gravity in the functional space (Villéger et al. 2008; **Chapter III**).

Many of the diversity indices are correlated with SR. This is to be expected as the addition of a species into an assemblage should also increase its diversity as the new species likely differs in its traits from the other species already present in the assemblage. Moreover, it is difficult to recognize whether the diversity patterns indicate ecological processes or result from random sampling processes. Therefore, null models are used to correct the diversity indices for the observed SR and to differentiate between random and ecological patterns. Null models are based on repeated randomizations of assemblages. Many ways of these randomizations exist; we used shuffling of the species identities on the phylogeny and in trait data matrix in **Chapters III and IV** as it is the method that does not alter SR recorded in assemblages and in the overall study area. The randomizations create assemblages that differ in their species composition (species identity). Species are randomly selected from 'a species pool', which is a collection of species found in the whole region, continent, or world. Randomizations are repeated many times and standardized effect sizes (SES) are usually computed (**Chapter III**) as a difference between observed value of the diversity index and the mean of the expected values, divided by standard deviation of the expected values. SES with high values indicate higher diversity than expected by chance and vice-versa with lower values.

2.3 Statistical analyses

We used several macroecological analytical approaches. First, in comparative (species-level) analyses we used a correction for phylogenetic relations between species (**Chapters I and II**). This approach assumes that closely related species are more similar in their traits and thus do not represent independent units. The correction was done by using generalized least squares regression method (GLS) and estimating Pagel's lambda

(Pagel 1999) that adjusts the analysis for the phylogenetic autocorrelation. As a source of phylogenies, we used birdtree.org (Jetz et al. 2012), where we downloaded 100 phylogenetic trees. As individual phylogenies slightly differ in topology and branch lengths, it was necessary to repeat the phylogenetic GLS analyses with 100 phylogenies and then average the results (**Chapter I**).

Second, in spatial (assemblage-level) analyses one needs to correct for spatial autocorrelation, where close assemblages are usually more similar (in their species composition or abiotic conditions) than distant ones. The correction was done by using information on geographical locations of assemblages (in form of latitude and longitude) to model spatial correlation structure in a spatial GLS model (**Chapters I–IV**). Because several correlation structures exist, the model was fitted with several of them and then we selected the best one based on the lowest value of AIC (**Chapters III and IV**). Another method of dealing with spatial autocorrelation is simultaneous autoregressive (SAR) models that work with the spatial distance and weighting of neighbourhood locations (Kissling & Carl 2008; **Chapter I**).

To complement the regression-based approaches and to differentiate between direct and indirect effects of explanatory variables on the response variable, we used structural equation modelling (SEM), also known as path analyses (Lefcheck 2016; **Chapter III**). This method enabled us to test hypothesized causal relationships by using pre-existing knowledge of the system and thus quantify the strength of presumed causal links between variables.

3 Results and discussion

3.1 Evolution of life history traits and morphology

Many hypotheses were proposed to explain interspecific variation in clutch size. Here we tested three of them: environmental productivity and its seasonality, nest predation, and fledgling development (**Chapter I**). We collected data on clutch sizes and other life history traits in 313 species of Australian songbirds from literature and tested which (if any) of these theories possibly explain interspecific variation of clutch size. Clutch size showed a broad taxonomical variability (**Chapter I**), ranging from one (e.g. family Menuridae) to six eggs (e.g. family Estrildidae). However, this variability was not so pronounced geographically, ranging from assemblages with mean clutch size of 2.6 eggs on the north and south-west of the continent to the clutch size of three eggs in the eastern Australia and the island of Tasmania. Although the visual pattern does not seem to support the latitudinal gradient in clutch size, we found a statistically significant increase in clutch size towards higher latitudes, which is in concordance with other studies that found a weak gradient even in the Southern Hemisphere (Yom-Tov et al. 1994, Young 1994, Jetz et al. 2008).

We did not find any effect of environmental productivity or its seasonality on clutch size (**Chapter I**) and thus cannot support the first hypothesis, which says that clutch size should increase in more productive and/or more seasonal environments (Lack 1947, 1948; Ashmole 1963). Although this relationship was demonstrated by previous studies (e.g. Ricklefs 1980, Yom-Tov 1994, Jetz et al. 2008, Griebeler et al. 2010, Hořák et al. 2015), it does not appear to be the main driver of the evolution of clutch size in Australian songbirds. An explanation might lie in quite unusual climatic conditions in Australia, as the continent is very arid, climatic seasonality there is not so distinct as in the Northern Hemisphere (Greenwood & Wing 1995) and is often unpredictable due to the ENSO events (Power et al. 1999). High aridity and unpredictability of the environment might have led to the evolution of overall small clutches. Environmental productivity is related to water availability, which is low in Australia (Fig. 2) and could have pushed the evolution of clutch size to smaller numbers of eggs. Also, according to the bet-hedging theory it should be more favourable to have small clutches in unpredictable environments so that parents do not lose as much energy during an unsuccessful nesting event and have an opportunity to re-nest (Murphy 1968, Slatkin 1974). Moreover, climatic conditions might have influenced clutch size evolution, but we could not be able to detect it due to our methodology.

We used satellite images of NDVI, which showed plant productivity but high values of NDVI might not represent optimum breeding conditions (Foster 1974) or reflect the actual food availability.

Further, neither nest predation showed any effect on clutch size (**Chapter I**). The problem with predation and its rates might lie in the changes in predator communities and introductions of new predators after the European settlement (Ford et al. 2001, Salo et al. 2007, Dickman 2009, Remeš et al. 2012a, Remeš et al. 2012b), which then might have changed the (possibly existing) historical patterns. However, we used data collected from records across large spatial and temporal scales, which should be less sensitive to these changes.

Out of the three hypotheses tested we found most support for the one concerning fledgling developmental traits (**Chapter I**). We found a positive relationship between clutch size and nestling period when controlled for either adult survival or climate and nest predation. According to Martin (2014), length of the nestling period affects the investment per offspring for parents by setting the gradient in nestling development. The combination of the length of the breeding season and adult survival then represents the total reproductive effort per breeding attempt which should emphasize the effect of the length of the nestling period. We also tested the assumption that high post-fledging survival is mediated by well-developed offspring allowed by long nestling periods (Martin 2014, 2015). We found that relative body mass at fledging was positively related to nestling period, while relative wing length was not, which only partly supported Martin's hypothesis (**Chapter I**). These analyses were carried on only a limited sample size of 18 species due to the difficulty of obtaining necessary data. However, the positive effect of relative body mass at fledging and the length of nestling period on post-fledging survival was found in birds globally (Remeš & Matysioková 2016, Martin et al. 2018), bringing more support for Martin's hypothesis.

Factors affecting the evolution of clutch size are complex and many theories were proposed to disentangle them. Even though we tested three of such theories and controlled for other possible effects (such as body mass, nest type, migratory strategy, length of the breeding season etc.; **Chapter I**), there might still remain other factors influencing clutch size. For example, it appears that old endemic families have smaller clutches (Woinarski 1985, Yom-Tov 1987), while cooperative breeders larger clutches. One might presume that helpers can help to raise more offspring, but this positive relationship was not proved to be true in Australian songbirds (Poiani & Jermiin 1994).

In case of a key morphological trait, avian beak, it is thought that the evolution of its shape and size is attributed mainly to dietary preferences, as known from the famous example with Darwin's finches (Grant et al. 1976, Grant & Grant 2002). Recently, an effect of thermoregulation and thus climatic conditions was suggested to shape beak size as well, yet the effects are still poorly understood. Therefore, we studied whether summer or winter climatic conditions affect evolution of beak size in 158 species of Australasian honeyeaters and allies (Meliphagoidea). This clade is ideal for these purposes, because its species are diverse in their beak morphologies, widespread across Australia, Tasmania, and New Guinea, yet mostly confined to these regions. We found that the evolution of beak size was mostly driven by winter temperatures (**Chapter II**). This gives some support for Allen's rule (Allen 1877), which says that individuals at higher latitudes (i.e. in colder climates) should have smaller body appendices due to the thermoregulation requirements. However, it is in contrast with results of Greenberg et al. (2012b) who found that the summer heat stress drives beak size evolution in North American Emberizid sparrows. Still, they observed larger beaks in coastal areas, which are climatically quite mild (Danner & Greenberg 2015). In the case of Australasia, beak size showed clear latitudinal gradient where species with larger beaks inhabited New Guinea and the northern regions of Australia, while the south and the centre of Australian continent were occupied by species with smaller beaks (**Chapter II**). Thus, larger beaks appear to be in coastal regions, which are quite mild and non-seasonal, while seasonal areas (with harsh winters) favourite smaller beaks.

It would be surely interesting to supplement the analyses of climate dependencies with analyses testing the effect of diet on the evolution of beak size. However, it is difficult to obtain suitable data concerning diet (**Chapter II**). For example, the most available form of diet data is the division of species according to diet categories such as seeds, fruit, or insect (e.g. Elton traits database; Wilman et al. 2014). However, such categories are not suitable to study their relationship with beak size. Instead, the role of dietary items' size (Grant et al. 1976) or foraging behaviour (Miller et al. 2017) might play more prominent role in driving beak size evolution. However, such detailed data are hard to obtain, especially for species inhabiting New Guinea and remote islands. Moreover, diet could play an important role in shaping beak shape, not size, and the shape could just scale with climate. Furthermore, the effect of diet and climate can differ at various spatial scales. For example, we would expect to find stronger influence of climate on larger spatial scales comprising of whole continents, while at small spatial scales with narrow climatic conditions, the effect of climate could not be apparent and instead we expect the increasing influence of diet on driving beak size. Thus, it is important to replicate such studies on various spatial scales and in different regions and taxa to better understand the evolution of key morphological traits.

3.2 Spatial patterns in avian diversity

We mapped spatial patterns of species richness of all Australian species of birds and other diversity metrics and studied direct and indirect effects of various environmental conditions on shaping these patterns (**Chapter III**). We used four indices to compute phylogenetic diversity (PD) and three indices and two sets of traits (based on either morphological or ecological properties) to compute functional diversity (FD). We used path analyses that can distinguish between such direct and indirect effects and included various environmental variables that could have significant effect, such as water availability, topography, height of the forest canopy, and diversity of habitats. Quantifying and identifying these effects is important for understanding current patterns of biodiversity and how these patterns originated.

All three aspects of diversity (SR, PD, and FD) showed strong spatial patterns. SR was highest along the eastern coast and on the south-east of the continent (Fig. 3), while residual PD (SES values) was higher than expected along the eastern coast and on the north (**Chapter III**). Spatial patterns in FD based on either morphological or ecological sets of traits were not consistent, but there was still a visible transition from central arid to coastal areas, which was apparent across assemblages in all diversity metrics. High SR and PD in the wet areas along the coasts is in agreement with the previous findings by Hawkins et al. (2003, 2005) and points to the presence of phylogenetically rich assemblages with species accumulated from various distant clades. Similar pattern is shown also by Australian mammals (Nipperes & Matsen 2013, Coelho et al. 2019), but it is opposite in Australian lizards and mice (Lanier et al. 2013). Wet forests along the eastern coast represent remnants of original habitats, which covered the whole continent of Australia more than 20 Mya when the aridification began (Byrne et al. 2008, Byrne et al. 2011). High richness in this environment thus might be caused by long time for diversification and accumulation of lineages (Wiens et al. 2011). Moreover, newly arisen arid environments might have caused higher extinction rates and thus reduce diversity (Pulido-Santacrus & Weir 2016). Adaptations to these harsh conditions should include effective temperature regulation and water economy (Wolf 2000, Fristoe et al. 2015), which might have prevented the colonization of the arid environment. For example, it was shown that in case of Australian honeyeaters (family Meliphagidae), only a few clades were able to invade and adapt to the newly arisen arid environment from the moist one in which the family originated (Miller et al. 2013, Joseph et al. 2014).

In the path analyses, only SR showed both direct and indirect dependencies on water availability, habitat diversity, and canopy height, while PD and FD indices did not correlate with environmental variation in most cases (**Chapter III**). Precipitation has a large influence on diversity patterns in Australian flora and fauna (Hawkins et al. 2003, Byrne et al. 2008, 2011) and we confirmed its direct effect on SR of Australian birds. However, in terms of the mechanism, probably mostly plants and ectotherms are affected by water availability directly, while endotherms are instead more influenced by extreme climatic events (McKechnie et al. 2012). Water availability also showed indirect effects on SR via increasing vertical (canopy height) and horizontal (habitat diversity) vegetation complexity (**Chapter III**), probably because structurally more complex habitats offer more resources and ecological space. The effect of canopy height (as a surrogate for vegetation complexity) on SR was previously shown in amphibians and primates (Gouveia et al. 2014, Roll et al. 2015), but it was not true in birds and mammals (Roll et al. 2015). However, this effect might differ between continents and biomes.

Climatic and environmental variables showed significant effects only on SR, but not on PD and FD (**Chapter III**). It thus appeared that while patterns of SR were affected by water availability, patterns in PD were probably mostly tied to the history of the continent, while patterns in FD were mostly correlated with SR with no effect of environmental variables we studied. However, to properly analyse patterns in FD, inclusion of more detailed ecological traits applied in local communities is needed.

Therefore, to study coexistence of species and their packing in ecological space, we conducted a research of the relationships between species richness, specialization, and niche overlap (**Chapter IV**). We used 298 species of Australian songbirds with data on five ecological traits concerning type of habitat, diet preferences and foraging behaviour (meaning how and on what substrates and stratum they obtain food) and three spatial scales ranging from localities to bioregions. We expected that SR would correlate positively with specialization and negatively with niche overlap because of the division of ecological space and relaxed interspecific competition that could enable higher packing of species (Hutchinson 1959, MacArthur 1972, Eeley & Foley 1999, Mason et al. 2008, Pigot et al. 2016). We indeed found positive richness-specialization relationship, but it showed variability between traits and across spatial scales (**Chapter IV**). Niche overlap was related negatively to species richness in case of foraging method, which was to be expected as species rich assemblages should overlap less in their ecological characteristics to be able to coexist. Surprisingly, niche overlap correlated positively with species richness in diet and foraging substrate. However, although the effect sizes were positive, they were smaller than those from the null model expectations. This could mean that processes sorting species and lowering the overlap in their ecological niches might still be present.

Interspecific interactions and niche partitioning are assumed to play more prominent role at smaller spatial scales, while effects of abiotic conditions and historical background should be more important on larger scales (Whittaker et al. 2001, Hawkins et al. 2003, Ricklefs 2006, Belmaker & Jetz 2011, Devictor et al. 2010, Ferger et al. 2014, Royan et al. 2016, Fergnani & Ruggiero 2017). Therefore, we expected to see stronger correlation coefficients at the small spatial scale of localities and their weakening towards grid cells (intermediate scale) and bioregions (largest spatial scale; Fig. 4). However, this was not the case and the richness-specialization relationship was as steep, or even steeper, at the regional scale as on the local scale (**Chapter IV**). Species richness was thus probably not driven by competition and partitioning of resources and current assemblage compositions probably mostly reflected historical effects and not current ecological processes (Hawkins et al. 2005, **Chapter III**).

Furthermore, we tested the expectation that specialization should be highest in assemblages that contain more species than is expected based on given environmental conditions (**Chapter IV**). First, we used multi-predictor regressions relating species richness to both specialization and variables concerning productivity (expressed as moisture) and vegetation structure (combination of vegetation height and cover), which are important predictors of species richness in general (Hurlbert 2004, Evans et al. 2006, **Chapter III**). Second, we used quantile regression analysis that related specialization to residuals of the richness-environment model (**Chapter IV**). We expected to find higher specialization in higher quantile cut-offs, i.e. in assemblages that contain more species than is expected for given environmental conditions; however, this was not the case. The richness-specialization relationship did not display the increase in higher cut-offs, again showing that spatial patterns in species richness were probably not related to competition between species and partitioning of resources. Interestingly, the relationship was strong also in assemblages that were species-poor for a given environment. This might be caused by the aridity gradient in Australia – species richness in Australia is lowest in arid areas (**Chapter III**) and present species might show high specialization to be able to endure extremely harsh conditions (Wiens et al. 2013).

We focused not only on specialization, but also on niche overlap between species. The reason is that the specialization index we used does not differentiate whether species in the same assemblage are specialized on the same trait categories or not (**Chapter IV**). We expected to find a negative correlation between specialization and niche overlap, which would suggest that interspecific competition might be relaxed. However, this was the case only in foraging stratum and substrate, while the rest of the traits showed positive correlations. The reason might be too wide ecological categories that might not reflect the actual niche partitioning. For example, in case of diet, species that specialize on foraging on different plants can fall into the same category of e.g. granivory and thus appear to be 'competitors'. However, even these species might differ in methods they use to obtain food and other foraging strategies. We found that niche partitioning is detectable in case of foraging substrate (**Chapter IV**) indicating that at least some partitioning of niche is present on local scales.

4 Conclusions

In this thesis I focused on studying interspecific variability, evolution, and geographical patterns in life history traits, morphology, and diversity of Australian birds. I showed that the evolution of clutch size and beak size were under the influence of different factors in Australia compared to other regions of the world. Moreover, diversity patterns and assemblage composition were probably mostly driven by historical effects rather than by current ecological conditions and interspecific interactions. The main conclusions of this work are as follows:

I. Clutch size of Australian songbirds showed low interspecific and spatial variability, but still increased away from the equator. Out of the three hypotheses tested, the role of nestling development in shaping the evolution of clutch size of Australian songbirds was most prominent. In contrast to many Northern Hemisphere studies, we found no relation between resource availability or nest predation and clutch size.

II. Winter, not summer, temperatures explained most of the variation in beak size in honeyeaters and allies across Australia and New Guinea. It appears that the need for heat retention in cold months affects the evolution of beak size in this group of Australasian songbirds.

III. Water availability had positive direct as well as indirect (via vegetation complexity) effects on species richness of Australian birds. However, phylogenetic and functional diversity were only poorly predicted by environmental conditions and were possibly more affected by the age of biomes and evolutionary history of the studied clades.

IV. Species richness and specialization of Australian songbirds showed both positive and negative mutual relationships depending on the ecological trait used (habitat selection, dietary preferences, or several types of foraging behaviour). The richness-specialization relationship was strongest at the regional scales, which is in contrast to the expectations that interspecific interactions should be most prominent on local spatial scales and shape the assemblage composition. However, it still appears that species partition their ecological space via the foraging on a particular vegetation stratum and substrate.

Future research regarding life history and diversity of Australian birds could surely profit from more field studies concerning avian reproductive and foraging strategies.

I showed a substantial deficiency in data on offspring development, specific body measurements, or detailed diet and foraging preferences. The addition of detailed field observations could certainly improve our knowledge of both evolution of life history traits and diversity patterns as they can help quantify processes affecting assemblage composition. However, it is important to put findings on these fine scales into context of large spatial scales and possibly also compare them with other regions beside Australia, preferably to other arid Southern Hemisphere areas. Moreover, applying various time scales can bring interesting insights into the evolution of Australian avifauna, either by the inclusion of paleoclimate and fossil data (though this might be challenging in case of birds) or by studying shifts in trait values or diversity patterns since the beginning of the European settlement. Extinctions of many species together with the introduction of new ones, which could fill in the new roles of competitors, predators, parasites, or prey, could have definitely affected the original Australian avifauna and alter macroecological patterns. Finally, macroecological studies still suffer from the lack of fully resolved molecular phylogenies which are essential in studying evolution of life history traits and phylogenetic diversity, and the use of purely correlative approach. It would be beneficial to employ frameworks based on species interactions, for example between birds and plants, such as pollinator-plants networks in, for example, Australian honeyeaters (family Meliphagoidae).

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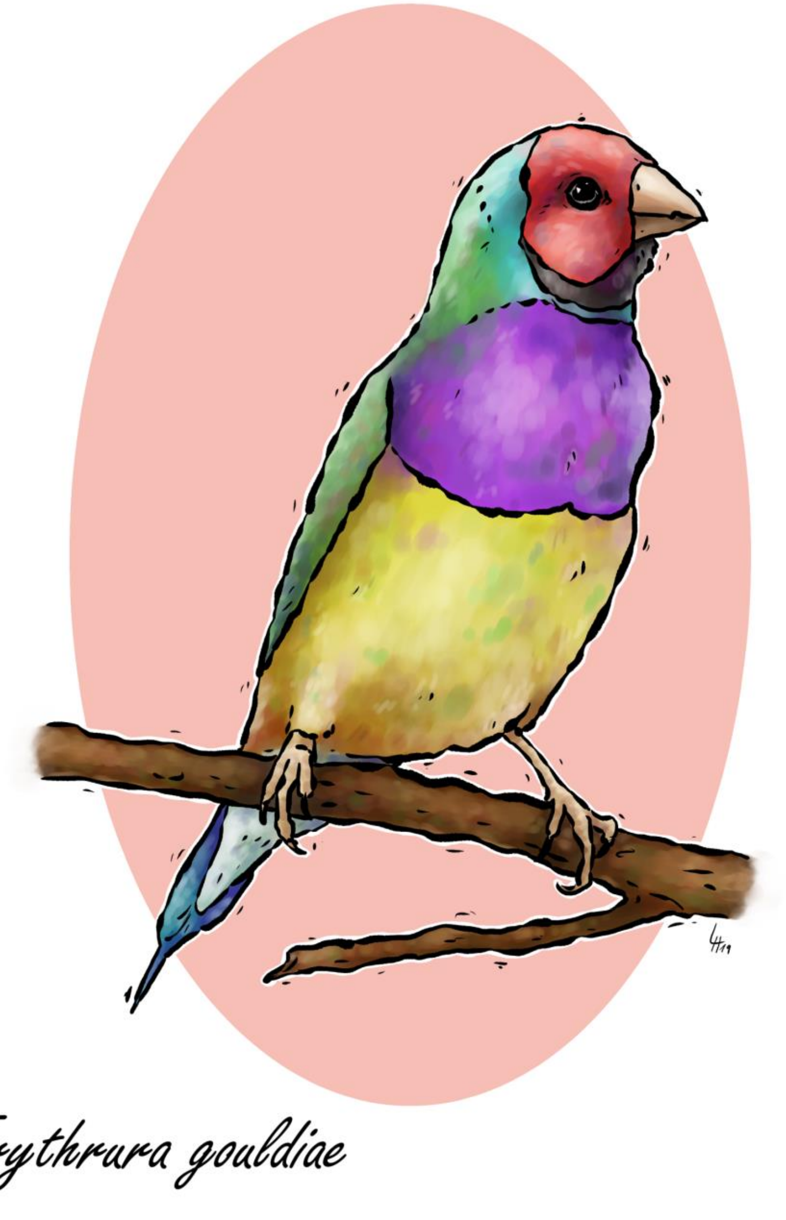
Chapter I

The evolution of clutch size in Australian songbirds in relation to climate, predation, and nestling development



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Gouldian Finches (*Erythrura gouldiae*) lay around six eggs per a clutch and represent one of the species with the largest clutch size found in Australian songbirds.

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The evolution of clutch size in Australian songbirds in relation to climate, predation, and nestling development

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ABSTRACT

The study of clutch size has been a productive approach to gaining better understanding of life-history evolution, especially in Northern Hemisphere birds. Factors driving life-history evolution in Southern Hemisphere species are less well understood. Moreover, studies often focus on single hypotheses for clutch size evolution and rarely test several hypotheses simultaneously. This severely limits more general conclusions of life-history evolution. We assembled an extensive dataset on 313 species (*ca.*98%) of Australian songbirds (Passeriformes) and tested three hypotheses for the evolution of clutch size in birds: (1) resource availability and their seasonality (Lack's and Ashmole's hypotheses), (2) nestling mortality (age-specific mortality and Skutch's hypotheses), and (3) fledgling developmental gradient (Martin's hypothesis). The mean clutch size of Australian songbirds was 2.69 eggs and increased in higher latitudes. Clutch size was positively related to the length of the nestling period and in species with short nestling periods offspring left the nest with lower body mass, consistent with Martin's hypothesis. In contrast to many Northern Hemisphere studies we did not detect any direct effect of the productivity of environment, its seasonality or nest predation rate. Our work provides one of only a handful of comprehensive tests of clutch size evolution in Southern Hemisphere birds. Its findings stress the importance of breaking the Northern temperate bias of life-history studies.

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Introduction

Patterns in clutch size variation among birds have been well documented, yet the mechanisms generating these patterns on both interspecific and intraspecific levels are still not fully understood. First, Lack (1947, 1948) and Ashmole (1963) stressed the importance of resource availability for optimal clutch size. Lack (1947, 1948) proposed that available resources determine how many offspring parents are able to rear: more resources per capita allow for larger clutch size. Ashmole (1963) later suggested that per-capita food availability during the breeding season is driven by the interaction between population density (which is regulated during the winter months), resource availability, and its seasonality. In areas with high seasonality of resources and low-resource winter periods, high over-winter mortality of individuals reduces population density. This results in high availability of food per capita in the following breeding season. Birds can then have larger clutches because they are able to nourish more offspring. Clutch size is thus predicted to increase with increasing seasonality of resources. Several studies have confirmed this prediction both across and within species (Ricklefs 1980; Koenig 1984; Yom-Tov 1994; Dunn *et al.* 2000; Yom-Tov and Geffen 2002; Jetz *et al.* 2008; Hořák *et al.* 2015; partial support in Evans *et al.* 2005; Samaš *et al.* 2013). Moreover, its logic was backed by modelling studies (McNamara *et al.* 2008; Griebeler *et al.* 2010). However, Ashmole's mechanism is certainly not the only process affecting clutch size evolution in birds, because there is usually substantial residual variation in clutch size across species and space after accounting for seasonality (Ricklefs 1980; Jetz *et al.* 2008). Moreover, it does not account for migrants, which are not exposed to harsh winter conditions, immigrate to highly seasonal areas, and exploit local resources during the breeding season, even though their mortality rates might increase during the migration. Most importantly, Ashmole's hypothesis has been tested simultaneously with other hypotheses to judge its relative importance in explaining clutch size variation across species only a few times (Hořák *et al.* 2011; Samaš *et al.* 2013).

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Supplemental data for this article can be accessed here

Second, according to Skutch (1949), larger broods are more likely to be depredated than smaller ones, because nests with more offspring attract the attention of predators more than nests with fewer offspring due to more frequent feeding visits by parents. Parents are thus selected to decrease their food delivery rates. Although they can partly compensate by delivering larger food items, lower delivery rates result in the reduction of clutch size (Martin *et al.* 2000), because parents are not able to nourish many offspring. Low food delivery rates under high nest predation were documented by Martin *et al.* (2000, 2011), suggesting that this mechanism might at least partially explain clutch size variation among species. Predictions of Skutch's hypothesis are in accordance with the age-specific mortality hypothesis, whereby under high nest predation rate it should be advantageous to decrease clutch size and thus save energy for easier re-nesting in the case of clutch or brood loss (Ricklefs 1968; Stearns 1976; Martin 1995). On the other hand, when mortality is high in adults (e.g. due to predation or starvation in the lean season), it is better to invest more energy (and thus increase clutch size) in the current reproductive attempt (Williams 1966; Sæther 1988; Martin 1995; Ghalambor and Martin 2001; but see Lloyd *et al.* 2014). These two hypotheses (i.e. age-specific mortalities) were suggested to explain increasing clutch size with latitude, because nest predation and adult survival rates are probably higher in the tropics than in the temperate zone (Skutch 1949; Slagsvold 1982; Yom-Tov *et al.* 1992; Martin *et al.* 2000; Ghalambor and Martin 2001). However, geographic gradients in nest predation rates seem to differ between regions (Martin 1996; Martin *et al.* 2000; Remeš *et al.* 2012a) and differences in adult survival between temperate and tropical regions can be sometimes weak or absent (e.g. Karr *et al.* 1990). Thus, it remains to be demonstrated how well age-specific mortalities predict clutch size in different parts of the world, especially when tested simultaneously with other relevant hypotheses.

Third, Martin (2014) proposed a new hypothesis that follows the basic idea of nest predation being the main driver of clutch size evolution, but with additional mechanisms. According to this hypothesis, higher nest predation risk leads to shortened nestling periods to avoid nest depredation and nestlings consequently fledge with underdeveloped wing feathers (Cheng and Martin 2012) and low body mass (Remeš and Martin 2002; Remeš and Matysioková 2016). Wing length and body mass at fledging vary between species and this gradient sets the amount of energy that must be spent on every offspring after fledging. More energy is needed for less developed fledglings as they are less agile, more dispersed, it takes them longer to develop self-feeding, and they have higher mortality rates (Martin 2014; Remeš and Matysioková 2016). The mortality rate of offspring, together with the daily energy expenditure of parents for the whole brood, then determines clutch size. This hypothesis predicts larger clutch sizes in species with longer nestling periods for a given adult body mass. Martin (2014, 2015) found support for his hypothesis in songbirds from North America, Malaysia, and Venezuela, but it now needs to be tested on additional datasets and on species from other parts of the world, preferably together with other relevant hypotheses.

Most studies concerning the evolution and geographic variation of clutch size and life histories in general were conducted on species inhabiting the Northern Hemisphere. Comparatively little is known about birds from the tropics and the Southern Hemisphere (Martin 1996, 2004, 2015). However, these species are distinct by their generally slow life histories, including longer breeding seasons and smaller clutches compared to birds from the same Northern latitudes (Cody 1966; Wyndham 1986; Martin *et al.* 2000; Jetz *et al.* 2008; Freeman and Mason 2014), and the latitudinal gradient of clutch size on the Southern Hemisphere is weak (Yom-Tov *et al.* 1994; Young 1994; Jetz *et al.* 2008). Australia represents a unique study system with highly endemic and diverse avifauna (Holt *et al.* 2013). Climatic and environmental conditions vary substantially both across latitude and from inland to coast, which makes this area ideal for studying life-history hypotheses based on such pronounced differences. Most of the continent is arid while productive environments with high precipitation are distributed along the northern, eastern, and southern coasts, creating somewhat unusual spatial pattern of climatic variability. Moreover, Australian avifauna is quite well studied compared to other Southern Hemisphere birds and provides a great opportunity for studying life histories of resident species of birds in the Southern Hemisphere.

In this study we put together a large dataset of several intrinsic and extrinsic traits obtained from the literature and test simultaneously for the first time all the hypotheses described above on Australian songbirds. We test the effects of (1) resource availability (Lack's and Ashmole's hypotheses), (2) the rate of nest predation (age-specific mortality and Skutch's hypotheses), and (3) the length of the nestling period and relative fledging mass and wing length (indirect test of the new Martin's hypothesis). Our study thus contributes to the understanding of the relative strengths of competing hypotheses for clutch size evolution in Australian songbirds, and more generally of the evolution of life histories in Southern Hemisphere birds.

Methods

Species-level data

Our species-level dataset consisted of 11 intrinsic and 2 extrinsic traits of Australian songbirds (Passeriformes) obtained from the literature. Altogether, we covered 313 species out of 318 species of songbirds (i.e. *ca.*98%) listed in our main data and taxonomy source, the 'Handbook of Australian, New Zealand and Antarctic Birds' (HANZAB; Higgins *et al.* 2001, 2006; Higgins and Peter 2002). Here we searched for the following data for each species: average clutch size (number of eggs; mean of completed clutches), nest type (open vs. closed nests, the latter including both cavities and domed nests), nestling period duration (number of days from hatching to leaving the nest), length of breeding season (months when the species breeds), migration strategy (sedentary species vs. migrants, which also included partial migrants and nomadic species), mean body mass of adults (grams), and type of foraging behaviour (foraging in air or elsewhere; as aerial foragers we considered species catching flying insects both by constant flying and from a perch). We obtained daily nest predation rates (DPR) from Remeš *et al.* (2012a) supplemented with additional literature (Supplement S1), and annual adult survival, relative wing length (wing length at fledging divided by wing length of adults) and relative body mass (body mass at fledging divided by body mass of adults) from the primary literature (Supplements S2 and S3).

Since HANZAB sometimes gives multiple values for individual species, we always calculated arithmetic means of all available values for a given species. To see whether these multiple values of our response variable were consistent, we calculated repeatability of clutch size, which proved to be high (ICC = 0.8, CI = 0.75–0.84, *n* = 313). For this calculation, we used the 'ICCest' function from the 'ICC' package in R (R Core Team 2015) which estimates the Interclass Correlation Coefficient using variance components from a one-way ANOVA (Wolak *et al.* 2012).

To estimate environmental productivity for each species in our dataset, we needed information on the geographic ranges of all species. Data on the geographic ranges of Australian birds were provided by BirdLife International and NatureServe (2011) as GIS shapefiles. We wanted to use only breeding ranges where the species are currently present. We thus adjusted range polygons according to their coding of species' presence (1 – extant, 2 – probably extant, 3 – possibly extant, 4 – possibly extinct, 5 – extinct, 6 – presence uncertain) and season (1 – resident, 2 – breeding season, 3 – non-breeding season, 4 – passage, 5 – seasonal occurrence uncertain) to keep only polygons with codes 1, 2, and 3 for species' presence (extant) and 1 and 2 for season (breeding area).

Using these breeding ranges, we estimated the environmental productivity for each species. As a proxy of environmental productivity, we used the Normalised Difference Vegetation Index (NDVI) available from the Australian Government's Bureau of Meteorology (2015). We used the Monthly NDVI Average for Australia dataset with mean monthly values of the NDVI for the years 2008–2014 to calculate the maximum breeding season NDVI and NDVI seasonality in the breeding range of each species. To do that, we first rasterised ranges in Australia and Tasmania to fit the 0.05 × 0.05° geographic (longitude × latitude) resolution of the NDVI data. Then we calculated mean monthly NDVI values for all cells within the geographic range of every species. Finally, we calculated two values for every species: (i) maximum breeding season NDVI as the value of the month with the highest NDVI out of species' breeding months, and (ii) NDVI seasonality as a difference between maximum breeding season NDVI and the month with the minimum value of the NDVI.

Assemblage-level data

For mapping the spatial variation in clutch size, we needed to convert species data into assemblage-level data. To obtain these assemblage-level data, we started with creating a grid across Australia and Tasmania and chose the resolution of 1 × 1° (longitude × latitude) as the smallest size of the cell that leads to unbiased results when using coarse range data (Hurlbert and Jetz 2007). We then removed cells containing islands (except Tasmania) and those with less than 50% of mainland in Quantum GIS v1.8 (QGIS Development Team 2014). The final grid consisted of 686 cells. We used this grid to obtain assemblage-level data on clutch size. We used breeding ranges (see above) to generate presence–absence data for all species in each cell of our grid. Species present in each grid cell composed the local assemblage. We obtained values of clutch size in each cell as the mean of the clutch size in all species present in that cell (i.e. assemblage means).

Statistical analyses

An assemblage-level spatial model was fitted to describe effects of latitude and longitude on clutch size. The model consisted of one dependent variable (clutch size) and two predictors (latitude and longitude) with their interaction. We first fitted the simple linear model with centred and scaled geographical position of grid cells (n = 686) as statistical units. However, geographical data often show spatial autocorrelation that might negatively affect analyses, so we tested for spatial autocorrelation in the residuals of the regression model using Moran's I (Moran 1950). The data points were spatially non-independent, so we fitted new regression analysis using a simultaneous autoregressive error model ($\mathrm{SAR}_{\mathrm{err}}$), which accounts for spatial autocorrelation (Kissling and Carl 2008).

For the phylogenetic analyses, we used species-level data and set up a priori models with their respective predictor variables (Table 1). Each model consisted of focal predictors stemming from the particular hypothesis and covariates that were previously shown to correlate with clutch size, including nest type (species nesting in a closed nest are expected to have larger clutches than species nesting in an open nest; Slagsvold 1982; Jetz *et al.* 2008), migration strategy (migrants tend to have smaller clutches than resident species; Yom-Tov and Geffen 2002; but see Jetz *et al.* 2008), body mass (larger species of passerines usually lay fewer eggs; Averill 1933), aerial foraging (aerial foragers can have smaller clutches than species with other foraging strategies; Martin 1995, 2014), and the length of the breeding season (as a surrogate for the number of broods per year; according to the principle of allocation, species with short breeding seasons should have time to rear only a few larger clutches, while species with long breeding seasons should have time to rear more clutches and allocate available resources among them; Cody 1966; Martin 1995). There are other factors, which may influence the evolution of clutch size, such as cooperative breeding and diet. However, due to conflicting or lack of evidence that these variables do have effects on clutch size, we did not include them in our analyses (for more information see the Discussion).

The lack of available data for some species limited our dataset. We obtained data for all 313 species only on clutch size and the length of the breeding season. Across the traits, the mean number of species with available data was 217.3 (median = 283, n = 13 traits); the smallest number of species was available for relative wing length at fledging (19 species). For each analysis, data are needed for all traits used in that particular analysis and since different variables are missing in different species, this further reduces sample size. None of the analyses were therefore conducted on the full (n = 313) number of species. The sample size used in each analysis is shown in Table 1.

In the first model, we used two indices expressing per capita food availability, namely max NDVI as a surrogate of the maximum productivity during the breeding season and NDVI seasonality as a surrogate of how productivity varies across the year (Lack's and Ashmole's hypotheses). For this analysis we used only non-migratory species (n = 224), because Ashmole's predictions cannot be applied to migrants. DPR in the second model tests the nestling mortality hypothesis and the length of the nestling period in the third model tests Martin's hypothesis concerning relative development of nestlings. Martin (2014, 2015) used also adult survival, relative wing length and relative body mass at fledging, but because limited availability of data would dramatically reduce species sample (n = 52; adult survival), we fitted one model with nestling period only, and another model that included also adult survival. The reduction of sample would be even more pronounced in analyses with relative wing length (n = 18) and relative body mass (n = 25). We thus fitted two models (one for relative wing length and one for

Table 1. The three main hypotheses for the evolution of clutch size that we tested, together with associated statistical models

Hypothesis	No. of species	Response variable	Predictors
Lack and Ashmole (productivity)	224	Clutch size	**Max NDVI**, **NDVI seasonality**, nest type, body mass, aerial foraging, season length
Skutch (nest predation)	97	Clutch size	**DPR**, nest type, migration, body mass, aerial foraging, season length
Martin (development)	191	Clutch size	**Nestling period**, nest type, migration, body mass, aerial foraging, season length
Martin (adjusted for adult survival)	52	Clutch size	**Nestling period**, **adult survival**, nest type, migration, body mass, aerial foraging, season length
Martin (relative wing length)	18	Relative wing length	**Nestling period**, body mass
Martin (relative body mass)	25	Relative body mass	**Nestling period**, body mass
All three together	93	Clutch size	**Max NDVI**, **NDVI seasonality**, **DPR**, **nestling period**, nest type, migration, body mass, aerial foraging, season length

These models were tested in the phylogenetic context. Target variables of each hypothesis are in bold font, covariates in normal font.

relative body mass) with only the length of the nestling period and adult body mass as predictors (Table 1). Finally, we put all variables into one model and tested all hypotheses simultaneously (Table 1). To avoid further reduction of sample size we did not omit migrants from this joint analysis. Instead we accounted for them by adding interactions between max NDVI and migration and between NDVI seasonality and migration. However, because the interactions were not significant (Table S5), we excluded them from the final model.

All models were fitted using species-level phylogenetic analyses. We used the phylogenetic generalised least squares (PGLS) method using the 'gls' (package 'nlme' of R language; R Core Team 2015) function. We accounted for phylogenetic uncertainty by running PGLS models across 100 phylogenies obtained from birdtree.org (Jetz *et al.* 2012). We used both Hackett and Ericson constraint but the results were similar, so we present only the results obtained with Hackett constraint. As a correlation structure for PGLS models we used Pagel's lambda, which is based on the Brownian motion model and optimally adjusts the analysis for phylogenetic autocorrelation in model residuals (Freckleton *et al.* 2002). We obtained R^2 values using the fast likelihood code of Freckleton (2012). There were 100 outcomes of every PGLS analysis (one for every phylogenetic tree), so we present the averages of parameters in the main text, but provide confidence intervals for the estimates in the Supplement. In every analysis we always transformed data to approach the normal distribution. Since the number and identity of species differed between analyses (see above), the type of transformation differed between analyses as well. Transformation used in a particular analysis is always clearly stated in a given table. After transformation we scaled the data so that their mean was zero and variance was one, and set statistical significance at $\alpha = 0.05$. All models were fitted in R v3.0.2 (R Core Team 2015).

Results

We collected data on the clutch size of 313 Australian species of songbirds, which ranged from 1 to 6 eggs (mean 2.69 ± 0.92 SD, $n = 313$; Figure 1). The mean clutch size of avian assemblages in grid cells ranged from 2.6 to 3.0 eggs (grand mean 2.86 ± 0.08 SD, $n = 686$ grid cells; Figure 2). Clutch size was smallest in assemblages in south-western Australia and north Queensland and largest in eastern and south-eastern Australia and in Tasmania (Figure 2). Interestingly, large clutch sizes in Tasmania are driven by introduced species, not by Tasmanian endemics (Figure S1). When testing the effect of geography statistically, clutch size significantly increased with increasing latitude from the equator towards the south ($\mathrm{SAR_{err}}$: Est = 0.54, SE = 0.23, $z = 2.39$, $p = 0.02$), but not with longitude ($\mathrm{SAR_{err}}$: Est = −0.08, SE = 0.29, $z = -0.26$, $p = 0.80$) and did not change with their interaction ($\mathrm{SAR_{err}}$: Est = 0.28, SE = 0.20, $z = 1.41$, $p = 0.16$). The effect of latitude remained significant even when Tasmania was excluded from the analysis ($\mathrm{SAR_{err}}$: Est = 0.68, SE = 0.25, $z = 2.65$, $p = 0.01$), confirming that the latitudinal trend was not driven by introduced species (with large clutches) being relatively important in assemblages on the species-depauperate island of Tasmania.

In phylogeny-based analyses conducted across species, clutch size was not correlated with either max annual NDVI or NDVI seasonality (Lack and Ashmole's hypotheses; Figure 3; Table 2). Similarly, neither daily nest predation rate (DPR; Skutch's hypothesis) nor nestling period length predicted clutch size significantly (Martin's hypothesis; Figure 3; Table 2). However, nestling period became statistically significant when DPR and both NDVI measures were accounted for in the most complete model testing all three main hypotheses (Figure 3; Table 2). Clutch size was then increasing with increasing length of the nest-

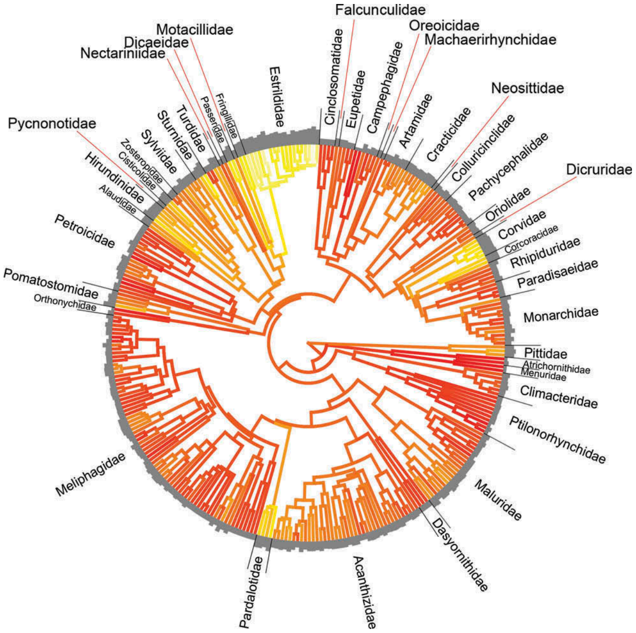

Figure 1. Clutch size in Australian songbirds depicted on a phylogenetic tree. Clutch size (number of eggs in a clutch) ranges from 1 to 6 eggs (columns) and is strongly linked to phylogeny (phylogenetic signal λ ~ 0.95; see Table 2). Dark shades represent small clutch size and light shades represent large clutch size, respectively. The depicted phylogeny is a Bayesian maximum clade credibility tree of 313 species based on 100 phylogenies, which we obtained from birdtree.org (Jetz et al. 2012).

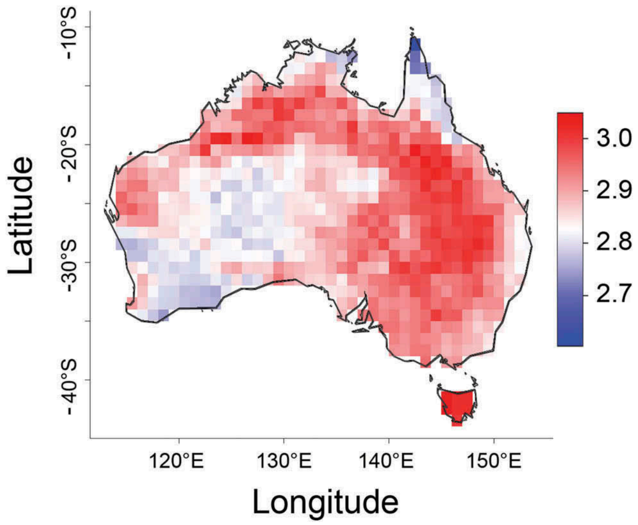

Figure 2. Geographic variation of clutch size in Australian songbirds. Mean clutch size (number of eggs in a clutch) of songbirds (n = 313) in Australia and Tasmania for assemblages within 1 × 1° grid cells (n = 686).

ling period. We did not include adult survival, relative wing length and relative body mass during fledging in our models, because their inclusion would lead to a substantial reduction in sample size. However, to evaluate Martin's (2014) finding that the effect of the nestling period was significant when statistically accounting for adult survival, we included adult survival into the model testing Martin's (2014) hypothesis. In this model, the effect of the nestling period remained statistically significant (Table S6). Moreover, we also tested whether relative body measurements at fledging correlated with the length of the nestling period, as assumed by Martin (2014). This relationship was significant only for relative body mass, where relative body mass increased with increasing length of the nestling period (Table S9), but not for relative wing length (Table S10).

Discussion

Clutch size in birds generally increases with latitude, from the tropics to temperate and arctic areas (Jetz *et al.* 2008). However, while this increase is strong in the Northern Hemisphere, it is generally weaker in the Southern Hemisphere (Yom-Tov *et al.* 1994; Jetz *et al.* 2008). This is partly caused by the absence of land in higher latitudes in the Southern Hemisphere and consequently lack of data. Although clutch size varied substantially across species (1–6 eggs; Figure 1), it did not vary as much spatially across the assemblages of species (assemblage averages ranged from 2.6 to 3.0 eggs; Figure 2). Despite this, we detected a significant increase in clutch size with latitude, which agrees with previous findings.

Productivity

Lack (1947, 1948) and Ashmole (1963) suggested that resource availability and its seasonality could affect the evolution of clutch size in birds. We did not find any statistically significant effect of the maximum environmental productivity during the breeding season (NDVI) or its seasonality on clutch size. We thus do not confirm findings of previous studies showing that clutch size increases with increasing environmental seasonality (Cody 1966; Jetz *et al.* 2008; Hořák *et al.* 2015) and, by implication, seasonality of resource availability (Ricklefs 1980). We offer two potential explanations for these conflicting results.

First, Australia is a climatically extraordinary continent with most of the interior area arid, while many coastal areas are dominated by humid forests. Moreover, climatic seasonality is not as profound in Australia (Figures S2 and S3) as in the Northern Hemisphere (Greenwood and Wing 1995) and resource availability thus probably does not change so

Table 2. Results of phylogenetic generalised least squares models of clutch size in relation to productivity (Lack's and Ashmole's hypotheses), predation (nest predation hypothesis), length of the nestling period (Martin's hypothesis), and all three hypotheses tested together

Response: Sqrt Clutch size	Productivity (adj. $R^2 = -0.004$, $\lambda = 0.93$)			Nest predation (adj. $R^2 = 0.02$, $\lambda = 0.96$)			Development (adj. $R^2 = 0.05$, $\lambda = 0.95$)			All three together (adj. $R^2 = 0.06$, $\lambda = 0.97$)		
Predictors	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P	Estimate ± SE	F	P
Max NDVI	−0.01 ± 0.05	0.10	0.83	–	–	–	–	–	–	−0.07 ± 0.10	0.51	0.50
Sqrt NDVI seasonality	−0.06 ± 0.04	2.32	0.16	–	–	–	–	–	–	−0.01 ± 0.08	0.09	0.84
Sqrt DPR	–	–	–	−0.12 ± 0.07	2.88	0.10	–	–	–	−0.05 ± 0.07	0.51	0.50
Ln Nestling period	–	–	–	–	–	–	0.09 ± 0.08	1.31	0.28	0.32 ± 0.12	7.06	0.01
Migration (Sedentary)	–	–	–	0.02 ± 0.07	0.16	0.74	−0.07 ± 0.04	3.53	0.08	0.03 ± 0.08	0.19	0.71
Nest type (Open)	−0.07 ± 0.09	0.70	0.42	−0.14 ± 0.14	1.08	0.31	−0.08 ± 0.10	0.70	0.41	−0.01 ± 0.14	0.02	0.92
Ln Body mass	0.05 ± 0.08	0.44	0.55	−0.12 ± 0.12	0.93	0.36	0.06 ± 0.09	0.52	0.54	−0.28 ± 0.14	3.92	0.05
Aerial (Yes)	0.02 ± 0.04	0.51	0.50	0.12 ± 0.08	2.13	0.15	0.05 ± 0.04	1.43	0.28	0.09 ± 0.08	1.35	0.25
Season length	0.03 ± 0.04	0.54	0.51	−0.02 ± 0.07	0.17	0.75	0.02 ± 0.04	0.37	0.61	0.04 ± 0.07	0.40	0.55

Models were run on 100 phylogenies, and means of parameters and test statistics are presented. Levels of binary predictors for which the estimates are valid are listed in parentheses. Focal predictors of each hypothesis are in bold font. 'Sqrt' = square root transformed.

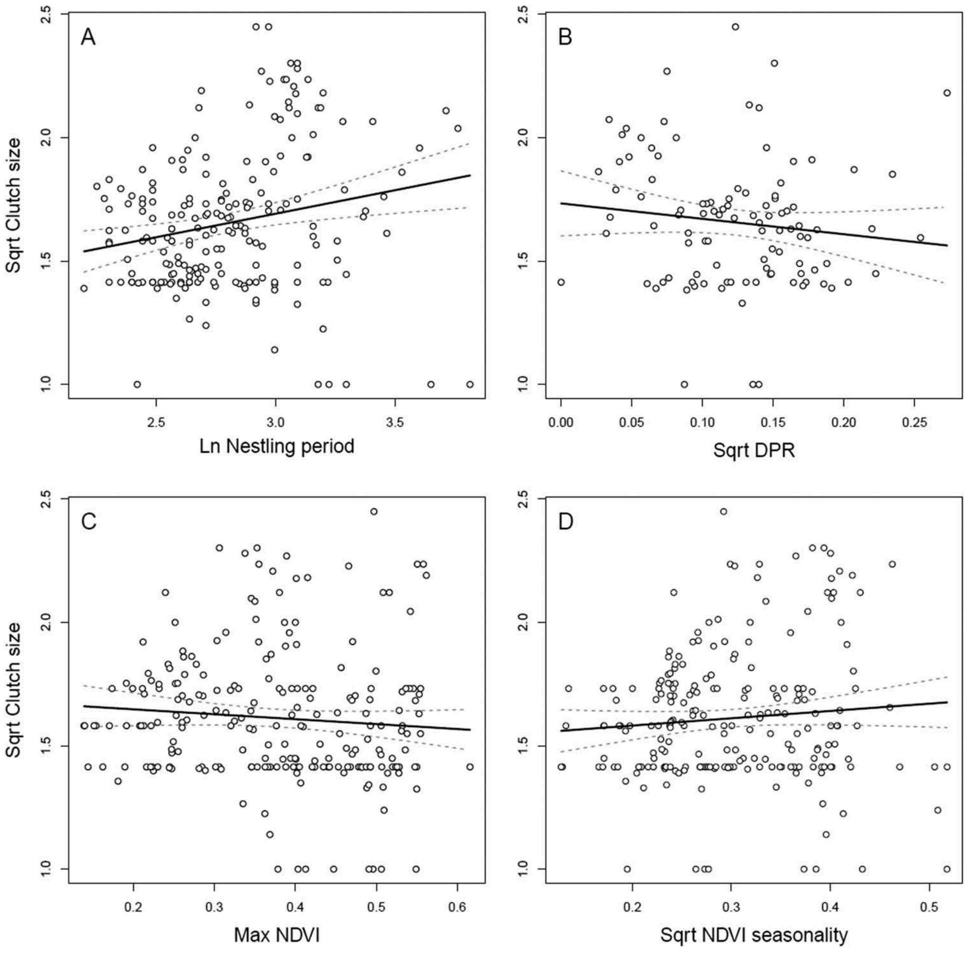

Figure 3. Relationships between clutch size (square root transformed) and focal predictors of the tested hypotheses: (A) nestling period (n = 208; ln transformed), (B) DPR (n = 102; square root transformed), (C) maximum breeding season NDVI (n = 224), and (D) NDVI seasonality (n = 224; square root transformed). Only the relationship of clutch size to nestling period was statistically significant in the phylogenetic analyses (A). Solid lines represent linear regression lines; dashed lines are 95% confidence intervals.

markedly throughout the year. However, the Australian climate is also driven by El Niño-Southern Oscillation (ENSO) events (Power *et al.* 1999), which induce strong and unpredictable changes in temperature and precipitation. These three climatic peculiarities can have significant consequences for life-history evolution. Owing to low seasonality, bird numbers might not be so tightly regulated by conditions during the lean season, which is a prerequisite for the mechanism suggested by Ashmole (1963). Further, bet-hedging theory suggests that in unpredictable environments (e.g. highly arid ones or those driven by ENSO events; Power *et al.* 1999), the probability of breeding success is reduced and parents are thus selected to invest less energy into single clutches and lay fewer eggs (Murphy 1968; Slatkin 1974). For instance, the clutch size of southern African birds was found to be smaller in arid areas when controlled for seasonality, thereby supporting the bet-hedging strategy (Lepage and Lloyd 2009). Moreover, productivity is tied closely to water availability, which plays an important role in avian reproduction as well (Coe and Rotenberry 2003), and thus the extensive aridity of Australia might have constrained the diversification of avian life histories.

Second, many Australian bird species reproduce during the months that have comparably low plant productivity (Figure S2 B), which might be caused by the occurrence of a marked wet season in the tropical areas, during which NDVI values increase, but might not represent ideal conditions for breeding (Foster 1974). Moreover, NDVI values can differ across habitats even within a climatic zone (Burbidge and Fuller 2007) and the NDVI probably does not fully account for seasonal changes in various types of food. Species with different diet specialisation, for instance, do not breed simultaneously, for example Australian insectivores breed earlier than seedeaters (Ford 1989), and this might not be well captured by the NDVI. Furthermore, even though food availability is seasonal in Australia, the seasonality is lower and without sharp peaks compared to the Northern Hemisphere, which might lead to overall smaller clutches of Australian songbirds compared to Northern Hemisphere songbirds (Woinarski 1985; Ford 1989). In addition, the timing of breeding in the tropics might be affected not only by food availability but also by annual variation in nest predation or the timing of energetically demanding moult (Stutchbury and Morton 2001). Taken together, the NDVI can be a good predictor of the best time for breeding in temperate areas but not in the tropics and (southern) subtropics, which might hamper its predictive value for clutch size in these regions.

Nest predation

The nest predation hypothesis suggests that clutch size decreases with increasing nest predation rate (Skutch 1949; Slagsvold 1982). Although several studies from other continents confirmed a negative correlation between clutch size and nest predation rates (Europe: Slagsvold 1982; North and South America: Martin *et al.* 2000; Ghalambor and Martin 2001), we did not find similar evidence in Australia. One might argue that historically existing correlation between clutch size and nest predation could be obscured by increases and decreases of populations of different species of predators in Australia compared to pre-European settlement (Ford *et al.* 2001; Remeš *et al.* 2012a), including the introduction of effective exotic predators (Salo *et al.* 2007; Dickman 2009; Remeš *et al.* 2012b). However, we doubt this is a sufficient explanation for the pattern in clutch size we found, because our data include records on clutch sizes and predation rates over large spatial and temporal scales and therefore should be robust to recent biotic changes. Rather, Australian songbirds might be geared towards small clutches and spreading the risk by other factors (e.g. overall aridity and low productivity), making the effect of nest predation difficult to detect. Notice in this respect that the effect of nest predation was not negligible, occurred in the expected direction, and was almost statistically significant (Table 2; Figure 3).

Nestling development

Martin (2014) predicted that clutch size would increase with the length of nestling period. We confirmed this prediction, but only when we controlled for adult survival (Table S6) or climate and nest predation (Table 2). Adult survival together with the length of the breeding season set the total parental reproductive effort (Martin 2014). Accordingly, nestling period became significant only when the analysis was adjusted for total reproductive effort. One is tempted to suggest that this makes sense, as Martin (2014) proposes that the per-offspring investment is set by the nestling period (via the nestling development gradient). The effect of nestling period would then become apparent when statistically accounting for factors affecting total reproductive effort per breeding attempt. However, caution is needed here, because the significance of the length of nestling period might have been caused simply by the sampling effect. The analyses re-run with the length of the nestling period as the only predictor (for the subset of 52 and 93 species; Martin's hypothesis adjusted for adult survival and the joint analysis; Tables S7 and S8) revealed that this was perhaps the case, as nestling period was significant even without the presence of adult survival, DPR, or NDVI among predictors. On the other hand this result shows that nestling period itself as well as total reproductive effort (nestling period together with adult survival) are significant predictors of clutch size at least for these subsets of species. Thus, only further detailed studies can show whether sampling effect, or real biological effects are more important.

Martin's (2014, 2015) hypothesis further assumes that species with long nestling periods enjoy benefits of well-developed offspring at fledging leading to high post-fledging survival. We tested the relationship between nestling development and the length of the nestling period and confirmed that relative body mass at fledging increased with increasing nestling period length in accordance with Martin's (2015) findings, but the effect of nestling period length on relative wing length at fledging was not significant. However, this latter analysis was probably hampered by the very limited sample size (18 species). Furthermore, Remeš and Matysioková (2016) recently confirmed that species with long nestling periods and high relative body mass at fledging enjoyed high post-fledging survival. Thus, these studies (Remeš and Matysioková 2016; this study) confirm two important components of the new hypothesis for clutch size evolution in songbirds (Martin 2014, 2015).

Other factors that may influence clutch size

Besides effects that we investigated, quite a large difference in clutch size seems to be present between old endemic families and those that underwent most of their evolution and diversification elsewhere and (re-)colonised Australia later (Moyle *et al.* 2016), and which, in general, have larger clutches (Corvidae and most of the families between Alaudidae and Estrildidae in Figure 1). Old endemics and old invaders to Australia have smaller clutches than the 'new' arrivals (Woinarski 1985; Yom-Tov 1987). Besides historical effects, cooperative breeding or diet might also covary with clutch size. Based on simple graphical inspection of data, it appears that families with mostly cooperatively breeding species have somewhat larger clutches (Artamidae, Corcoracidae, Cracticidae, Maluridae, Pomatostomidae; Figure 1). Helpers might help raise larger clutches as they possibly provide extra food to offspring and help with nest defence. However, Poiani and Jermiin (1994) found the opposite effect in Australian passerines, where clutch size in cooperative breeders was smaller than that of non-cooperatively breeding species. This shows that the effect of cooperative breeding on clutch size will be complex (if any), because additional adult help might instead lift the load from the other provisioners, which does not affect chicks but increases adult survival. Moreover, the occurrence and degree of cooperative breeding might differ greatly between individual family groups within species and also might be facilitated by low environmental seasonality (Ford *et al.* 1988), and thus its relation to clutch size might be confounded by environmental factors. These hypotheses remain to be tested rigorously.

In this study, clutch size was positively associated with latitude and out of the three hypotheses we tested, guarded support was received by Martin's (2014) new hypothesis stressing the role of the nestling development gradient. Since this developmental gradient is often driven by nest predation (Remeš and Martin 2002; Cheng and Martin 2012; Remeš and Matysioková 2016), nest predation seems to be indirectly driving clutch size evolution, at least in some Australian songbirds. However, our test of Martin's hypothesis was indirect and on a small sample of species. We thus critically need more direct tests involving nestling developmental traits, especially wing length and body mass at fledging (Martin 2015).

In sum, we show that the evolution of clutch size in Australian songbirds might be under the influence of different factors compared to other continents. Australian birds, with their wide range of life histories, including a high incidence of cooperative breeding, and occupying a large array of habitats, provide great opportunity to shed new light on the evolution of clutch size and other life-history traits in birds.

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Supplemental Material

The evolution of clutch size in Australian songbirds in relation to climate, predation, and nestling development

Authors

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Supplement S1. The list of literature sources used to obtain additional data on daily predation rate (DPR).

Supplement S2. The list of literature sources used to obtain data on adult survival.

Supplement S3. The list of literature sources used to obtain data on relative wing length and relative body mass during fledging.

Figure S1. Differences in geographic variation of clutch size with emphasis on Tasmanian and introduced species.

Figure S2. Variation in productivity in species-level data.

Figure S3. Geographic variation in productivity in Australia and Tasmania.

Table S1. Full results of PGLS model of clutch size in relation to productivity (Lack's and Ashmole's hypotheses).

Table S2. Full results of PGLS model of clutch size in relation to predation (Skutch's hypothesis).

Table S3. Full results of PGLS model of clutch size in relation to length of the nestling period (Martin's hypothesis).

Table S4. Full results of PGLS model of clutch size in relation to productivity, predation, and length of the nestling period (all three hypotheses tested together).

Table S5. Full results of PGLS model of clutch size in relation to productivity, predation, and length of the nestling period (all three hypotheses tested together) fitted with an interaction between maximum NDVI and migration and between NDVI seasonality and migration.

Table S6. Full results of PGLS model of clutch size in relation to length of the nestling period (Martin's hypothesis) adjusted for adult survival.

Table S7. Full results of PGLS model of clutch size in relation to length of the nestling period (Martin’s hypothesis) fitted for 93 species (exact species used in Table S4).

Table S8. Full results of PGLS model of clutch size in relation to length of the nestling period (Martin’s hypothesis) fitted for 52 species (exact species used in Table S6).

Table S9. Full results of PGLS model of relative body mass in relation to length of the nestling period.

Table S10. Full results of PGLS model of relative wing length in relation to length of the nestling period.

Supplement S1.

The list of literature sources used to obtain additional data on daily predation rate (DPR).

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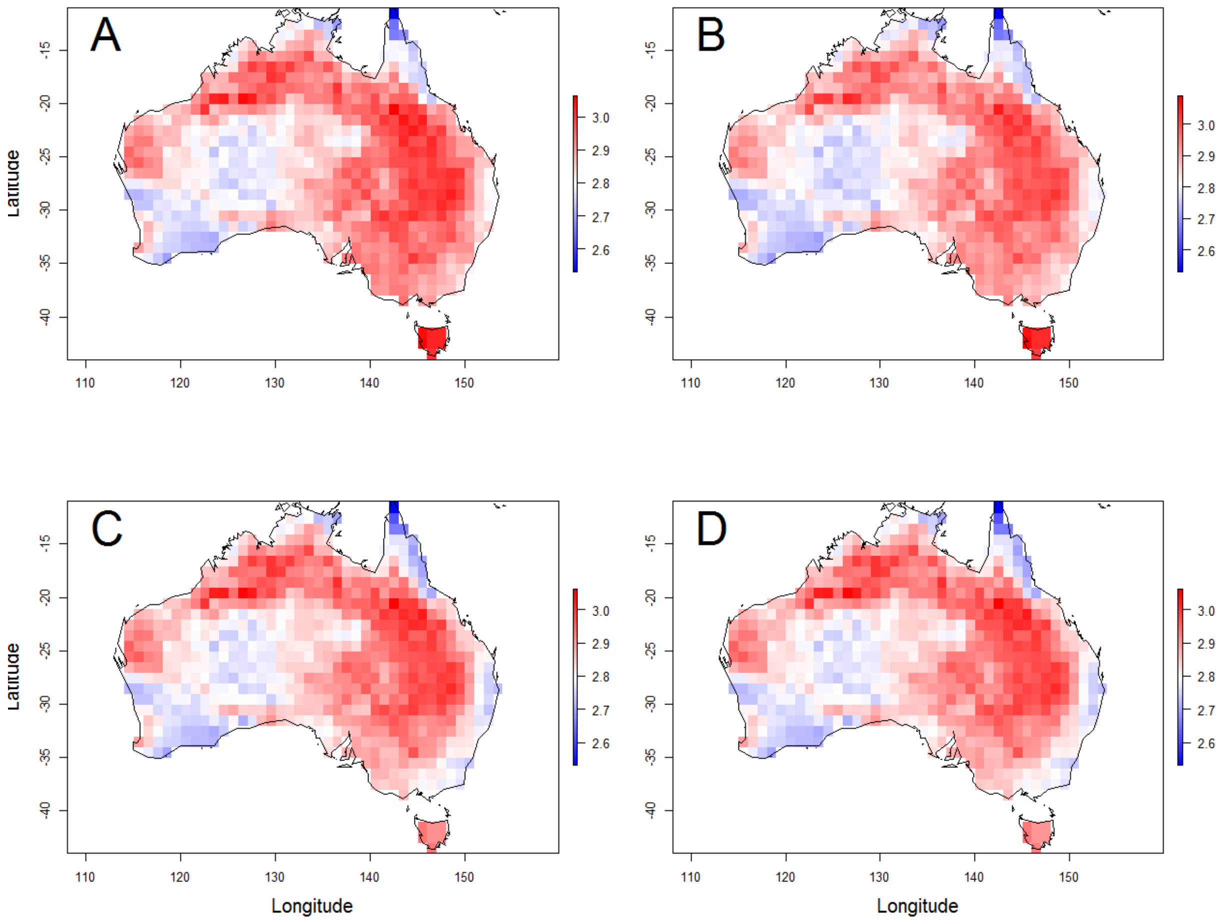

Figure S1.

Differences in geographic variation of clutch size with emphasis on Tasmanian and introduced species: (A) clutch size of all Australian songbirds (*n* = 313), (B) clutch size without Tasmanian endemics (*n* = 303), (C) clutch size without recently introduced species (*n* = 302), and (D) clutch size without both Tasmanian endemics and introduced species (*n* = 292).

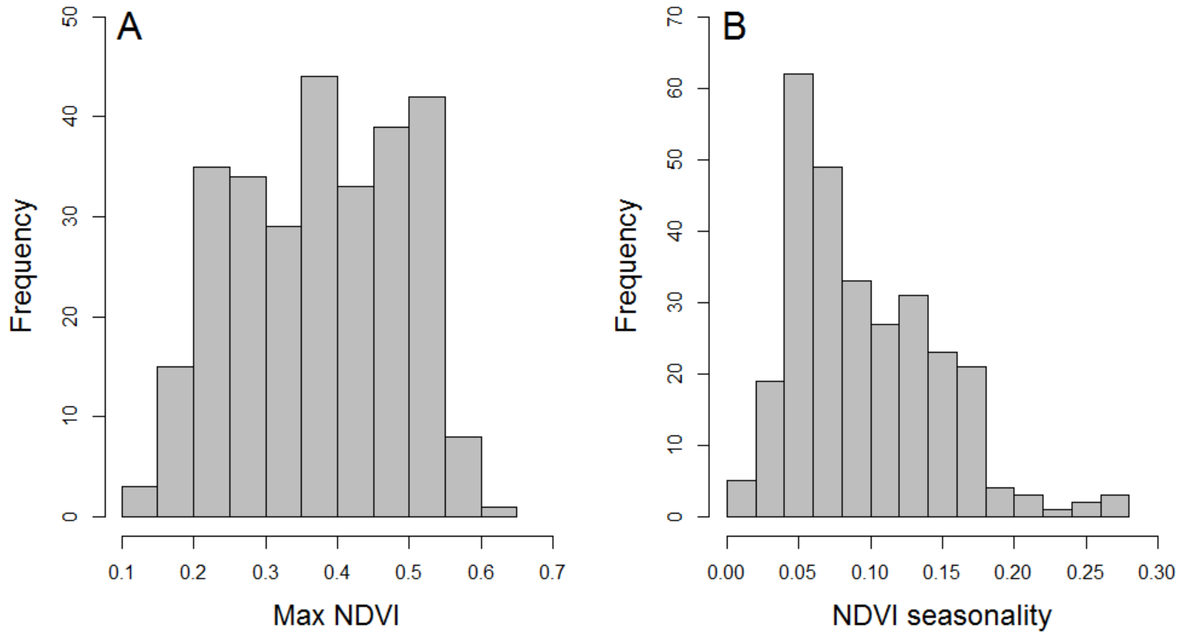

Figure S2.

Variation in productivity in species-level data: (A) inter-species variation in Maximum NDVI, (B) inter-species variation in NDVI seasonality.

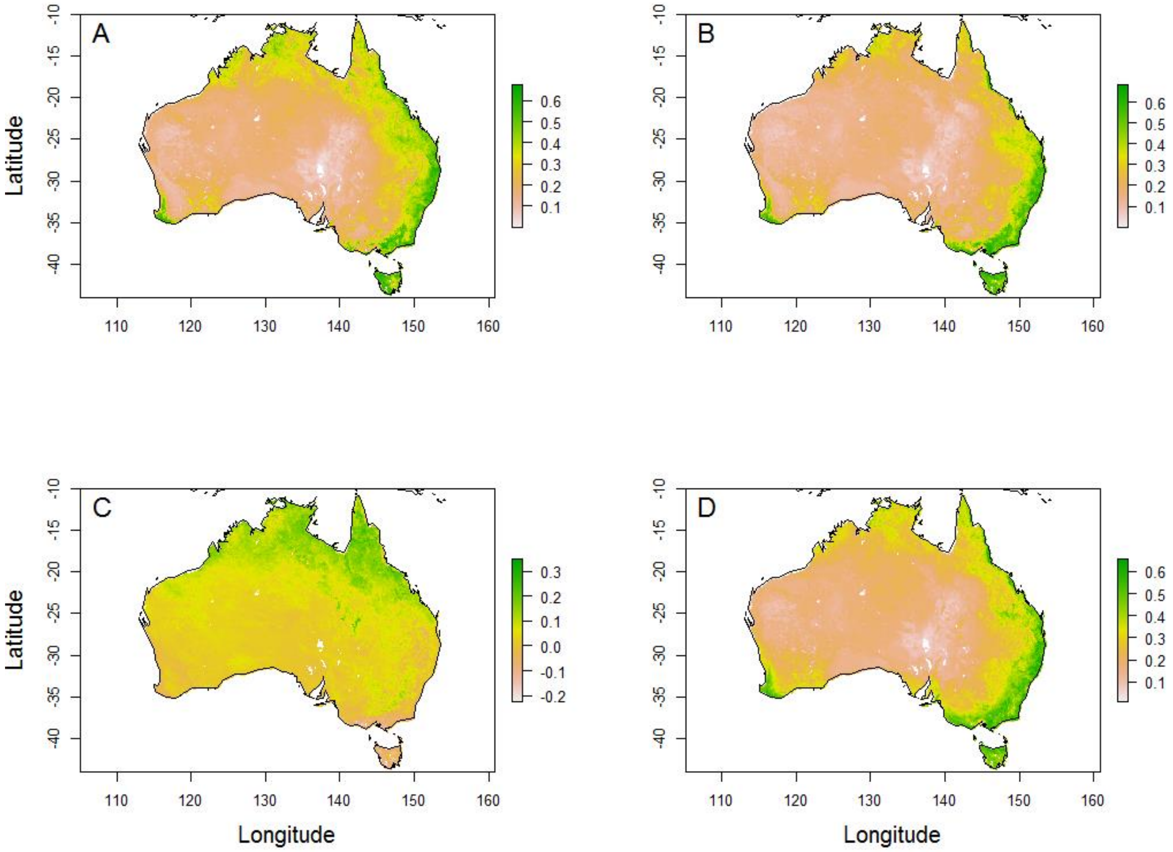

Figure S3.

Geographic variation in productivity in Australia (including Tasmania): (A) month with the highest mean NDVI (April), (B) month with the lowest mean NDVI (December), (C) difference in NDVI values between April and December, (D) mean NDVI from all twelve months. The maps were created from raw NDVI data and serve only for illustrative purposes. In the analyses were used more appropriate NDVI values computed for each species based on its range and length of the breeding season.

Table S1.

Full results of PGLS model of clutch size in relation to productivity (Lack's and Ashmole's hypotheses). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictors of this hypothesis are in bold.

Response: Sqrt Clutch size (*n* = 224)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Max NDVI	-0.001	-0.029	0.029	0.049	0.046	0.051	0.098	0.000	0.445	0.827	0.506	0.989
Sqrt NDVI seasonality	-0.064	-0.088	-0.043	0.043	0.040	0.046	2.325	1.018	4.205	0.157	0.042	0.314
Nest type (Open)	-0.074	-0.101	-0.045	0.091	0.088	0.094	0.697	0.254	1.257	0.422	0.263	0.615
Ln Body mass	0.049	0.013	0.084	0.079	0.077	0.081	0.444	0.027	1.172	0.547	0.280	0.871
Aerial (Yes)	0.025	0.009	0.034	0.036	0.029	0.040	0.509	0.083	0.909	0.497	0.342	0.774
Season length	0.027	0.004	0.044	0.040	0.037	0.042	0.539	0.015	1.318	0.505	0.252	0.902
Adj. R^2	-0.004	-0.012	0.005									
λ	0.928	0.898	0.958									

Table S2.

Full results of PGLS model of clutch size in relation to predation (age-specific mortality and Skutch's hypotheses). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Sqrt Clutch size (*n* = 97)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Sqrt DPR	-0.123	-0.158	-0.090	0.073	0.069	0.076	2.876	1.572	4.401	0.104	0.039	0.213
Nest type (Open)	-0.144	-0.180	-0.115	0.140	0.134	0.145	1.080	0.684	1.661	0.308	0.201	0.410
Migration (Sedentary)	0.023	-0.006	0.051	0.073	0.067	0.079	0.157	0.001	0.568	0.744	0.453	0.973
Ln Body mass	-0.118	-0.163	-0.071	0.125	0.121	0.129	0.928	0.338	1.719	0.355	0.193	0.563
Aerial (Yes)	0.117	0.099	0.140	0.080	0.067	0.090	2.132	1.625	2.823	0.152	0.097	0.206
Season length	-0.020	-0.050	0.006	0.066	0.053	0.072	0.173	0.001	0.598	0.747	0.441	0.980
Adj. R^2	0.020	0.002	0.046									
λ	0.964	0.926	1.000									

Table S3.

Full results of PGLS model of clutch size in relation to length of the nestling period (Martin's hypothesis). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Sqrt Clutch size (*n* = 193)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Ln Nestling period	0.087	0.049	0.117	0.078	0.071	0.081	1.307	0.397	2.297	0.278	0.131	0.529
Nest type (Open)	-0.082	-0.105	-0.059	0.099	0.096	0.105	0.699	0.366	1.164	0.415	0.282	0.546
Migration (Sedentary)	-0.071	-0.089	-0.054	0.039	0.031	0.042	3.527	1.886	6.851	0.075	0.014	0.172
Ln Body mass	0.059	0.016	0.120	0.092	0.088	0.095	0.517	0.031	1.742	0.536	0.190	0.862
Aerial (Yes)	0.050	0.016	0.078	0.044	0.038	0.050	1.431	0.207	2.939	0.281	0.088	0.650
Season length	0.019	-0.001	0.039	0.036	0.031	0.039	0.366	0.001	1.477	0.613	0.229	0.971
Adj. R^2	0.045	0.020	0.057									
λ	0.945	0.915	1.000									

Table S4.

Full results of PGLS model of clutch size in relation to productivity, predation, and length of the nestling period (all three hypotheses tested together). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictors of each hypothesis are in bold.

Response: Sqrt Clutch size (*n* = 93)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Sqrt DPR	-0.051	-0.074	-0.027	0.074	0.069	0.078	0.511	0.134	1.013	0.498	0.317	0.716
Ln Nestling period	0.323	0.286	0.351	0.122	0.115	0.127	7.056	5.761	8.062	0.010	0.006	0.019
Max NDVI	-0.067	-0.097	-0.024	0.096	0.081	0.103	0.506	0.076	0.958	0.499	0.331	0.789
Sqrt NDVI seasonality	0.003	-0.050	0.035	0.079	0.055	0.090	0.088	0.000	0.672	0.844	0.451	0.996
Nest type (Open)	-0.007	-0.041	0.021	0.144	0.138	0.149	0.016	0.000	0.083	0.919	0.776	0.995
Migration (Sedentary)	0.029	0.000	0.054	0.077	0.068	0.084	0.190	0.000	0.548	0.709	0.461	0.984
Ln Body mass	-0.280	-0.314	-0.244	0.142	0.138	0.145	3.922	2.961	4.823	0.053	0.031	0.089
Aerial (Yes)	0.094	0.079	0.114	0.081	0.067	0.089	1.352	1.038	1.777	0.252	0.186	0.311
Season length	0.042	0.017	0.061	0.068	0.058	0.073	0.401	0.074	0.796	0.547	0.375	0.786
Adj. R^2	0.057	0.040	0.076									
λ	0.973	0.928	1.000									

Table S5.

Full results of PGLS model of clutch size in relation to productivity, predation, and length of the nestling period (all three hypotheses tested together) fitted with an interaction between maximum NDVI and migration and between NDVI seasonality and migration. The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictors of this hypothesis are in bold.

Response: Sqrt Clutch size (*n* = 93)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Sqrt DPR	-0.065	-0.103	-0.040	0.074	0.069	0.079	0.811	0.305	1.901	0.394	0.172	0.583
Ln Nestling period	0.325	0.281	0.368	0.121	0.114	0.127	7.268	5.700	9.092	0.009	0.003	0.019
Max NDVI	-0.062	-0.112	-0.022	0.096	0.082	0.103	0.371	0.037	0.835	0.532	0.254	0.815
Sqrt NDVI seasonality	0.034	-0.017	0.079	0.082	0.056	0.095	0.087	0.000	0.806	0.675	0.384	0.944
Nest type (Open)	-0.008	-0.044	0.023	0.144	0.136	0.149	0.018	0.000	0.099	0.912	0.754	0.995
Migration (Sedentary)	-0.041	-0.164	0.012	0.086	0.076	0.100	0.222	0.000	0.645	0.660	0.084	0.987
Ln Body mass	-0.309	-0.358	-0.263	0.144	0.138	0.149	4.654	3.375	6.251	0.037	0.015	0.070
Aerial (Yes)	0.070	-0.001	0.105	0.083	0.074	0.091	0.844	0.019	1.662	0.416	0.201	0.892
Season length	0.032	-0.014	0.061	0.069	0.058	0.075	0.287	0.002	0.826	0.640	0.366	0.961
Max NDVI:Migration	0.075	-0.579	0.966	0.308	0.214	0.422	1.630	0.002	7.318	0.402	0.009	0.963
NDVI seasonality:Migration	-0.047	-0.706	0.573	0.245	0.145	0.336	2.346	0.188	7.330	0.227	0.008	0.667
Adj. R^2	0.072	0.032	0.132									
λ	0.984	0.943	1.000									

Table S6.

Full results of the PGLS model of clutch size in relation to length of the nestling period (Martin's hypothesis) adjusted for adult survival). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Ln Clutch size (*n* = 52)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Ln Nestling period	0.661	0.586	0.721	0.188	0.156	0.201	12.451	9.770	16.107	0.001	< 0.001	0.003
Adult survival	-0.075	-0.109	-0.037	0.090	0.077	0.098	0.723	0.183	1.305	0.421	0.260	0.671
Nest type (Open)	-0.310	-0.354	-0.266	0.170	0.158	0.183	3.341	2.528	4.161	0.078	0.047	0.119
Migration (Sedentary)	0.031	-0.012	0.073	0.092	0.078	0.102	0.184	0.000	0.736	0.724	0.401	0.984
Ln Body mass	-0.059	-0.124	0.017	0.187	0.169	0.195	0.135	0.003	0.442	0.743	0.510	0.959
Aerial (Yes)	-0.145	-0.254	-0.068	0.116	0.098	0.128	1.859	0.298	6.521	0.258	0.036	0.589
Season length	-0.026	-0.043	-0.008	0.071	0.053	0.083	0.157	0.012	0.399	0.713	0.531	0.915
Adj. R^2	0.265	0.224	0.475									
λ	0.953	0.890	1.000									

Table S7.

Full results of PGLS model of clutch size in relation to length of the nestling period (Martin's hypothesis) fitted for 93 species (exact species as used in Table S4). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Sqrt Clutch size (*n* = 93)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Ln Nestling period	0.327	0.289	0.357	0.118	0.111	0.123	7.686	5.946	8.949	0.007	0.004	0.017
Nest type (Open)	-0.004	-0.044	0.025	0.143	0.137	0.147	0.016	0.000	0.093	0.919	0.761	0.996
Migration (Sedentary)	-0.001	-0.039	0.036	0.069	0.062	0.075	0.089	0.000	0.329	0.817	0.568	0.987
Ln Body mass	-0.280	-0.316	-0.247	0.139	0.135	0.142	4.084	3.191	5.046	0.048	0.027	0.078
Aerial (Yes)	0.102	0.084	0.124	0.079	0.069	0.087	1.679	1.196	2.323	0.203	0.131	0.277
Season length	0.044	0.014	0.069	0.066	0.057	0.071	0.467	0.061	1.047	0.521	0.309	0.806
Adj. R^2	0.071	0.051	0.089									
λ	0.974	0.936	1.000									

Table S8.

Full results of PGLS model of clutch size in relation to length of the nestling period (Martin's hypothesis) fitted for 52 species (exact species as used in Table S6). The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Ln Clutch size (*n* = 52)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Ln Nestling period	0.649	0.583	0.699	0.187	0.154	0.200	12.170	9.751	16.132	0.001	< 0.001	0.003
Nest type (Open)	-0.308	-0.354	-0.261	0.170	0.157	0.182	3.327	2.452	4.213	0.078	0.046	0.124
Migration (Sedentary)	0.014	-0.029	0.061	0.089	0.076	0.099	0.099	0.000	0.522	0.806	0.474	0.993
Ln Body mass	-0.078	-0.143	0.009	0.185	0.166	0.194	0.218	0.009	0.580	0.670	0.451	0.925
Aerial (Yes)	-0.150	-0.263	-0.064	0.116	0.098	0.128	2.000	0.311	7.260	0.244	0.024	0.584
Season length	-0.027	-0.043	-0.010	0.071	0.052	0.083	0.167	0.018	0.417	0.703	0.523	0.895
Adj. R^2	0.270	0.224	0.477									
λ	0.953	0.884	1.000									

Table S9.

Full results of PGLS models of relative body mass in relation to length of the nestling period. The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Relative body mass^2 (*n* = 25)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Ln Nestling period	0.832	0.804	0.850	0.167	0.164	0.170	24.884	22.738	25.845	< 0.001	< 0.001	< 0.001
Ln Body mass	-1.079	-1.127	-1.036	0.174	0.167	0.182	38.278	36.671	39.361	< 0.001	< 0.001	< 0.001
Adj. R^2	0.613	0.600	0.622									
λ	0.262	0.000	0.573									

Table S10.

Full results of PGLS models of relative wing length in relation to length of the nestling period. The model was run on 100 phylogenies. For parameter estimates from the 100 models, we provide the mean, SE, and lower (LCI) and upper (UCI) 95% confidence limits. Focal predictor of this hypothesis is in bold.

Response: Relative wing length (*n* = 18)

Predictors	Estimate			SE			F			P		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Nestling period	0.042	-0.034	0.114	0.227	0.221	0.235	0.060	0.001	0.253	0.837	0.622	0.982
Ln Body mass	-0.583	-0.668	-0.501	0.255	0.245	0.264	5.239	3.886	6.646	0.039	0.021	0.067
Adj. R^2	0.198	0.157	0.237									
λ	0.968	0.745	1.000									

Chapter II

Smaller beaks for colder winters: Thermoregulation drives beak size evolution in Australasian songbirds

Malurus cyaneus

Friedman N.R., ***Harmáčková L.****, Economo E.P. & Remeš V.*
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Superb Fairywrens (*Malurus cyaneus*) belong to the family Maluridae, one of the three Australasian families of songbirds we used for studying the evolution of beak size. Fairywrens have typically quite short beaks with only slight curvature.

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Smaller beaks for colder winters: Thermoregulation drives beak size evolution in Australasian songbirds

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Birds' beaks play a key role in foraging, and most research on their size and shape has focused on this function. Recent findings suggest that beaks may also be important for thermoregulation, and this may drive morphological evolution as predicted by Allen's rule. However, the role of thermoregulation in the evolution of beak size across species remains largely unexplored. In particular, it remains unclear whether the need for retaining heat in the winter or dissipating heat in the summer plays the greater role in selection for beak size. Comparative studies are needed to evaluate the relative importance of these functions in beak size evolution. We addressed this question in a clade of birds exhibiting wide variation in their climatic niche: the Australasian honeyeaters and allies (Meliphagoidea). Across 158 species, we compared species' climatic conditions extracted from their ranges to beak size measurements in a combined spatial-phylogenetic framework. We found that winter minimum temperature was positively correlated with beak size, while summer maximum temperature was not. This suggests that while diet and foraging behavior may drive evolutionary changes in beak shape, changes in beak size can also be explained by the beak's role in thermoregulation, and winter heat retention in particular.

KEY WORDS: Allen's rule, beak size, Meliphagoidea, thermoregulation.

Many phenotypic traits are multifunctional, and thus understanding their evolution in terms of adaptation and constraint can be a challenge (Gould and Lewontin 1979; Wainwright 2007). Even if a trait is critically important for maintaining one function, trait divergence among species may be driven by selection on a second, sometimes less obvious, function (Cox et al. 2003; Ellers and Boggs 2003). Bird beaks exhibit a stunning diversity in size and shape (Cooney et al. 2017), and no doubt this diversity reflects the functional importance of beaks in a variety of selective contexts (Willson et al. 1975; Gill 2007). Bird beaks are obviously critical for foraging, and the relationship among beak size, shape, and diet in Darwin's finches (Grant et al. 1976; Grant and Grant 2002) is now the cornerstone of many introductory lectures on natural selection. However, beaks have also been shown to function as thermoregulatory structures. They can function akin to radiators as they shed heat through convection without losing water (Tattersall et al. 2009; Greenberg et al. 2012a), an effect that can be augmented by vasodilation or reduced by vasoconstriction (Hagan and Heath 1980). Thus, a large beak may be adaptive in hot environments, but present a problem for heat retention in cold environments (Danner and Greenberg 2015). Given these different functions—heat radiation, heat retention, and foraging—it is unclear which factors are most responsible for the evolution of bird beak size during diversification.

Thermal constraints are known to lead to large-scale variation in morphology. In particular, Allen's rule (Allen 1877) is a classic ecogeographic pattern for endothermic organisms that describes a gradient in extremity length varying with climate. It predicts that selection will lead to individuals in higher elevations and latitudes exhibiting relatively smaller extremities as a means of thermoregulation (Lomolino et al. 2006). Researchers have long documented Allen's rule as a geographic gradient in limb length among individuals of many bird and mammal species (Yom-Tov and Nix 1986; Bried et al. 1997; VanderWerf 2012). Although Allen's Rule was earlier thought to be limited to local adaptation within species (Mayr 1956), several studies have since established this pattern as one that applies also across species (Cartar and Morrison 2005; Nudds and Oswald 2007). However, these focused on limb length as the object of selection for thermoregulation.

Examinations of Allen's rule in beak length have been rare until recently, as Greenberg and colleagues have established the repeated adaptation of North American sparrow species' beak size to salt marsh habitats (Greenberg and Droege 1990; Grenier and Greenberg 2005). Both among and within salt marsh sparrow populations, summer temperatures are good predictors of beak surface area (Greenberg and Danner 2012; Greenberg et al. 2012b; Greenberg and Danner 2013). However, it is apparent that winter temperatures can also influence beak size, and a framework was presented by Greenberg et al. (2012a; Danner and Greenberg 2015) to test which season is the critical period for thermoregulation. As with limb length, Allen's rule in beak size has recently been extended as a pattern observed across species (Symonds and Tattersall 2010). However, the key question remains: If thermal effects are important, is winter or summer the critical season driving interspecific variation in beak size?

Australia provides a testing ground uniquely suited to disentangle the critical season hypothesis, as its central arid and semiarid zones exhibit challenging high temperatures in summer and relatively low temperatures in winter. Thus, if selection acts primarily on individuals unable to shed heat during summer, we should expect to see larger beak sizes among species exposed to hot summers. However, if selection acts primarily on individuals unable to conserve heat during winter, we should expect to see smaller beak sizes among species exposed to cold winters. To test these hypotheses, we focused on a diverse clade of Australasian songbirds, the honeyeaters and allies (Meliphagoidea). These species are ideal for such analyses, as they are widespread across Australasia, but largely confined to it (Marki et al. 2017). Thus, their in situ diversification across the different climate regimes of Australasia (e.g., Miller et al. 2013) provides a natural experiment of the effects of these regimes on beak morphology.

Methods

MEASUREMENTS AND METRICS

We used measurements taken from vouchered museum specimens of Meliphagoidea at the Australian National Wildlife Collection (ANWC). We measured beak length (culmen base to tip), beak depth (at distal end of nares), and beak width (at distal end of nares). NRF performed all measurements, sampling an average of five adult male specimens in breeding condition per recognized species (estimated from skull pneumatization and gonad size), with attempts to sample at least two individuals per subspecies group (Schodde and Mason 1999). We included those species for which we were able to obtain data on beak morphology, spatial distribution, and position on a multilocus phylogeny. This led to a taxonomic sampling of 94 species in Meliphagidae, 40 species in Acanthizidae, and 24 species in Maluridae. We estimated beak surface area using the conical equation described in Danner and Greenberg (2015). Body mass was included from measurements taken at the time of collection and reported in the ANWC specimen database (Schodde and Mason 1999); in the few cases when these were unavailable we used the median of estimates from the *Handbook of the Birds of the World* (hereafter HBW; del Hoyo et al. 2007, 2008).

Most honeyeater species exhibit some degree of curvature in their beak, potentially decreasing the conical estimate of beak surface area's accuracy. To support the accuracy of our beak size and area estimates, we used 2D geometric morphometric data from specimens photographed at the Natural History Museum in Tring, U.K. to provide supplementary estimates of size and surface area that account for curvature. We placed five landmarks and 19 semilandmarks around in the outline of each species' beak in *tpsDig* 2 (version 2.22; Rohlf 2015) using the arrangement shown in Figure 5. We used the R package *geomorph* (version 3.0.3; Adams and Otarola-Castillo 2013) to measure the area of this shape and the scaling factor of its Generalized Procrustes alignment as independent estimates.

CLIMATE

We calculated climate averages for each species as the mean of all raster values contained within a species' range (Birdlife International and NatureServe 2011) using the R package *raster* (Hijmans 2015). As a measure of winter minimum and summer maximum temperatures, we used bioclim data at a resolution of 10 min (bio5 and bio6 in Hijmans et al. 2005). These represent the maximum temperature of a region's warmest month and the minimum temperature of its coldest month, averaged across years from 1950 to 2000. For migratory species, we used the breeding range to calculate summer climate variables, and the nonbreeding range to calculate winter climate variables. As the importance of convective versus evaporative heat exchange is likely to change depending on the availability of water during summer heat, we included a metric of aridity (hereafter "summer heat stress"). For this metric, we extracted summer precipitation (bio18 in Hijmans et al. 2005) to express "summer heat stress" as its statistical interaction with summer maximum temperature (see next).

SPATIAL DISTRIBUTION

To visualize spatial distributions of beak size traits, we accounted for allometry using residuals of their regression against body mass (these characters were not used for comparative analyses described below). We used the *Spatial Analysis in Macroecology* software package (version 4.0; Rangel et al. 2010) to estimate both species richness and average trait values for each taxonomic family at every grid cell (0.5° × 0.5°). These grids were then trimmed to include only cells with at least two species present. We used *QGIS* version 2.14 to produce choropleth figures describing species richness and the spatial distribution of beak size traits (QGIS Development Team 2015).

COMPARATIVE METHODS

Correcting for phylogenetic nonindependence is critical to the comparative method. We conducted a separate analysis for each family by taking advantage of their recent multilocus phylogeny (Lee et al. 2012; Nyári and Joseph 2012; Joseph et al. 2014). This approach has the advantage of both using high-quality molecular phylogeny and at the same time assessing between-family heterogeneity in evolutionary patterns. To estimate time-calibrated branch lengths for these trees, we used penalized likelihood in *ape* to constrain branch lengths by divergence time estimates in the references listed above (Paradis et al. 2004; Paradis 2013).

Just as closely related species are not phylogenetically independent, they are not spatially independent either (Freckleton and Jetz 2009). Indeed, even when using correction for spatial autocorrelation spurious correlations often result from comparisons of species' climate variables and traits, apparently due to an autocorrelation of ecology and historical biogeography (Tello and Stevens 2012; Warren et al. 2014; Friedman and Remeš 2016). To avoid these pitfalls, we used a phylogenetic generalized least squares framework that combines correction for both phylogenetic and spatial relationships (Freckleton and Jetz 2009; hereafter "spatial PGLS"). This model includes estimates of both a phylogenetic effect parameter (λ) and a spatial effect parameter (Φ). Scripts to run this analysis in the R programming environment are available from R. Freckleton upon request as stated in the original publication (Freckleton and Jetz 2009). We used this spatial PGLS method to test for significant relationships between morphological characters and environmental factors in each family using a multivariate analysis. In this analysis, we included winter minimum temperature, summer maximum temperature, and precipitation as predictors.

To correct for allometric scaling of beak size, we included body mass as a covariate in each analysis. This approach is preferred among contemporary phylogenetic comparative studies because the use of residuals may cause collinearity issues (Freckleton 2009; Symonds and Tattersall 2010; Baab et al. 2014; Benson-Amram et al. 2015). To display allometric relationships outside the context of our phylogenetically corrected analyses, we used residuals from the regression of $\log_{10}$ beak size against $\log_{10}$ body mass (for linear beak measurements, body mass was raised to the one-third power; for beak surface area body mass was raised to the two-third power).

To estimate the effect size of each predictor as the standardized regression coefficient, we scaled each climate predictor by its standard deviation so that its variance equaled 1. Below, we present results from bivariate analyses, as well as analyses using multivariate models.

Results and Discussion

Our analyses illuminate the roles of different selection pressures in the evolution of beak size in Australasian honeyeaters and allies. In particular, we found a consistent evolutionary correlation between winter temperature and beak size (Figs. 1 and 2A). In areas with low winter minimum temperature, bird species tend to have low beak surface area, length, and width (Fig. 2C; weaker effects were observed for depth). The relationship between winter temperature and beak size was consistent in its direction and was significant across each clade examined in this study. In contrast, we found little evidence that beak size was associated with summer maximum temperatures (Fig. 2B and D).

Among multivariate analyses including summer heat stress (i.e., interaction between summer maximum temperature and summer precipitation), beak size measures were significantly correlated with winter minimum temperatures in most models (Table 1). Five of 12 comparisons, and at least one from each clade we examined, showed significant relationships between low winter temperatures and small beak sizes. In particular, winter temperatures were associated with beak surface area and beak length in Meliphagidae and Maluridae, and with beak width in Acanthizidae. On the contrary, summer heat stress was not significantly associated with beak size in models that included winter temperatures (Fig. 3, Table 1). Maps of average beak sizes across Australasia showed a similar pattern: species of each family tended to exhibit relatively larger beaks in northern Australia and New Guinea, and smaller beaks in central and southern Australia (Fig. 4).

We observed the greatest effect of winter temperatures on beak length in Meliphagidae and Maluridae, and on beak width in Acanthizidae (Fig. 2C). The relationship between winter temperature and beak surface area, the most important beak characteristic in terms of thermoregulation, was consistent across all families for univariate analyses. Furthermore, measurements of beak area and scale accounting for curvature in Meliphagids showed similar results (Fig. 5). These results provide support for the evolutionary relationship between climate and extremity length, particularly beak size (see also Campbell-Tennant et al. 2015; Gardner et al.

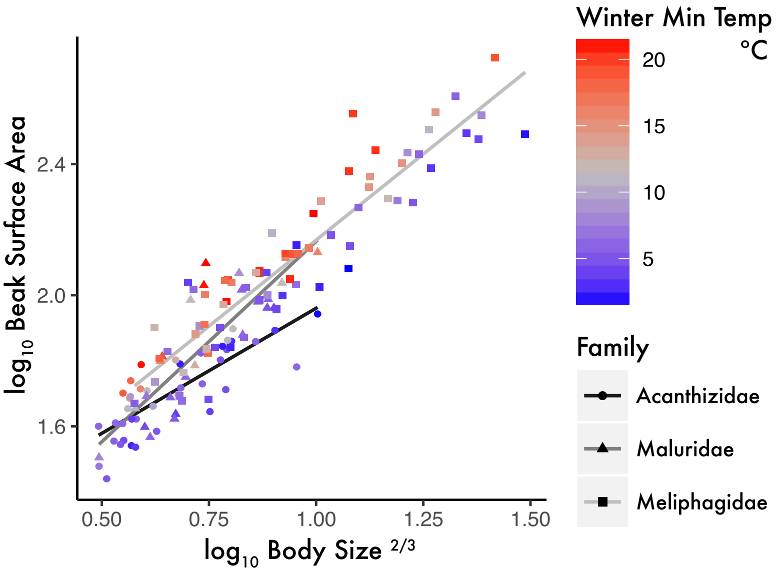

Figure 1. Allometric plot of $\log_{10}$ beak surface area against $\log_{10}$ body mass, with body mass raised to the two-third power to account for the dimensional difference between area and volume. Minimum winter temperatures, averaged across species ranges, are shown as the color of the points in the scatterplot, while taxonomic families are depicted with different symbols. Ordinary least squares linear models are shown to aid visualization of climate patterns relative to allometry relationships, with lines colored by family. Most species in regions with warm winters have large beaks for their body mass, whereas most species in regions with cold winters have small beaks for their body mass.

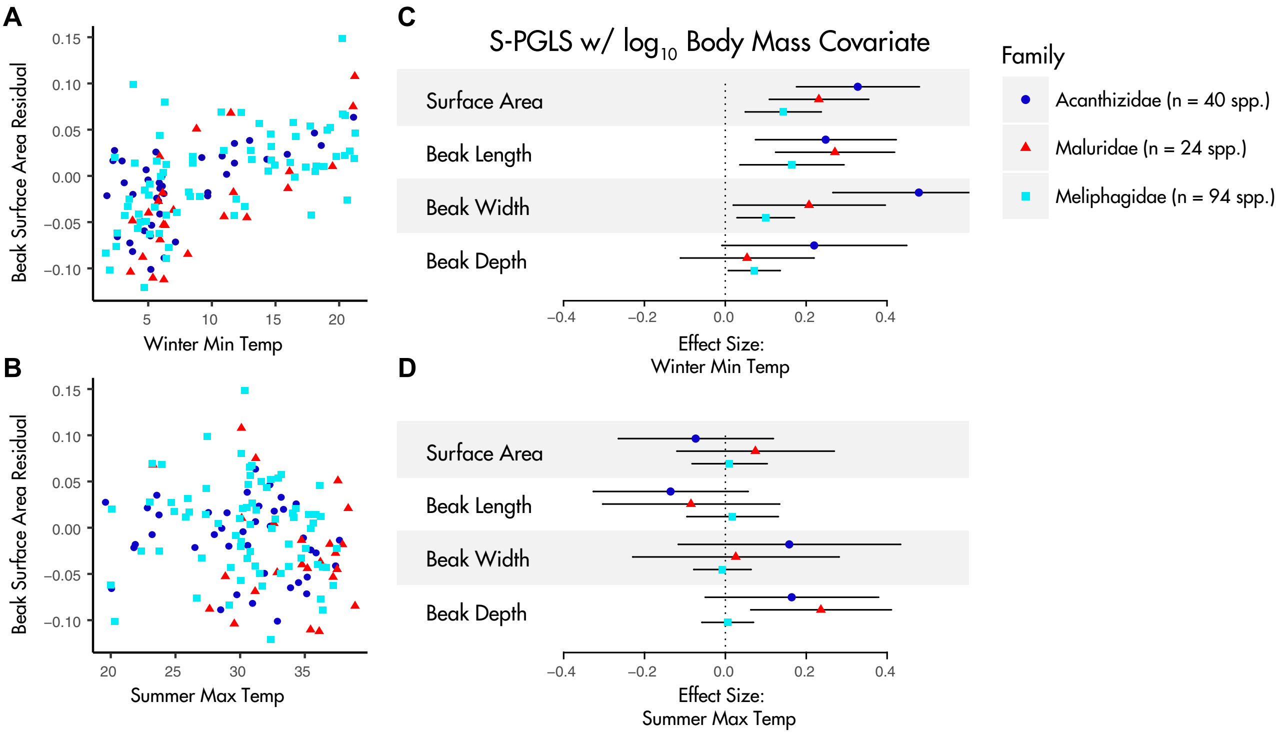

Figure 2. (A–B) Comparisons of beak surface area, as residuals of the relationship shown in Figure 1 to climate averages. (C–D) Effects of climate averages on four measures of beak size, shown as effect sizes (standardized β) with 95% confidence intervals. These effect sizes describe bivariate spatial PGLS models comparing trait values across species and including body mass as a covariate to account for allometry. Taxonomic families are represented by the symbols shown in the legend in the upper right.

Table 1. Results of multivariate PGLS models fit with both phylogenetic and spatial autocorrelation parameters. Bold values are significant at a level of $\alpha = 0.05$ or better.

		Meliphagidae			Acanthizidae			Maluridae		
Dependent variable	Model component	Covariance parameters	*t*-Value	*P*-value	Covariance parameters	*t*-Value	*P*-value	Covariance parameters	*t*-Value	*P*-value
Beak conical Surface area	Summer heat Stress	$\lambda_{opt} = 0.85$	−0.174	0.863	$\lambda_{opt} = 0.34$	0.996	0.326	$\lambda_{opt} = 0.87$	0.499	0.623
	winter minimum temperature	$\Phi_{opt} = 0$	2.543	**0.013**	$\Phi_{opt} = 0$	1.968	0.057	$\Phi_{opt} = 0$	4.144	**< 0.001**
	Body mass		15.134	**< 0.001**		8.646	**< 0.001**		3.819	**0.001**
Beak length	Summer heat stress	$\lambda_{opt} = 0.99$	−0.728	0.469	$\lambda_{opt} = 0.99$	1.143	0.260	$\lambda_{opt} = 0$	0.775	0.448
	Winter minimum temperature	$\Phi_{opt} = 0.13$	2.820	**0.006**	$\Phi_{opt} = 0$	1.666	0.104	$\Phi_{opt} = 0$	4.208	**< 0.001**
	Body mass		10.754	**< 0.001**		4.267	**< 0.001**		7.682	**< 0.001**
Beak width	Summer heat stress	$\lambda_{opt} = 0.83$	0.503	0.616	$\lambda_{opt} = 0.52$	0.342	0.734	$\lambda_{opt} = 0.99$	−0.324	0.749
	Winter minimum temperature	$\Phi_{opt} = 0$	1.943	0.056	$\Phi_{opt} = 0$	3.128	**0.003**	$\Phi_{opt} = 0.40$	0.711	0.485
	Body mass		21.857	**< 0.001**		4.298	**< 0.001**		1.452	0.162
Beak depth	Summer heat stress	$\lambda_{opt} = 0.99$	1.005	0.319	$\lambda_{opt} = 0.59$	0.379	0.707	$\lambda_{opt} = 0.56$	1.314	0.204
	Winter minimum temperature	$\Phi_{opt} = 0$	1.312	0.194	$\Phi_{opt} = 0$	1.260	0.216	$\Phi_{opt} = 0$	0.755	0.459
	Body mass		19.404	**< 0.001**		4.415	**< 0.001**		2.718	**0.013**

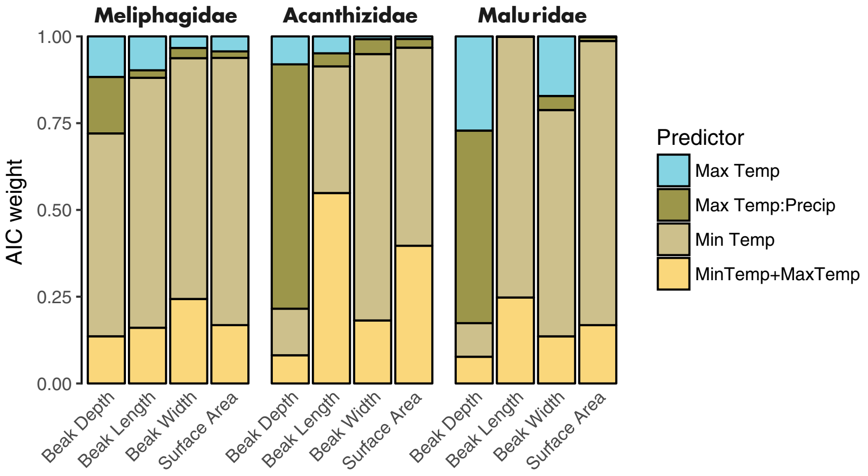

Figure 3. Comparison of model support across spatial PGLS analyses. Bar plots show Akaike weights for models including combinations of predictor variables that reflect a priori hypotheses. Models that include minimum temperature have majority support in all analyses explaining beak surface area. Summer heat stress (MaxTemp:Precip) models are a better fit as explanations of beak depth in Acanthizidae and Maluridae. However, these associations with summer heat stress were not statistically significant when winter minimum temperature was included in multivariate analyses (Table 1).

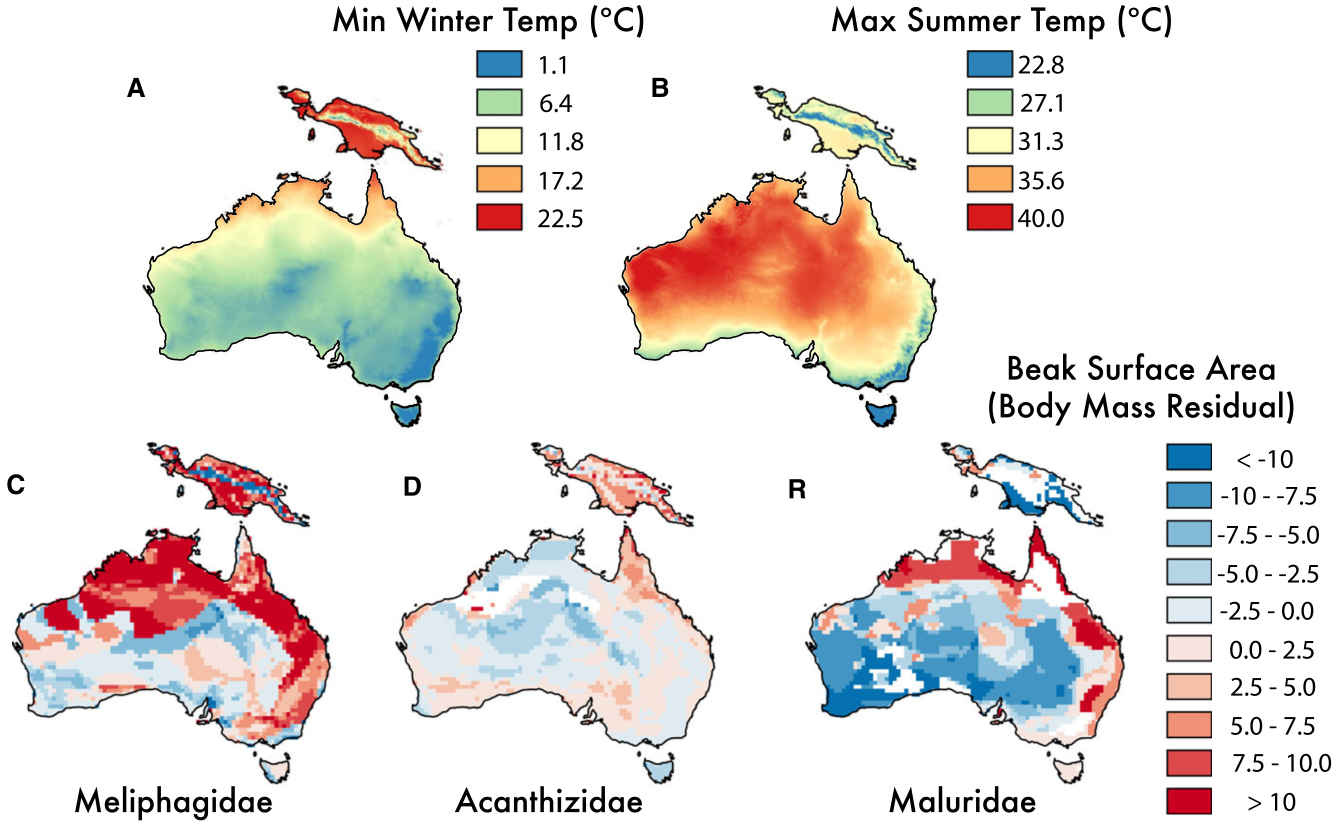

Figure 4. Geographic distribution of minimum winter temperature (A) and maximum summer temperature (B) from the bioclim dataset (Hijmans et al. 2005). Beak surface area averaged across species present in 0.5° grid cells (as residuals of regression with body mass) for Meliphagidae (C), Acanthizidae (D), and Maluridae (E). Larger beaks are shown in red and smaller beaks are shown in blue. Cells with less than two species present were excluded (white).

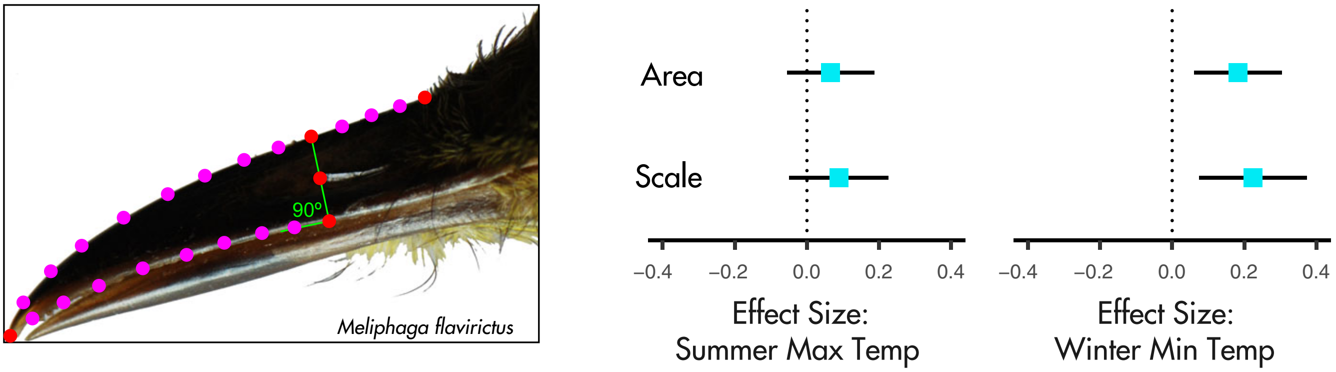

Figure 5. At left, landmark (red) and sliding semilandmark (magenta) positions used in scoring beak area and size. Semilandmarks were set at equal intervals between landmarks. At right, effect sizes (standardized β) of spatial PGLS models comparing climate predictor variables to landmark-based measures of beak area and size; lines represent 95% confidence intervals.

2016). Furthermore, our results show support for winter and not summer temperatures driving beak size evolution across several clades adapting to a broad range of climates. This pattern is not predicted by proximate explanations for Allen's rule that rely on a direct effect of temperature on skeletal development (Serrat et al. 2008; Burness et al. 2013), as developing songbirds grow exceptionally fast and thus reach their adult size prior to the onset of winter temperatures (Starck and Ricklefs 1998). However, birds can exhibit seasonal variation in size of the keratin-based rhamphotheca, resulting in a slight increase in beak length during the breeding season (Morton and Morton 1987; Greenberg et al. 2012a). In our study, we measured specimens in breeding condition, thus we can to some extent control for—but cannot describe—seasonal variation of the rhamphotheca.

Among seasons, we found that winter temperatures were often significantly correlated with beak size, whereas summer temperatures and summer heat stress were never correlated with beak size. This suggests that selection in winter produces the most detectable effect at a broad phylogenetic scale, not that summer temperature has no impact on beak size. The evidence from North American sparrows clearly supports a gradient in beak size driven by summer heat stress (Greenberg et al. 2012b). However, this summer effect was observed most prominently in coastal regions where winters are relatively mild (Danner and Greenberg 2015). Similarly, we observed large beak sizes for species in coastal northern Australia, where summers are hot and winters tend to be mild (Fig. 4). However, we observed small beak sizes for species in inland Australia, where summers are still hot but winter temperatures can be harsh as well. Although selection on beak size in winter and summer appears to interact negatively across Australia's broad aridity gradient, these effects may interact positively along steep altitudinal gradients, where regions tend to be either hot or cool year-round. This could explain the drastic contrasts in beak size we observed between the central highlands and coastal lowlands of New Guinea in Meliphagidae and Acanthizidae (Fig. 4), as well as those observed in Hawaiian elepaios (VanderWerf 2012). Path analysis studies (Hardenberg and Gonzalez-Voyer 2013) are needed to describe the effects of complex interactions between seasonal climates and elevation on morphological evolution.

In this study, we cannot rule out a major role for diet in the evolution of beak size and shape in Meliphagoidea. Although preferences for seeds, insects, or the nectar in flowers are available in most species descriptions, these dietary categories may be less important than the size of preferred items in driving the evolution of divergent beak sizes (Grant et al. 1976). The manner in which these items are procured (e.g., pursuit and hawking vs. probing and gleaning) and the substrate they occupy likely also influence adaptive beak evolution (Miller et al. 2017). Such detailed descriptions are typically unavailable for taxa in remote regions like New Guinea and the South Pacific islands, making comparative studies difficult. Lastly, particular food sources may increase or decrease in availability due to climate, making it difficult to rule out diet in explaining differences in beak size between regions. Thus, our results highlight the importance and need for thorough descriptions of foraging niche at a broad taxonomic scale to better tease out the relative roles of diet and thermoregulation in driving beak evolution.

It has long been clear that bird species employ a diverse range of specialized beak shapes that are a close fit to their diets (Beecher 1951; Wooller and Richardson 1988). However, our results from a phylogenetic comparative study of Australasian songbirds suggest that such structures likely also scale with the demands of climate. Shorebirds provide an excellent example, where bill size has dramatically increased with probing behavior (Barbosa and Moreno 1999). But such species can be observed with their bills tucked into insulating plumage when not in use, likely mitigating their thermoregulatory costs (Midtgård 1978).

For decades, the evolution of beak size in Galapagos finches has been an instructive model system for the study of adaptation, and findings using this system have largely highlighted the importance of trophic processes in the evolution of beak size (Grant et al. 1976; Grant and Grant 2002). However, as island endemics, these species are only subject to the climates present in a narrow (if dynamic) geographic range (Grant and Boag 1980). We predict that if our study were repeated in that clade it would be difficult to find a similar effect of climate on beak size evolution; this contrast underscores the importance of broad comparative studies in evolutionary research. In contrast, our study of honeyeaters and allies across Australasia spans both tropical and temperate zones including a continental gradient in precipitation and an extended range of elevations up to 4500m (Fig. 4). We interpret our findings to suggest that at greater spatial or temporal scales (Meliphagoidea originated 25–30 million years ago in the early Oligocene; Moyle et al. 2016, Marki et al. 2017), the beak's thermoregulatory role may explain a more considerable amount of evolutionary change than previously thought. The relative importance of this mechanism versus foraging niche divergence in explaining beak evolution will be an exciting avenue of future research. Ultimately this finding highlights the diversity of selective pressures acting on species morphological traits (Schluter et al. 1991) and the contrasting patterns they may produce at different spatial and temporal scales (Carroll et al. 2007).

AUTHOR CONTRIBUTIONS

NRF and VR planned the study. NRF and LH collected the data. NRF performed the analyses and wrote the paper with help from EPE, and editing contributions by all authors.

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DATA ARCHIVING

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Supporting Information

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Figure S1. Species richness of three Australasian songbird clades, estimated from the sampling used in this study.

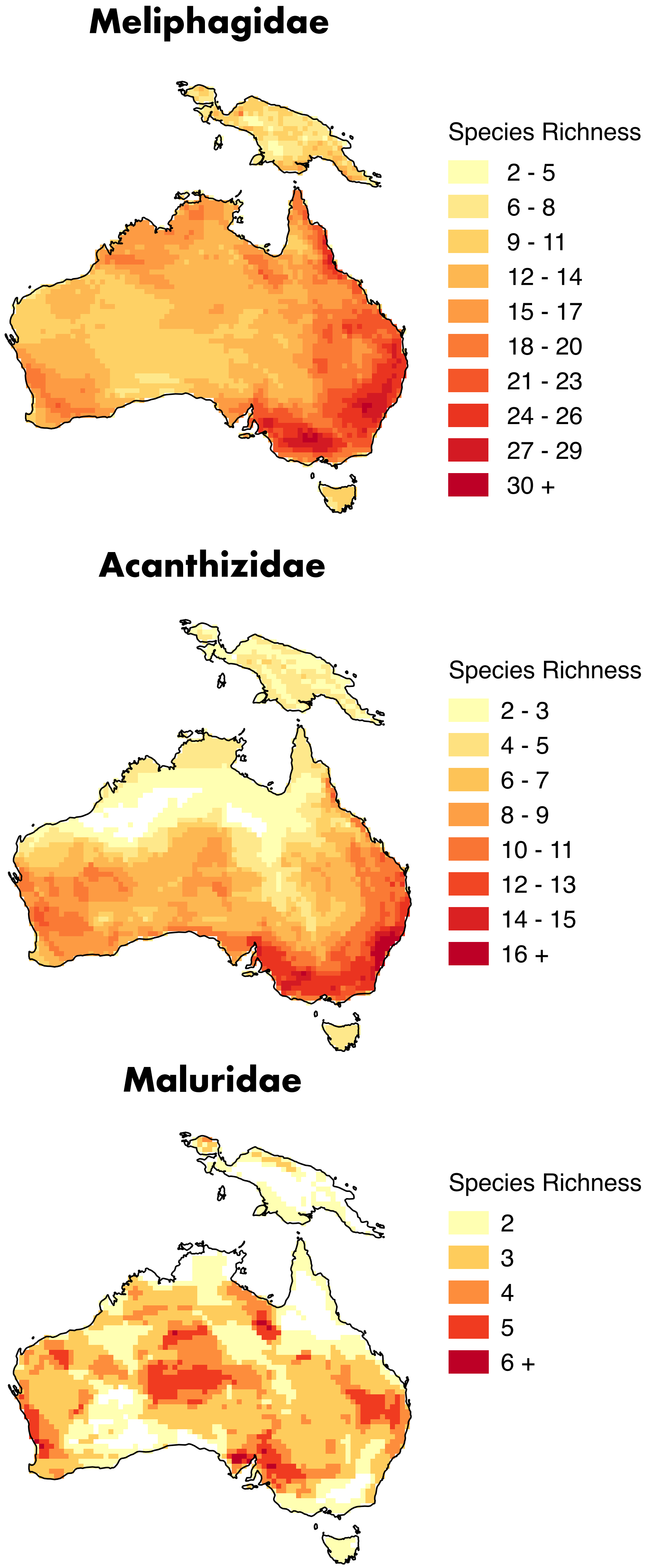

Figure S1: Species richness of three Australasian songbird clades, estimated from the sampling used in this study. Note that this sampled richness may differ from estimates of species richness assembled from all recognized taxa, particularly in New Guinea.

Chapter III

Disentangling direct and indirect effects of water availability, vegetation, and topography on avian diversity

Platycercus eximius

Remeš V. & ***Harmáčková L.***
Scientific Reports (2018) 8: 15475

Eastern Rosellas (*Platycercus eximius*) show distinct morphological and ecological traits such as short beak and tarsi, long tail, and forage primarily on seeds. We used such traits for computation of diversity indices.

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Disentangling direct and indirect effects of water availability, vegetation, and topography on avian diversity

Vladimír Remeš & Lenka Harmáčková

Climate is a major driver of species diversity. However, its effect can be either direct due to species physiological tolerances or indirect, whereby wetter climates facilitate more complex vegetation and consequently higher diversity due to greater resource availability. Yet, studies quantifying both direct and indirect effects of climate on multiple dimensions of diversity are rare. We used extensive data on species distributions, morphological and ecological traits, and vegetation across Australia to quantify both direct (water availability) and indirect (habitat diversity and canopy height) effects of climate on the species richness (SR), phylogenetic diversity (PD), and functional diversity (FD) of 536 species of birds. Path analyses revealed that SR increased with wetter climates through both direct and indirect effects, lending support for the influence of both physiological tolerance and vegetation complexity. However, residual PD and residual FD (adjusted for SR by null models) were poorly predicted by environmental conditions. Thus, the FD and PD of Australian birds mostly evolved in concert with SR, with the possible exception of the higher-than-expected accumulation of avian lineages in wetter and more productive areas in northern and eastern Australia (with high residual PD), permitted probably by older biome age.

Current climatic conditions, especially energy and precipitation, are major determinants of species richness[1–3]. This effect can be direct, due to a subset of species tolerating harsh climates (the physiological tolerance hypothesis)[4] or indirect due to wetter and warmer environments facilitating more complex habitats providing more ecological niches (the vegetation structure hypothesis)[5,6]. These indirect effects include taller vegetation with increased vertical vegetation complexity[7–9], more habitat types[10,11], and possibly greater food availability (e.g. invertebrate biomass)[12]. All these effects suggest that there is more available energy supporting more individuals, which allows more populations to potentially co-exist with densities sufficient to avoid local stochastic extinction. In addition, these effects might be modified by spatial heterogeneity resulting in an increase in microhabitats, which could further influence diversity (e.g. topographic heterogeneity[13]; see Fig. 1a). Both direct and indirect climatic effects on species richness (SR) have been demonstrated on spatial and environmental SR gradients[9,12,14–18]. However, effects of climate on residual phylogenetic diversity (PD) and functional diversity (FD) adjusted for SR have been quantified only rarely[19–21], and studies comparing both direct and indirect effects of climate on residual PD and FD are even rarer[22].

A comprehensive assessment of all dimensions of diversity should provide a new insight into the origin and maintenance of diversity[23–28]. For example, climatic tolerance could limit the number of species capable of colonizing a challenging environment (e.g. desert) leading to low SR, but these species could ecologically diversify to fill available niches, which would lead to high residual FD[29]. Moreover, although SR might increase with ecological factors, e.g. productivity, residual FD might be better predicted by the evolutionary time available for species differentiation, as is the case in mammals globally[30]. Additionally, climatic history can complicate inference as climate change can drive diversity. For example, areas with faster climate change during the late Quaternary were taxonomically poorer in amphibians, birds, and mammals[31]. Additionally, regions with long existence and climatic stability were biologically diverse[32,33] and areas with greater climatic stability since the last interglacial

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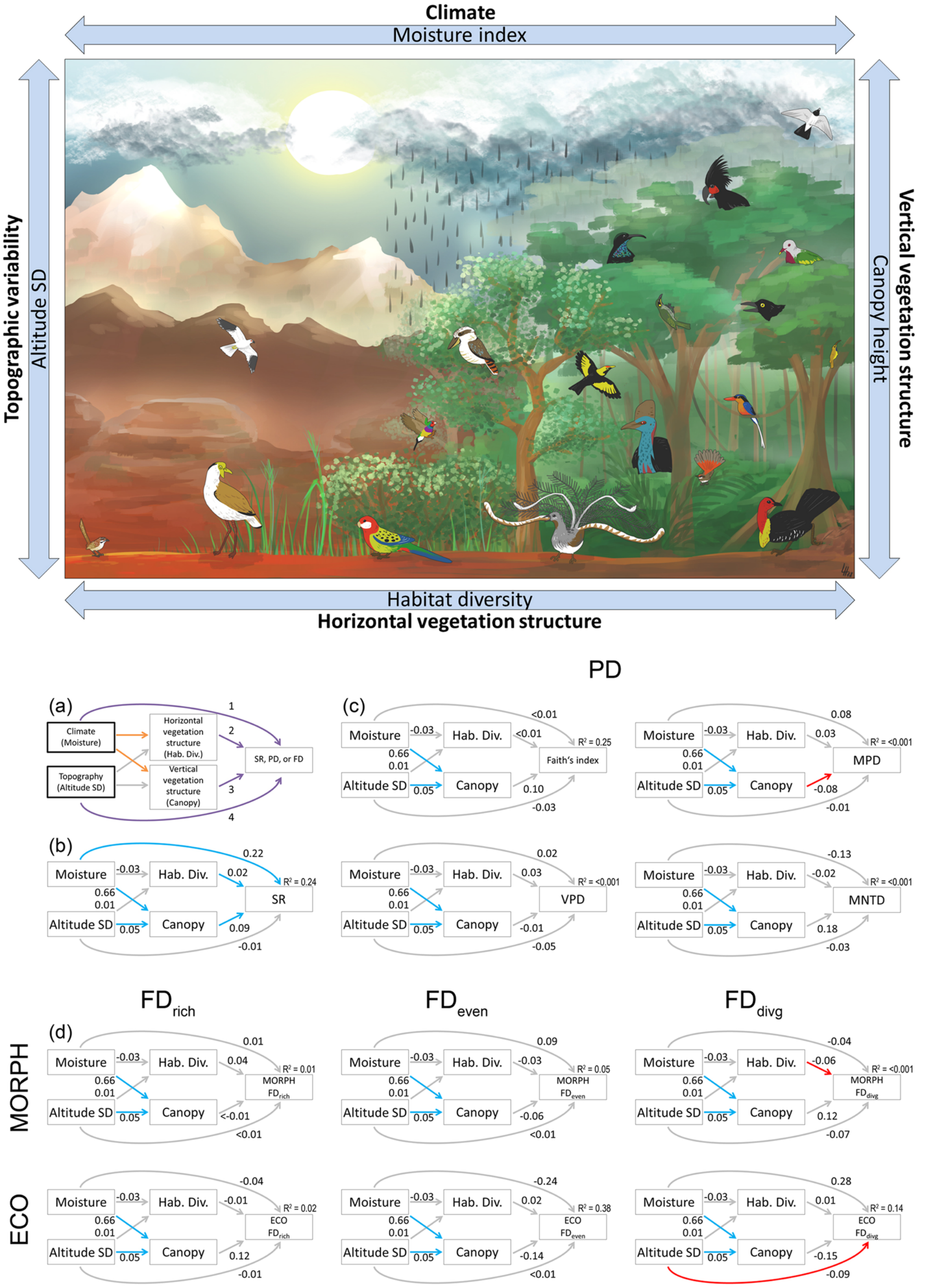

Figure 1. Results of path analyses. Top figure (drawing by L. Harmackova) and panel (a) show the conceptual framework to quantify direct and indirect effects of climate (water availability quantified by moisture index) on species richness (SR), phylogenetic (PD), and functional diversity (FD). In panel (a) climate can affect diversity either directly due to species physiological tolerance (1: the physiological tolerance hypothesis[4]) or indirectly by facilitating richer vegetation, which in turn provides more niches[5,6]. More niches can arise by means of higher horizontal vegetation diversity (2: habitat diversity[11]) and/or higher vertical vegetation diversity (3: canopy height[7,8]). We also include a direct effect of a major source of abiotic heterogeneity (4: topographic heterogeneity defined as the Standard Deviation (SD) of Altitude[13]). Abiotic factors are in thick box. Colour codes are as follows: Magenta = direct effects of variables on diversity; Orange = direct effects of climate on vegetation structure; Grey = other logical links between variables. For details, see the main text. (**b**–**d**) Results of path analyses for SR (**b**), residual PD (**c**), and residual FD (**d**). Blue arrows are statistically significant positive effects, red arrows are significant negative effects, and grey arrows are nonsignificant effects. Numbers along paths are standardized effect sizes for individual paths. Numbers above response variables are pseudo-Rsq values, which were the same for Hab. Div. (<0.01) and Canopy (0.37) in all path models and thus are not depicted in the figure.

period (last 125 000 years) had higher residual PD in birds globally[28]. Furthermore, the FD of European plants and PD of European dragonflies were lower than expected for given SR in northern areas of the European continent due to the legacy of glacial climate change[34–36]. It is clear that multiple dimensions of diversity should be considered when exploring the processes influencing the distribution of diversity in space.

Australia is uniquely suited to resolving the direct and indirect effects of climate on the distribution of biodiversity. This continent experienced dramatic changes in its environment involving intense aridification in the past 15–20 million years[37–39]. Species-rich and phylogenetically diverse assemblages are usually situated in the remnants of the original wet forests on the east coast[40] existing from at least the early Paleogene ca. 55 Mya[39] and probably even from before the separation of Australia from the rest of Gondwana some 80 Mya[41,42]. However, the Australian arid zone (now comprising ca. 70% of the continent) also provided an opportunity for the extraordinary diversification of many lineages of animals and plants, which required multiple adaptations to challenging abiotic conditions[37]. The Australian arid zone was invaded relatively recently, which was demonstrated by phylogeny-based studies confirming the mesic origins of arid-adapted lineages[38,43]. Moreover, FD might also be elevated in certain lineages in the arid zone. For example, local assemblages of reptiles in Australian deserts are much more diverse in terms of both SR and functional type than anywhere else in the world[44] and certain species even seem to fulfil the ecological roles of insects or mammals[45]. Furthermore, the SR of Australian honeyeaters (Meliphagidae), which originated ca 25 Mya in Australian wet forests[46,47] decreases towards dry areas[43] and only five lineages have become endemic for the arid zone[48]. However, their ecological and behavioural (foraging behaviour) diversity does not decline as fast with aridity as their SR, showing that the arid-adapted species have ecologically diverged to a similar degree as their mesic counter-parts[29].

To disentangle direct and indirect effects of climate on biodiversity in an ancient and rich radiation of vertebrates, we studied patterns in SR, PD, and FD in Australian and Tasmanian birds across major climatic and environmental gradients. We used four PD indices and three FD indices based on three sets of ecologically important traits linked to ecological niches (breeding habitat, diet, and foraging substrate) to build on previous studies[40] and investigate the effects of water availability and available niche space on SR, PD and FD. Specifically, we (i) mapped the geographical distribution of the residual PD and residual FD of Australian and Tasmanian birds adjusted for SR by null models and identified areas deviating from our null expectations, and (ii) fitted path models to link SR and residual PD and residual FD to water availability, topography, canopy height, and habitat diversity. By using path models (Fig. 1a), we quantified both the direct and indirect effects of a major climatic variable driving Australian environments, namely water availability, to provide comprehensive insights into the processes determining the accumulation and maintenance of biodiversity in Australian and Tasmanian avifauna. It should be noted that we focused only on the current climate and environment as potential explanations for bird diversity, because finding data of sufficient detail and scope for past climates and environments was not possible.

Materials and Methods

Data. To map PD and FD in assemblages we created a geographical grid with a 1 × 1 degree resolution (longitude x latitude; equivalent to ca. 10,000 km^2) across Australia and Tasmania in R software ver. 3.4.3[49]. We eliminated cells in which land constituted less than 50% so that the final grid consisted of 692 cells, where one grid cell represented one assemblage. We used the distribution ranges of mainland Australian and Tasmanian species of birds ($n = 536$) obtained from[50] to generate presence-absence data for all species in each assemblage. We used only breeding ranges where the species were extant and the area of the range occupied at least 10% of a cell. The assemblages were then characterized by the list of species present in each cell. For our continent-wide analyses, we preferred coarse-grained range extents rather than point occurrence records, e.g. from The Atlas of Living Australia (www.ala.org.au), because the former are less susceptible to sampling bias that might compromise data on local scales[51]. Phylogenetic trees for the computation of PD indices were obtained from the publicly available archive at birdtree.org (Hackett constraint)[52]. We created one Bayesian maximum clade credibility tree out of 500 phylogenies using TreeAnnotator software embedded in BEAST[53]. However, to ensure that phylogenetic uncertainty did not compromise the calculation of PD indices, we calculated all PD indices (see below) across 100 randomly chosen phylogenetic trees to quantify the variation in indices across trees.

We used species morphology and ecology to quantify FD. As dimensions of the species' ecological niche we used following three traits: (i) type of breeding habitat, (ii) diet, and (iii) foraging substrate. Data on morphological and ecological traits for every species were obtained from The Handbook of Australian, New Zealand and Antarctic birds[54–60]. Morphology included mean body mass (grams) and the length of wing, tail, tarsus, and bill (mm). Type of habitat was divided into 12 categories (forest, woodland, shrubs, savanna, grassland, reed, swamps, sand, freshwater, marine, rocks, and human settlement), diet into eight categories (plant material, fruit, nectar, seeds, insects and other invertebrates, fish, other vertebrates, and carrion), and foraging substrate into four categories (ground, vegetation, air, and water). Each category of each ecological trait received a value ranging from 0 to 5 according to the information in[54–60]. The value symbolized the proportional use by the species (e.g. 0 – not used, 2.5 – the given category represented one half of the use, 5 – only this category was used) so that the sum of all values in all categories in a given ecological trait for a given species was always equal to 5. It should be noted that using a scale from 0 to 5 was arbitrary and any similar scale would serve equally well (e.g. a percentage scale from 0 to 100).

To test both the direct and indirect effects of climate on diversity, we selected four variables as predictors in our analyses: two environmental variables (habitat diversity and canopy height), one climatic variable (moisture index), and one topographic variable (variability in elevation within geographic cells). We obtained these predictors as follows. First, we obtained data on land cover[61], canopy height[62], and water availability and elevation (The Atlas of Living Australia, http://www.ala.org.au, accessed 24 April 2017). The land cover dataset provides the proportional cover constituted by particular habitat types expressed in percentages and we used nine out of twelve metrics from this dataset (we removed habitats that occur only marginally in Australia, i.e. needle leaf trees, snow, and open water). Canopy height is the average height of the highest stratum of vegetation in a geographic cell (in metres). We characterized water availability by moisture index, which is the annual mean of the monthly ratio of precipitation to potential evaporation (pan, free water surface). It is a numerical indicator of the degree of dryness of the climate at a given location, whereby high values indicate relatively wet locations while low values indicate relatively dry locations. The Australian arid zone is usually defined by values less than 0.4[37]. We characterized topographic variability by the standard deviation of the elevation in 1,000,000 subcells within each grid cell (Altitude SD henceforth), where the original resolution of the elevation was 3.6 arc-seconds (equivalent to ca. 0.1 km). The original resolution of other datasets was 30 arc-seconds for land cover (equivalent to ca. 1 km), 1 km for canopy height, and 12 arc-minutes for climate (equivalent to ca. 22 km). We rescaled these datasets to match our grid by taking the mean value of the smaller pixels within our 1 × 1 degree mask (equivalent to the resolution of ca. 100 km). Canopy height and climate data were entered into our analyses unaltered. However, we transformed land cover metrics into an index of habitat diversity by computing Levins' index on the basis of the number of types of land cover and their relative proportions in each grid cell (for more information see)[10]. The values of this index range from zero, representing uniform grid cells dominated by one habitat type, to one, representing diverse grid cells that contain all habitat types represented equally. This metric thus includes information on both the number of habitat types and their proportions in a given cell and is more informative than, for example, the simple number of habitat types in a cell.

We selected the abovementioned predictors on the basis of previous work and strived to use predictors that are easy to understand and whose potential link to biodiversity is easy to interpret. At the same time, we focused on recent environments, because it was impossible to obtain sufficiently detailed information on past habitats and climates to factor them into our analyses. The first predictor, habitat diversity, relates to the number of habitat types and their relative areas; that is, areas with high habitat diversity (Levins' index → 1) might provide ecological space for more and diverse species[10,11]. The second predictor, canopy height, is expected to be important in that a higher canopy should provide more microhabitats and resources and thus support higher biodiversity[9]. It provides an index of vertical vegetation richness and productivity. The reasons for this are twofold: (i) The number of vegetation strata logically increases with tree height and we verified this assertion by correlating canopy height with leaf area index (LAI), which is defined as the one-sided green leaf area per unit ground surface area (in m^2/m^2; The Atlas of Living Australia, http://www.ala.org.au, accessed 24 April 2017). The correlation was sufficiently high (Log LAI vs. Sqrt Canopy height, $r = 0.82$), confirming our expectation. (ii) Net primary productivity increases with tree mass[63] and forest stand biomass[64], which again increases with maximum tree size[65]. The third predictor, topographic variability, is expected to be important in that high topographic heterogeneity (Altitude SD) might provide more niches for species with variable ecological requirements[13]. The fourth predictor, water availability, was previously reported to correlate positively with species richness in a wide range of plant and animal groups, especially on the southern hemisphere[3,40], and is considered a major driver of biome dynamics in Australia[37,38,66]. Thus, although other aspects of climate might affect diversity, we used the moisture index, which uniquely summarizes water balance by integrating water inputs from precipitation with water losses due to solar energy. An alternative index of water availability is precipitation deficit, which is the monthly difference between precipitation and potential evaporation (pan, free-water surface; The Atlas of Living Australia, http://www.ala.org.au, accessed 24 April 2017). However, correlation between the two indices of water balance was sufficiently high (Log Moisture index vs. Sqrt Precipitation deficit, $r = 0.96$) and thus we used only the moisture index. The spatial distribution of our predictors across Australia and Tasmania is apparent from Fig. S1 in Appendix S1.

Phylogenetic and functional diversity. We used indices to cover phylogenetic richness, divergence, and regularity[67].

1. For richness, we used Faith's index[23], which represents overall PD in an assemblage as the sum of branch lengths connecting all species in that assemblage.
2. For divergence, we used the Mean Nearest Taxon Distance index (MNTD)[68] and Mean Pairwise Distance (MPD)[68]. While MNTD represents the average phylogenetic distance between closest relatives in an assemblage, MPD represents the average pairwise phylogenetic distance among all species[25]. Thus, MNTD is informative for questions related to terminal branching, whereas MPD is informative for questions related to branching occurring deep within a tree[67]. All the three indices mentioned above showed good performance in extensive simulations[69].
3. For regularity, we used Variation of Pairwise Distances (VPD)[70], which represents variance in all pairwise phylogenetic distances. It should be noted that we inverted the sign of VPD so that high values mean higher regularity, whereas low values mean low regularity.

We used the functions 'pd', 'mpd', and 'mntd' from the 'picante' package ver. 1.6–2[71] to compute Faith's index, MPD, and MNTD; and the function 'taxondive' from the 'vegan' package ver. 2.4–6[72] to compute VPD in every grid cell (for more information on these indices see)[25]. Although in all analyses we used PD indices calculated on one Bayesian maximum clade credibility tree, we also recalculated all PD indices on 100 randomly sampled phylogenies to evaluate variation in indices stemming from phylogenetic uncertainty. We thus obtained estimates of all PD indices for all 692 geographic cells across 100 phylogenies. We then submitted these 100 sets of estimates to principal component analysis. The first axis from this principal component analysis accounted for 99.9% of variation in Faith's index, 99.4% in MPD, 99.2% in MNTD, and 90.4% in VPD, showing that potential effects of phylogenetic uncertainty were likely negligible.

We used appropriate indices to account for all three aspects of FD – namely, functional richness, functional evenness, and functional divergence, as proposed in[73–75] – while at the same time avoiding the poor-quality tree-based functional space indices as recommended in[76]. We calculated all three indices for the morphological traits and ecological characteristics of species (breeding habitat, food, and foraging substrate; see above). We calculated FD on morphology using scaled values (by subtracting the mean and dividing by one standard deviation) to avoid FD being dominated by overall body size. Thus, our FD indices for morphology are based on relative size proportions that are likely to reflect the ecological functions of species[77].

1. FD richness represents the overall volume of the functional space that is occupied by an assemblage[74]. FD richness is thus expected to be lower in assemblages with less diverse traits and a small number of species, while assemblages with high variability in functional traits and many species should exhibit higher FD richness. We calculated FD richness as the convex hull volume, which provides an n-dimensional measure of the volume of trait space occupied by species in an assemblage[78]. For ecological characteristics, we used the first five PCoA axes to calculate FD richness[76].
2. FD evenness measures how regularly the functional space is filled by species[74]. The FD evenness algorithm creates the minimum spanning tree that links the species in the functional space and quantifies their distances from each other on the branches of the tree. Small values of FD evenness represent clustered distances between species while high values represent an even distribution of species on the minimum spanning tree and in the functional space.
3. FD divergence quantifies the dispersion of species in the trait volume[74]. The FD divergence algorithm creates a centre of gravity of all species in an assemblage and calculates their mean distance from this centre. FD divergence is then computed as the sum of deviations of species from the mean distance divided by the absolute value of the same quantity, standardized by the mean distance (see)[74]. High values of FD divergence are thus the result of assemblages with species that are widely dispersed in trait space, and not clustered near the assemblage trait centroid. We used the 'dbFD' function from the 'FD' package ver. 1.0–12[79] to calculate FD richness, evenness, and divergence.

Null models. Some of the indices correlate with SR by definition and were shown to do so by simulations in previous studies (PD: Faith's index and MNTD[69]; FD: FD richness[74,75]). Thus, we corrected these indices for SR using null models (see below). Other indices have previously been shown by simulation to be largely independent of SR (PD: MPD[69]; FD: FD evenness and FD divergence[74,75]). However, these indices showed (nonlinear) relationships with SR in our data, or showed correlations between the variance of the index and SR (Fig. S2 in Appendix S1). Thus, to account for these empirically observed correlations with SR and for the sake of applying a consistent approach across all indices, we corrected all indices of PD and FD to ensure they were independent of SR (see also)[80]. We computed Standardized Effect Sizes (SES) for every grid cell (assemblage) as the difference between the observed value and the mean of the expected values divided by the standard deviation (SD) of the expected values. Thus, values of SES higher than 1.96 or lower than −1.96 are outside those expected by chance. To obtain the expected values of each index in each assemblage, we randomly generated samples of species from the pool of all Australian species. In particular, we used the SIM3 model from[81], whereby species number per site is fixed and all species are equiprobable, which has good overall performance when combined with Faith's index, MPD, and MNTD[69]. We performed SIM3 by shuffling species names either on the phylogeny for PD indices or in the trait data for FD indices and computed the indices with this randomized phylogeny or trait matrix (while the number of species in an assemblage remained unaltered, see above). We repeated this procedure 1000 times and then computed the mean and SD of the expected values of indices from these simulated data. Mutual correlations between SES of all indices together with species richness are shown in Fig. 2. In addition, to show the sensitivity of results to using null models, we also provide results of analyses where null models were used only in indices where the correlation of mean index value with SR was theoretically expected (Fig. S4 in Appendix S2).

Statistical analyses. To test both the direct and indirect effects of climate, we used structural equation modelling (SEM) where the SES value of the PD or FD index was the main variable to be explained and four other variables (see above and Fig. 1a) were linked in hypothesized causal relationships in the SEM[82]. To fit the SEM we used a piecewise approach in which the causal relationships were statistically defined and evaluated as mutually interconnected equations[83]. Specifically, we used the following three equations: Habitat diversity ~ Moisture index + Altitude SD; Canopy height ~ Moisture index + Altitude SD; and FD/PD index ~ Moisture index + Altitude SD + Habitat diversity + Canopy height. We used generalized least-squares to account for spatial autocorrelation and we chose the autocorrelation function with the lowest AIC value. We checked the autocorrelation of residuals to ensure that spatial effects were accounted for (Fig. S3 in Appendix S1). We calculated pseudo-Rsq values using the 'rsquared' function (the 'piecewiseSEM' package ver. 1.2.1)[83] for R software. All variables were tested for normal distribution; they were $\log_{10}$ or square root transformed if necessary and scaled (so that their mean was zero and standard deviation was one) prior to statistical analyses. As such, effect sizes from SEM were mutually comparable for individual paths. For details of our methodological choices see Appendix S3.

Results

Spatial patterns. There was a strong spatial gradient in the species richness (SR) of Australian birds, varying four-fold in 1 × 1 degree squares: it was highest (max. 291 species) in eastern Queensland and New South Wales and lowest (min. 73 species) in west-central deserts (south-eastern Western Australia); it was also low on Tasmania (Fig. 3a). More importantly, when adjusted for SR, the Standardized Effect Sizes (SES) of phylogenetic (PD) and functional diversity (FD) still showed marked spatial gradients, often resembling the gradient in SR (see Fig. 2 for correlations with SR and Fig. 3 for maps of SES). However, these patterns also differed for individual aspects of residual PD and FD, namely richness, divergence, and regularity/evenness. We mention and interpret only SES larger than 1.96 or smaller than −1.96, because only these differ significantly from expected values.

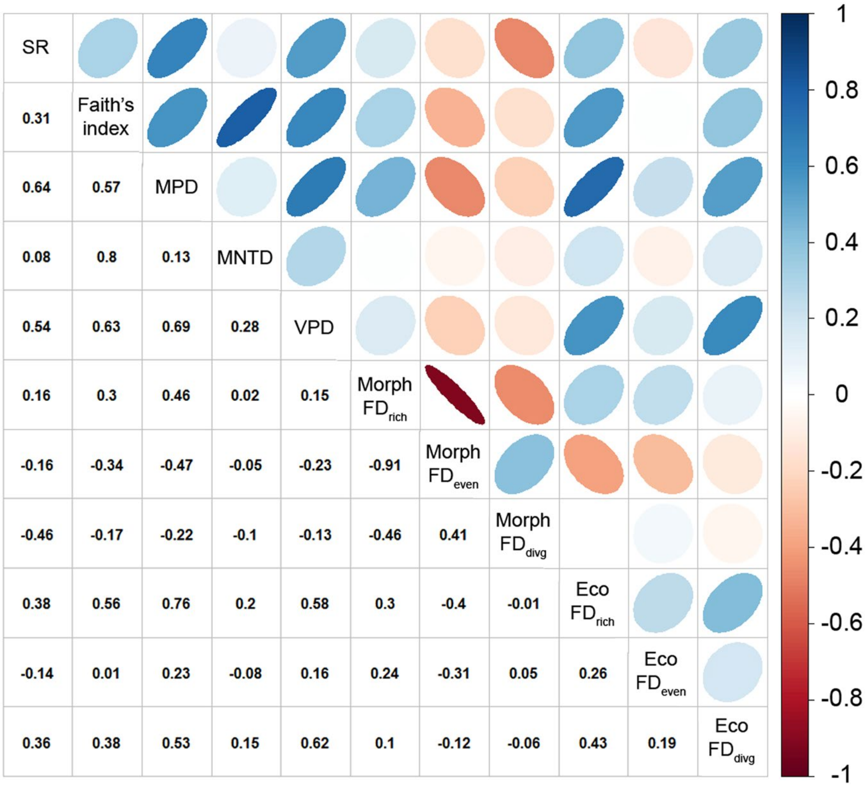

Figure 2. Mutual correlations between species richness (SR) and Standardized Effect Sizes (SES) of phylogenetic and functional diversity (FD) indices (FD$_{rich}$ is functional richness, FD$_{even}$ is functional evenness, and FD$_{divg}$ is functional divergence). Blue colour represents a positive correlation, while red colour denotes a negative correlation. The higher the correlation is, the thinner is the corresponding oval. Numerical values represent Pearson's correlation coefficient. It should be noted that (i) seemingly missing correlation ovals signal zero correlation (white colour) and (ii) we inverted the sign of SES for the variation of pairwise distances (VPD) so that high values mean higher regularity, whereas low values mean low regularity. Abbreviations not explained above: Morph = morphology, Eco = ecological traits, MPD = mean pairwise distance, and MNTD = mean nearest taxon distance.

Overall residual PD richness (Faith's index) and residual PD divergence for terminal branches (MNTD) were higher than expected for given SR along northern and eastern coasts (Fig. 3b,e). Residual PD divergence for deeper branches (MPD) and residual PD regularity (VPD) were higher than expected for a given SR again along northern and eastern coasts, while MPD was also higher in central-east Australia (Queensland outback and New South Wales) except for a small area in the southwest interior where MPD and VPD were lower than expected (southern Western Australia; Fig. 3c,d).

The distribution of residual morphological FD was quite irregular across Australia (Fig. 3). The strongest patterns were: (i) a negative correlation between the SES of FD richness and FD evenness (Figs 2 and 3f,g), and (ii) higher than expected residual FD divergence in north-western Australia (mostly Queensland) and on Tasmania (Fig. 3h). The spatial distribution of residual ecological FD richness was marked by exceptionally low values in the arid south-central part of Australia (the Nullarbor Plain and adjacent areas; Fig. 3i). In contrast, residual FD evenness was higher than expected across large parts of Australia (Fig. 3j), while the opposite was true for residual FD divergence across most of southern Australia (Fig. 3k).

Environmental predictors of SR, residual PD, and residual FD. Path analyses revealed both direct and indirect effects of our environmental predictors on SR (Fig. 1b, Table S1 in Appendix S4). SR increased with increasing water availability (increasing moisture index), higher habitat diversity, and higher canopy. At the same time, canopy height increased with increasing water availability and higher topographic heterogeneity (Fig. 1b, Table S1 in Appendix S4). Taken together, the direct effects of water availability on SR were higher (effect size 0.22) than indirect effects through canopy height (0.06; the magnitude of an indirect effect is the product of the direct effects connecting the two variables, i.e. 0.66 × 0.09), while the opposite was true for topographic heterogeneity, where indirect effects through canopy height, although weak (0.01), were higher than direct effects (zero).

Most aspects of residual PD and FD (i.e., Standardized Effect Sizes) were largely independent of our environmental predictors. The only statistically significant exceptions were (i) decreasing PD divergence for deeper branches (MPD) with higher canopy (effect size −0.08; Fig. 1c), (ii) decreasing morphological FD divergence with increasing habitat diversity (−0.06; Fig. 1d), and (iii) decreasing ecological FD divergence with increasing topographic heterogeneity (−0.09; Fig. 1d). However, some further non-negligible effects approached statistical

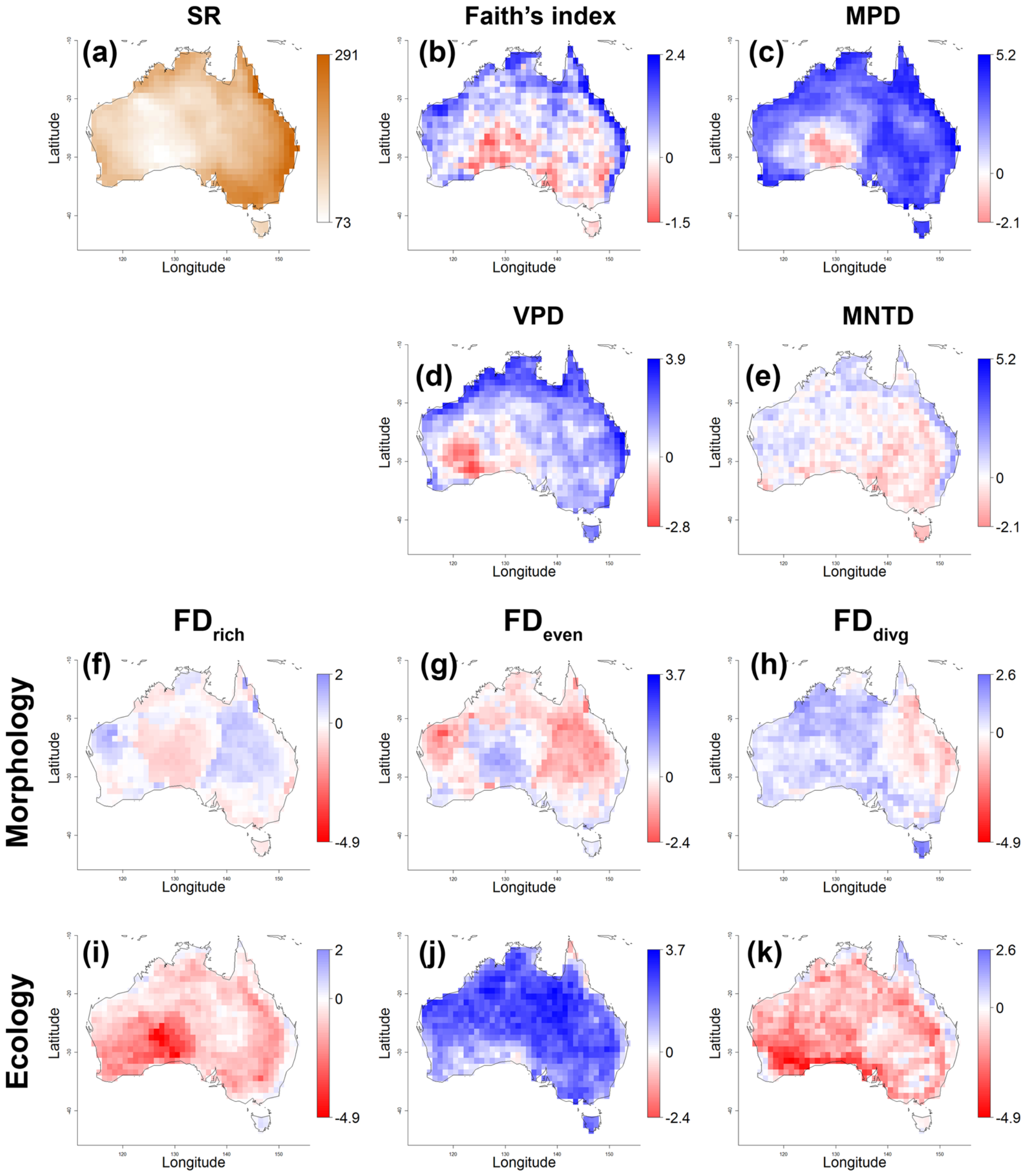

Figure 3. Spatial variation in (**a**) species richness (SR) and Standardized Effect Sizes (SES) of the (**b**–**e**) phylogenetic and (**f**–**k**) functional diversity of Australian birds. Blue colour shows SES values of indices higher than expected by chance for a given species richness, red colour shows values lower than expected. Similar metrics are presented on the same colour scale (mean pairwise distance (MPD) vs mean nearest taxon distance (MNTD), and morphology vs ecology for all functional diversity (FD) indices). It should be noted that (i) values of ca. ±1.96 deviate significantly from null expectations and (ii) we inverted the sign of SES for the variation of pairwise distances (VPD) so that high values mean higher regularity, whereas low values mean low regularity. FD$_{rich}$ is functional richness, FD$_{even}$ is functional evenness, and FD$_{divg}$ is functional divergence.

significance. If we highlight effects with size >0.1 and p-values between 0.05 and 0.07 (Table S1 in Appendix S4), we obtain the following further effects: (i) higher canopy correlates with higher phylogenetic divergence for terminal branches (MNTD, effect size 0.18; Fig. 1c), higher ecological FD richness (0.12), and lower ecological FD evenness (−0.14) and FD divergence (−0.15); and (ii) ecological FD divergence increases with increasing water availability (0.28; Fig. 1d).

Discussion

Understanding both the direct and indirect effects of climate on phylogenetic (PD) and functional diversity (FD) lags behind our understanding of these effects on species richness (SR). Yet, quantifying these effects is important for a deeper understanding of the origin and maintenance of biodiversity. By studying the spatial distribution of multiple dimensions of the biodiversity of birds across Australia and Tasmania, we demonstrated that avian SR, residual PD, and residual FD all showed strong spatial patterns, most differences being apparent between mesic and arid areas. However, whereas SR correlated with climatic and ecological factors, residual PD and residual FD (adjusted for SR by null models) were mostly independent of these same factors. These results show that both direct (physiological) and indirect (ecological) effects of climate are important in explaining SR at the spatial scale of this study, and reveal important ecological and evolutionary processes determining SR. Furthermore, the residual PD of birds in Australia is much less dependent on these same factors but might be under the influence of historical rather than current factors (e.g. available time), revealing an additional effect of time necessary for the accumulation of lineages in climatically stable and productive regions with old biomes. Lastly, residual FD (morphology, habitats, food, and foraging substrate) behaved spatially rather haphazardly and was not predicted by climate or environment, which suggests that the most relevant ecological and evolutionary effects were already captured by SR.

There were marked spatial gradients in all aspects of the biodiversity of Australian and Tasmanian birds. A conspicuous pattern was high SR in wetter areas along coasts[3,40], where assemblages were also phylogenetically rich, divergent, and regular (Fig. 3). These findings show that assemblages here are unexpectedly overdispersed in both deeper and terminal branches and that species are unexpectedly evenly spaced in the phylogenetic tree space. This finding is consistent with the higher than expected residual PD in tropical northern and north-western Australia (monsoonal Western Australia, Northern Territory, and Queensland) found in parrots[84] and birds on the global scale[28]. However, there seems to be limited consistency across classes. Studies variably report patterns of PD similar (Australian mammals)[85], different (arid-zone lizards and mice in Australia)[21], and even opposite (mammals globally)[86] to what we found in birds, making generalizations across taxa difficult. Further complexity was added by spatially inconsistent patterns of residual FD. The only generalization seemed to be the presence of low residual ecological FD in terms of overall richness and divergence in arid southwestern interior areas, which were also typified by very low SR and low residual PD. Overall, the only consistent patterns across all dimensions of diversity seemed to be high SR, residual PD, and some aspects of residual FD in coastal and mesic areas as compared to west-central parts of the arid zone. This seems to be in agreement with the notion of environmental harshness directly limiting the number of lineages that adapt and diversify in challenging conditions[37,43,48] or with the idea of vegetation structure indirectly driving the number of niches and the amount of energy available[5,6]. We tested both these hypotheses explicitly using path analyses.

When studying the direct and indirect effects of climate on diversity, we included precipitation, which has been demonstrated to be a major driver of biome and vegetation dynamics[66]; SR[40,87]; and clade diversification in Australia (reviewed in[37,38]). Accordingly, we observed positive direct effects of water availability on SR (Fig. 1b), in agreement with previous studies[3]. This effect might have been mediated by the physiological tolerance of species[4], whereby relatively few species/clades were probably able to invade challenging arid areas, which requires multiple adaptations concerning temperature regulation and water economy[88–90]. Accordingly, evidence indicates that physiological tolerance can at least partly determine species distributions[91–93]. On the other hand, direct effects of water availability on SR are more likely for plants and ectothermic animals, while endotherms such as birds are metabolically more resilient and thus likely to be affected only by rather extreme climatic events[94]. Consequently, an alternative factor might have been the shorter amount of time available for diversification, as the arid zone is comparatively young (15–20 My)[39]; in contrast, more humid, forested habitats were available for a comparatively long time in Australia (at least 55 My, probably even 80 My)[41,42], and niche conservatism[95] might have slowed-down the invasion of the arid zone[96]. A role for available time in driving patterns of diversity in Australian birds is supported by our observation of higher residual PD in areas of high SR (Fig. 3), suggesting the accumulation and retention of lineages in climatically stable and highly productive areas that were colonized early[97]. However, these historical effects can be robustly estimated only by using high-quality, dated molecular phylogenies to estimate the timing of the invasion of the arid zone by clades and to map their climatic niche on phylogenies[37,38], which is yet to be done for the majority of Australian birds[43], and indeed other clades.

We also identified an indirect effect of climate on diversity – specifically, species richness increasing with the increasing complexity of both horizontal (habitat diversity) and vertical (canopy height) vegetation structure, probably due to complex habitats providing more ecological niches and resources. These results confirm previous studies showing increasing SR with increasing habitat diversity[10,11]. We also confirmed the classical expectation that SR increases with increasingly rich vertical vegetation structure[7], of which canopy height is a good index (see Methods). This relationship was repeatedly observed on local scales[8,98–100], although the methodologies of some of these studies have been challenged[101]. These studies were recently extended to continental and global scales, using canopy height as a surrogate of vertical vegetation complexity. So far, results are mixed, with the SR of primates[9] and amphibians increasing with canopy height[102], which is not true in birds and mammals[102]. However, the relationships of SR to canopy height varied across continents[102], suggesting that either the effects of vertical vegetation complexity differ regionally, or that canopy height and vertical complexity correlate only on limited spatial scales – for example, within floristically similar regions. These alternatives remain to be tested.

The east coast of Australia (eastern Queensland, New South Wales, and Victoria) is covered with forests and woodlands and benefits from relatively high rainfall, productivity, and resource availability compared to the arid zone[37,38]. All these conditions are conducive to high SR, confirmed by our path analyses, whereby moist climates both directly and indirectly facilitated high SR in birds. Approximately the same regions were also typified by phylogenetically diverse assemblages. However, perhaps surprisingly, residual PD was not predicted well by habitats or water availability, and we suspect that historical factors may be more important in explaining residual PD. The reason is that forests have been available in eastern Australia since at least the early Paleogene ca. 55 Mya[39], while the arid zone is comparatively younger, arising in the last 15–20 My[37–39]. Accordingly, lineages in climatically stable environments had time to accumulate diversity and retain old lineages[32,103,104]. Conversely, the drying of the environment might have raised extinction rates, purging SR and PD[105]. Additionally, substantial immigration, origination, and the maintenance of new avian lineages in the new arid habitats could have been inhibited by low productivity and thus low energy availability[106] or priority effects[107]. However, a limited number of lineages have succeeded even in this challenging environment[37,88].

These ecological and evolutionary processes are exemplified for instance by Australian honeyeaters (Meliphagidae) and lizards. Honeyeaters originated in wet forests ca 25 Mya[46,47], enabling the accumulation of SR, and only five lineages subsequently became endemic for new arid environments, this leading to low PD[43,48]. However, these lineages display disproportionately high FD that at least partly offsets the decline in diversity towards arid areas[29]. Similarly, reptiles including lizards are more diverse in moist coastal areas[87], where many lineages accumulated and diversified; in contrast only a few taxa of arid-adapted lizards (with low PD) diversified and thrived in the new arid zone[108–110]. At the same time, these arid-adapted lizards are exceptionally functionally diverse, which at least partially compensates their limited lineage diversity, and this high functional diversity might have been enabled by a historically contingent lack of functionally equivalent competitors from other animal groups[44,45]. We observed similar effects on the scale of whole Australian avifauna, with the exception of higher residual FD in arid areas.

In summary, in this study we tested both direct and indirect effects of climate (water availability) on bird diversity in Australia and Tasmania. Both direct and indirect effects were significant for SR, as it was well predicted by water availability, habitat diversity, and canopy height. However, residual PD was not related to either climate or habitat; instead, it was probably related to the age of the biome, although this hypothesis remains to be rigorously tested. Analyses of residual FD did not add any further insights beyond the effects captured by SR.

Future studies should find at least six lines of research fruitful. First, improved dated molecular phylogenies will help to robustly estimate historical effects on phylogenetic diversity and the timing of the invasion and accumulation of lineages in the arid zone[37]. Second, simulations should be useful in identifying equilibrium (niches, energy) vs. non-equilibrium (time, diversification rate) drivers of diversity across the aridity gradient in Australia[30]. Third, the investigation of other climatic features, e.g. temperature or seasonality, could shed additional light on their role in shaping diversity. Fourth, although the effects of topographic heterogeneity in our study were negligible, more detailed investigation of altitude, topographic heterogeneity, and related climatic gradients is warranted. Fifth, given the several relationships of residual ecological FD to canopy height and water availability that approached statistical significance in this study, detailed investigation of functional diversity, preferably using more detailed traits and local communities, should prove useful in identifying further ecological and evolutionary processes driving diversity in Australia. Sixth, explicitly evolutionary analyses modelling trait evolution should reveal the potential interplay between species coexistence and trait evolution, especially on local scales where effects of species interactions are expected to be strong.

Data Availability

All primary data sufficient to replicate this study are included in this published article (and its Supplementary Information files).

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Author Contributions

V.R. and L.H. designed the study; L.H. performed research and data analyses with input from V.R., V.R. wrote the manuscript and L.H. contributed to the writing. Both authors gave final approval for publication.

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Supplementary information for:

Disentangling direct and indirect effects of water availability, vegetation, and topography on avian diversity

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Appendix S1. Supplementary figures.

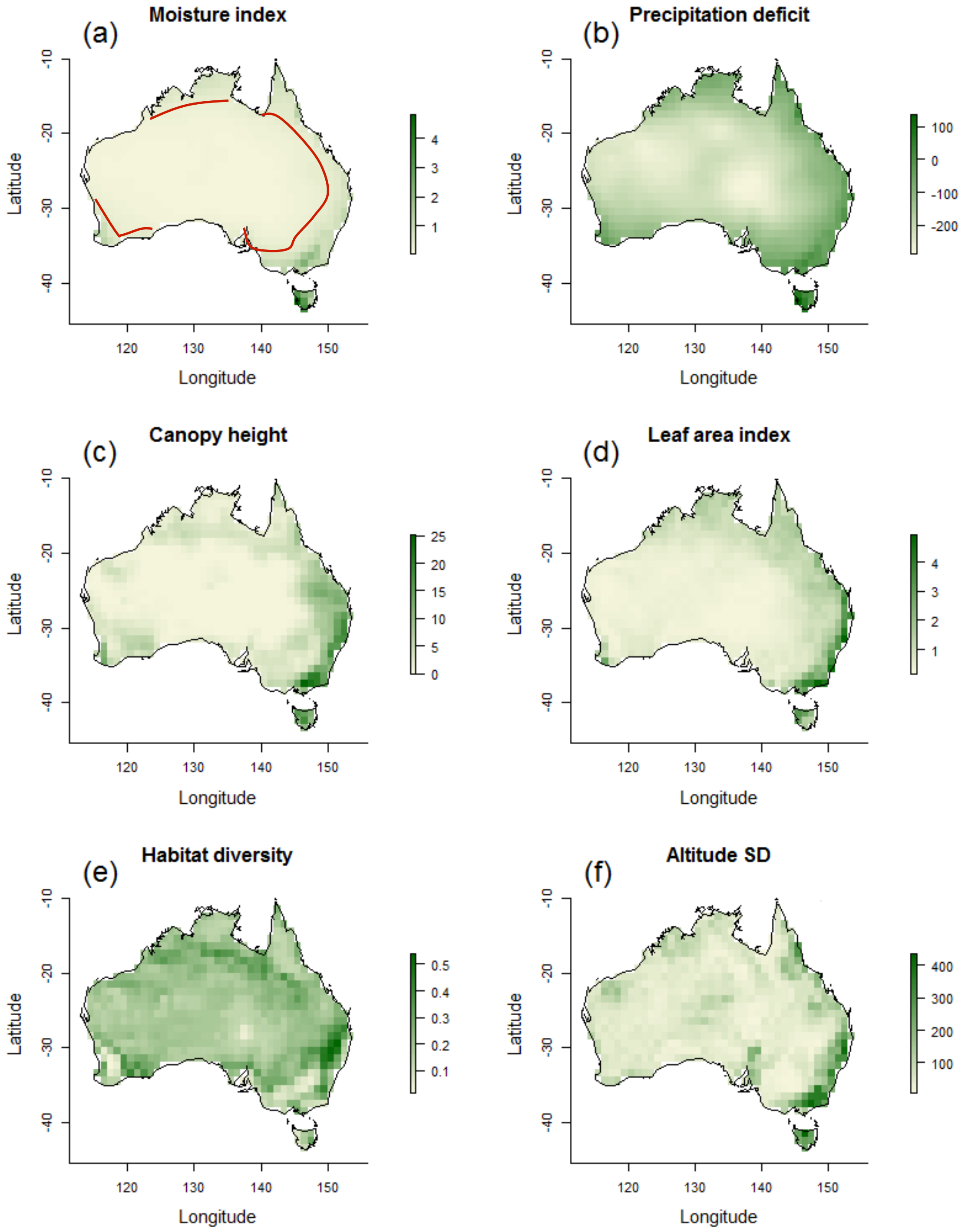

Figure S1. Spatial variation in climatic and environmental variables: Moisture index (a), Precipitation deficit (b), Canopy height (c), Leaf area index (d), Habitat diversity (Levins' index) (e), and Altitude Standard Deviation (f). Red line in (a) represents boundary between arid (values <0.4) and mesic areas.

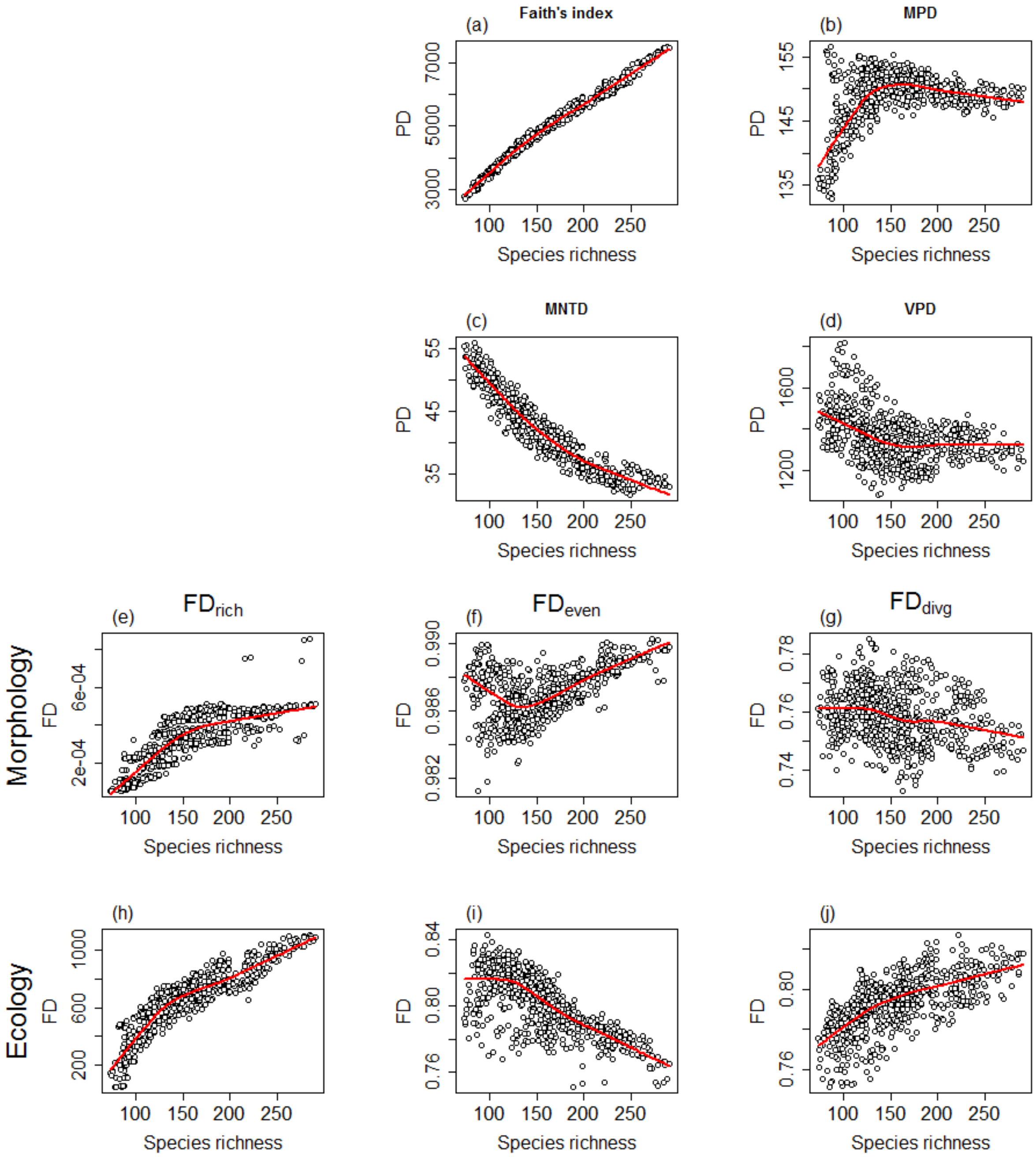

Figure S2. Correlations between species richness and raw phylogenetic and functional diversity indices. These indices were **not** adjusted for species richness by using null models. First two rows show correlations with phylogenetic indices: Faith's index (a), MPD (b), MNTD (c), and VPD (d). Remaining rows represent individual sets of traits: Morphology (e-g) and Ecology (h-j); while columns show functional indices: richness (FD_{rich}; e, h), evenness (FD_{even}; f, i), and divergence (FD_{divg}; g, j).

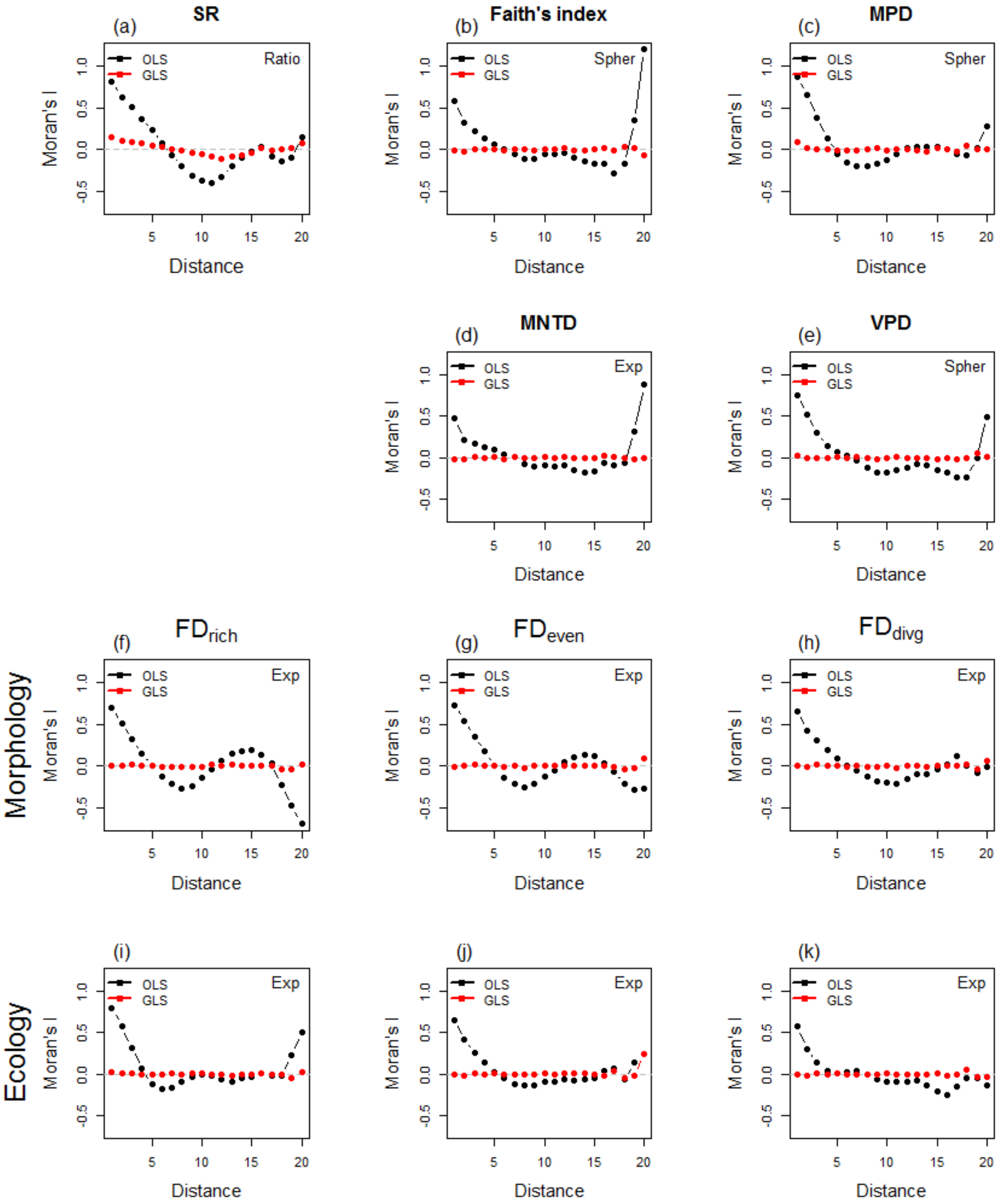

Figure S3. Spatial autocorrelation of residuals of ordinary least-squares (OLS; black) and generalized least-squares (GLS; red) regressions. As an exemplary model we show *SR/PD/FD index ~ Aridity + Altitude SD + Hab. Div. + Canopy height*. For more details on the variables see the main text. Residuals of the SR model are shown in (a), PD models in (b-e), and FD models in (f-k). Abbreviations in top right corner of each panel indicate the spatial correlation structure used in the particular GLS model: exponential (Exp), rational quadratic (Ratio), and spherical (Spher).

Appendix S2. Sensitivity of results to null models

Here we use null models adjusting for SR only for indices that correlate with species richness by definition and were shown to do so by simulations (PD: Faith's index and MNTD [70]; FD: FD richness [75,76]). Other indices were shown by simulation to be largely independent of species richness (PD: MPD [70]; FD: FD evenness and FD divergence [75,76]) or are expected not to be correlated (VPD [71]), and for these indices we use raw values unadjusted for SR in the following analyses. However, please note that this concerns only correlations of mean values of indices, not their variances, because the variance of some indices correlates with SR independent of mean index value (e.g. MPD where variance typically decreases with SR, see Fig. 6.2. in [25] and our Fig. S2b), and thus some bias in analyses might remain even in these latter indices.

To summarize, following indices were adjusted for SR using null models: Faith'sindex, MNTD, and FD richness, whereas following indices were not: MPD, VPD, FD evenness and FD divergence.

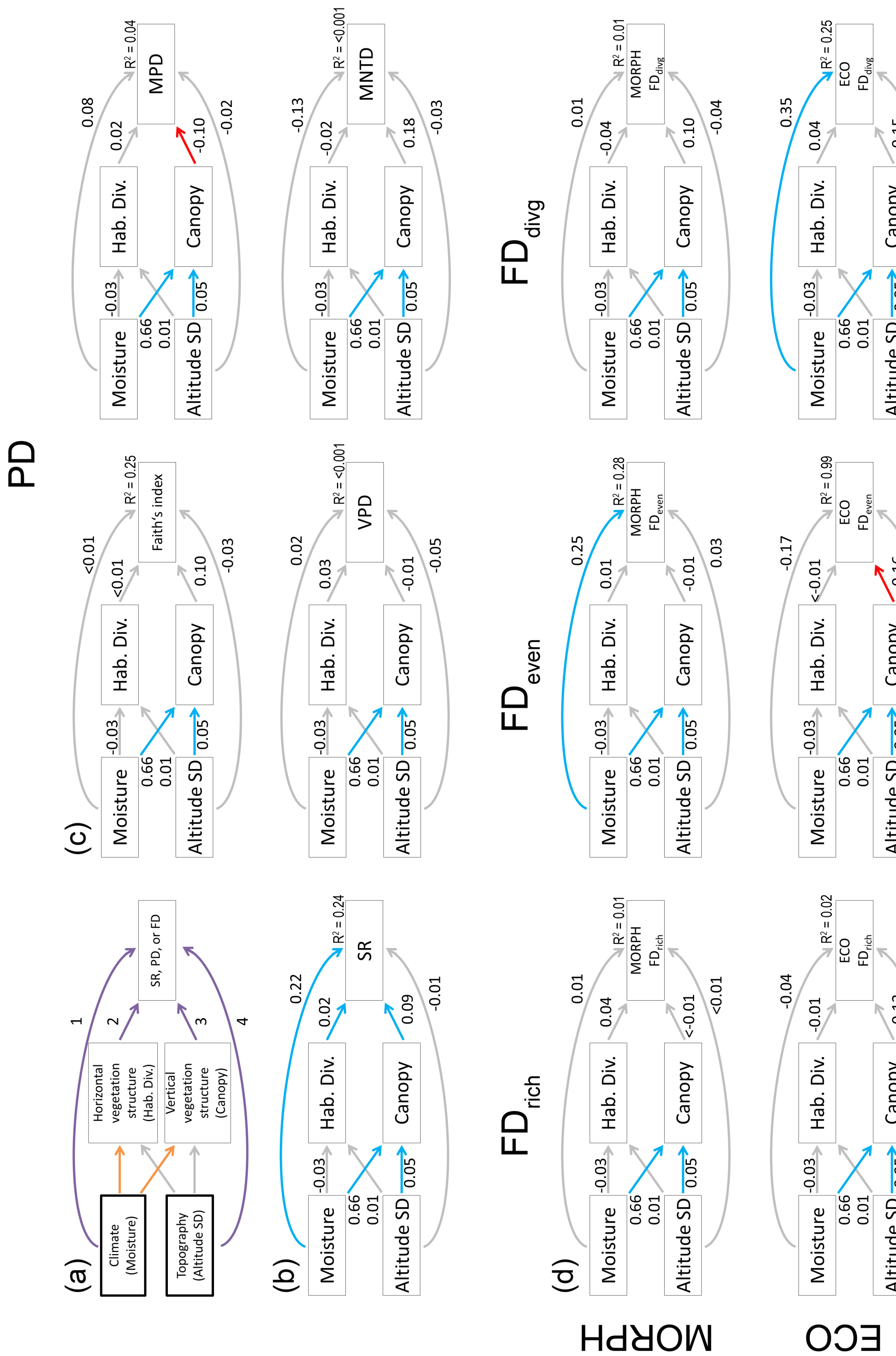
(a)
Climate (Moisture)
Topography (Altitude SD)
Horizontal vegetation structure (Hab. Div.)
Vertical vegetation structure (Canopy)
SR, PD, or FD
1
2
3
4
(b)
Moisture
Altitude SD
Hab. Div.
Canopy
SR
R² = 0.24
-0.03
0.66
0.01
0.05
0.02
0.09
0.22
-0.01
PD
(c)
Faith's index
R² = 0.25
<0.01
<0.01
0.10
-0.03
VPD
R² = <0.001
0.02
0.03
-0.01
-0.05
MPD
R² = 0.04
0.08
0.02
-0.10
-0.02
MNTD
R² = <0.001
-0.13
-0.02
0.18
-0.03
(d)
MORPH
ECO
FDrich
MORPH FDrich
R² = 0.01
0.01
0.04
<-0.01
<0.01
ECO FDrich
R² = 0.02
-0.04
-0.01
0.12
-0.01
FDeven
MORPH FDeven
R² = 0.28
0.25
0.01
-0.01
0.03
ECO FDeven
R² = 0.99
-0.17
<-0.01
-0.16
-0.02
FDdivg
MORPH FDdivg
R² = 0.01
0.01
-0.04
0.10
-0.04
ECO FDdivg
R² = 0.25
0.35
0.04
-0.15
-0.03

Figure S4. Results of path analyses. (a) Conceptual framework to quantify direct and indirect effects of climate (moisture index) on species richness (SR), phylogenetic (PD) and functional diversity (FD). Climate can affect diversity either directly due to species physiological tolerance (1: physiological tolerance hypothesis [4]) or indirectly by facilitating richer vegetation, which in turn provides more niches [5,6]. More niches can be brought about by higher horizontal vegetation diversity (2: habitat diversity [11]) and/or higher vertical vegetation diversity (3: canopy height [7,8]). We also include a direct effect of a major source of abiotic heterogeneity (4: topographic heterogeneity defined as SD of Altitude [13]). Abiotic factors are in bold frame. Colour codes are as follows: Magenta = direct effects of variables od diversity; Orange = direct effects of climate on vegetation structure; Grey = other logical links between variables. For details see main text. (b-d) Results of path analyses for SR (b), PD (c), and FD (d). Blue arrows are statistically significant positive effects, red arrows are significant negative effects, and grey arrows are nonsignificant effects. Numbers along paths are standardized effect sizes for individual paths. Numbers above response variables are pseudo-Rsq values, which were the same for Hab. Div. (<0.01) and Canopy (0.37) in all path models and thus are not depicted in the figure.

Appendix S3. Notes on methodological choices.

In our analyses we considered all bird species with current breeding range in Australia. However, that involves also species introduced into Australia quite recently, such as Eurasian blackbird (*Turdus merula*), Eurasian skylark (*Alauda arvensis*) or Scaly-breasted Munia (*Lonchura punctulata*). Previous studies of the effects of introduced species on PD and FD estimates provide mixed evidence. For example, some authors found that PD was indeed sensitive to non-native species, but those were distantly related to original mammal biota [112]. The presence of such species caused great increases in PD. On the other hand, other authors reported that introduced species of plants had actually negative effects on PD [113]. The effect of alien species on calculation of PD and FD indices might thus differ between regions and taxa. We believe that inclusion of recently introduced species did not bias our results from two reasons. First, Australian avifauna consists of over five hundred species; the lowest number of species in an assemblage in our study was 73 and the highest 291. These are considerable numbers compared to twelve introduced species used in our study, especially considering that median number of recently introduced species in one assemblage was three species. Second, most of recently introduced species have close relatives among native Australian birds (e.g. thrushes, larks, estrildid finches) and therefore it is questionable whether their presence in an assemblage should considerably affect calculations of PD and FD values.

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Appendix S4.

Table S1. Statistical results of path analyses. Standardized effects of predictor variables on Habitat diversity, Canopy height, SR, PD, and FD indices. Pseudo-R2 represents marginal coefficients of determination. Since the results of analyses with Habitat diversity and Canopy height as response variables are the same in each path analysis, we show them only once.

	Response	Predictor	Estimate ± SE	P	Pseudo-R^2
	Hab. Div.	log Moisture	-0.03 ± 0.11	0.80	<0.001
		log Altitude SD	0.01 ± 0.05	0.84	
	sqrt Canopy	log Moisture	0.66 ± 0.06	<0.001	0.37
		log Altitude SD	0.05 ± 0.01	<0.001	
SR	log SR	log Moisture	0.22 ± 0.04	<0.001	0.24
		log Altitude SD	-0.01 ± 0.01	0.30	
		Hab. Div.	0.02 ± 0.01	<0.001	
		sqrt Canopy	0.09 ± 0.03	<0.001	
PD	Faith's index	log Moisture	<0.01 ± 0.17	0.98	0.25
		log Altitude SD	-0.03 ± 0.04	0.41	
		Hab. Div.	<0.01 ± 0.03	0.99	
		sqrt Canopy	0.10 ± 0.08	0.24	
	MPD	log Moisture	0.08 ± 0.09	0.36	<0.001
		log Altitude SD	-0.01 ± 0.02	0.64	
		Hab. Div.	0.03 ± 0.02	0.06	
		sqrt Canopy	-0.08 ± 0.04	0.05	
	MNTD	log Moisture	-0.13 ± 0.16	0.43	<0.001
		log Altitude SD	-0.03 ± 0.05	0.55	
		Hab. Div.	-0.02 ± 0.04	0.58	
		sqrt Canopy	0.18 ± 0.10	0.06	
	VPD	log Moisture	0.02 ± 0.11	0.88	<0.001
		log Altitude SD	-0.05 ± 0.02	0.05	
		Hab. Div.	0.03 ± 0.02	0.09	
		sqrt Canopy	-0.01 ± 0.05	0.87	

		Response	Predictor	Estimate ± SE	P	Pseudo-R^2
FD	Morphology	FD_{rich}	log Moisture	0.01 ± 0.13	0.96	0.01
			log Altitude SD	<0.01 ± 0.04	0.96	
			Hab. Div.	0.04 ± 0.03	0.20	
			sqrt Canopy	<-0.01 ± 0.08	0.98	
		FD_{even}	log Moisture	0.09 ± 0.12	0.47	0.05
			log Altitude SD	<0.01 ± 0.04	0.80	
			Hab. Div.	-0.03 ± 0.03	0.26	
			sqrt Canopy	-0.06 ± 0.08	0.45	
		FD_{divg}	log Moisture	-0.04 ± 0.13	0.77	<0.001
			log Altitude SD	-0.07 ± 0.04	0.06	
			Hab. Div.	-0.06 ± 0.03	0.05	
			sqrt Canopy	0.12 ± 0.08	0.11	
	Ecology	FD_{rich}	log Moisture	-0.04 ± 0.12	0.75	0.02
			log Altitude SD	-0.01 ± 0.03	0.79	
			Hab. Div.	-0.01 ± 0.02	0.60	
			sqrt Canopy	0.12 ± 0.06	0.09	
		FD_{even}	log Moisture	-0.23 ± 0.14	0.10	0.38
			log Altitude SD	<0.01 ± 0.03	0.91	
			Hab. Div.	0.02 ± 0.03	0.41	
			sqrt Canopy	-0.14 ± 0.07	0.06	
		FD_{divg}	log Moisture	0.28 ± 0.15	0.06	0.14
			log Altitude SD	-0.09 ± 0.04	0.03	
			Hab. Div.	0.01 ± 0.03	0.82	
			sqrt Canopy	-0.15 ± 0.09	0.08	

Chapter IV

Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds

Phylidonyris novaehollandiae

Harmáčková L., *Remešová E. & Remeš V.*
(in review)

New Holland Honeyeaters (*Phylidonyris novaehollandiae*) represent highly a specialized species that feeds mainly on nectar obtained from flowers.

Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds

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Abstract

Ecological specialization enables the partitioning of resources and thus can facilitate the coexistence of species and promote higher species richness. Specialization and niche partitioning are expected to exert a decisive influence on local spatial scales, while species richness at regional scales should be shaped mostly by historical factors and abiotic conditions. Moreover, specialization is expected to be particularly important in communities that are exceptionally species rich for their environmental conditions. At the same time, niche overlap in these communities should be minimized to enable species coexistence. We tested these hypotheses by studying specialization-richness relationship and niche overlap in assemblages of 298 species of songbirds (Passeriformes) across Australia. We improved on previous studies by studying scales from truly local (2-6 ha) to regional (bioregions), and by using detailed data on habitats, diet, and especially foraging behaviour (method, substrate, and stratum), which might be particularly important in fine niche partitioning. We expected the richness-specialization relationship to be particularly strong on local spatial scales and in communities exceptionally species rich for given environmental conditions (approximated by moisture and vegetation complexity). We also expected low niche overlap in assemblages with specialized species. While the specialization and species richness were often positively related, the strength (and even the direction) of the relationship changed between traits and across spatial scales. Moreover, the strength of specialization-richness relationship was actually as strong, or even stronger, on regional scales as on local scales. On the other hand, we found the expected negative relationship between specialization and overlap in foraging stratum and substrate (in local communities), suggesting that species partition ecological space in terms of where they find food. Overall, our results suggest that ecological processes related to obtaining resources (foraging behaviour) are important in structuring avian communities across spatial scales.

Key words

Australia, Passeriformes, spatial scales, niche partitioning, community assembly, null models

Introduction

Niche partitioning is presumed to play a prominent role in shaping species richness by facilitating species coexistence. The assumption is that narrow specialization enables finer partitioning of resources and thus enhances local coexistence of species and allows higher species richness (Hutchinson, 1959; MacArthur, 1972; Eeley & Foley, 1999; Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008; Pigot, Trisos, & Tobias, 2016). Specialists (i.e. species with narrow niches) use only restricted range of available resources, while generalists can utilize many resources available in their environment (Futuyma & Moreno, 1988). Ecological specialization (or niche breadth) received much attention in attempts to explain patterns in species richness, but the evidence for its role in shaping spatial patterns in species richness is mixed (Belmaker, Sekercioglu, & Jetz, 2012;

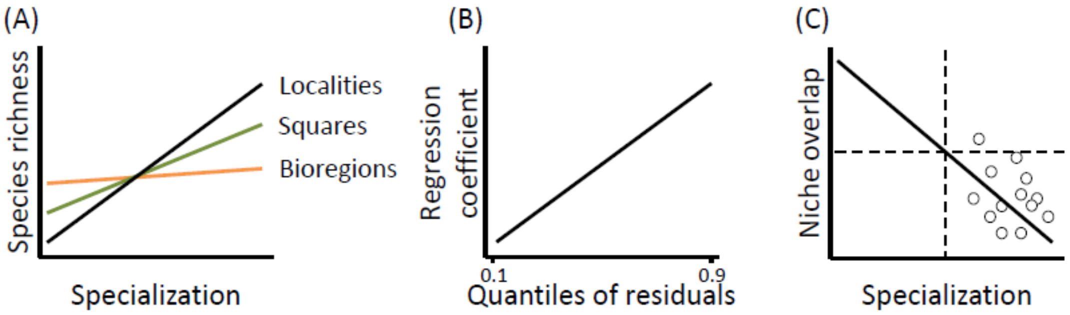

Figure 1. Graphical presentation of the tested hypotheses. (A) We expect an increasing strength of species richness-specialization relationship towards small spatial scales, provided niche partitioning drives species coexistence. (B) We expect a particularly strong species richness-specialization relationship (i.e., high regression coefficient) in assemblages exceptionally rich for given environmental conditions (i.e., those in high quantiles of residuals from a richness-environment regression), while weak richness-specialization relationship is possible in assemblages exceptionally depauperate in species for the given environment (i.e., those in low quantiles of residuals from a richness-environment regression). (C) To partition resources and avoid competition, specialization and niche overlap should be negatively correlated and assemblages should be concentrated in the lower right quadrant (highly specialized species which do not overlap in their resource use).

Pigot, Trisos, & Tobias, 2016). The reason might be that many studies focused on only one or a few coarse traits as a measure of ecological specialization (mostly habitat utilization and diet preferences; e.g. Brändle, Prinzing, Pfeifer, & Brandl, 2002; Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006; Belmaker, Sekercioglu, & Jetz, 2012; Reif, Hořák, Krištín, Kopsová, & Devictor, 2016), yet niche partitioning might take place on finer ecological scales, such as foraging behaviour (substrate or methods used for obtaining food). A classic example represents mixed flocks of titmice (family Paridae), where individual species differ in their foraging sites with larger-bodied species foraging on the inner parts of trees while smaller species using mostly outer branches (Lack, 1971; Suhonen, Alatalo, & Gustafsson, 1994; Jablonski & Lee, 1998). Therefore, even though they share habitat and diet preferences, the interspecific competition is relaxed via the division of foraging space, which thus facilitates species coexistence. However, we mostly lack information on fine niche partitioning in local assemblages (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006; Belmaker & Jetz 2011) and its relationship to species richness studied on a large sample of species.

While niche partitioning is assumed to be most important on fine spatial scales shaping local coexistence of species, the role of abiotic conditions and historical effects should be more prominent on coarser regional scales and thus shaping spatial variation in species richness (Whittaker, Willis, & Field, 2001; Hawkins et al., 2003; Ricklefs, 2006; Belmaker & Jetz 2011; Devictor et al., 2010; Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Royan et al., 2016; Fergnani & Ruggiero, 2017). However, most studies fail to work across several spatial scales and thus fail to identify relative roles of niche partitioning, abiotic conditions, and historical effects on different scales (Ricklefs, 2004; Belmaker, Sekercioglu, & Jetz, 2012). Yet, working across spatial scales is critical, because specialization can operate together with environmental productivity in shaping patterns in species richness at different spatial scales (Belmaker, Sekercioglu, & Jetz, 2012; Pellissier, Barnagaud, Kissling, Sekercioglu, & Svenning, 2018). Thus, specialization should be studied together with, and in relation to, resource availability at several spatial scales simultaneously (Futuyma & Moreno, 1988; Belmaker, Sekercioglu, & Jetz, 2012).

Although there is considerable evidence for positive relationships of species richness to various environmental factors (e.g. vegetation heterogeneity) and productivity (Hurlbert, 2004; Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Pellissier, Barnagaud, Kissling, Sekercioglu, & Svenning, 2018), environmental factors themselves do not explain how the assemblages originate and species coexist. Two scenarios were put forward for highly productive environments (defined e.g. by high vegetation heterogeneity or high net primary productivity) harbouring exceptionally species rich assemblages. First, one can expect a strong richness-specialization relationship due to the partitioning of niche and the division of ecological space in these highly productive assemblages (Evans, Jackson, Greenwood, & Gaston, 2006; Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008; Pellissier, Barnagaud, Kissling, Sekercioglu, & Svenning, 2018). Second, alternatively, high amount of resources could release species from interspecific competition and thus enable low specialization and/or high niche overlap (MacArthur, 1965; Evans, Jackson, Greenwood, & Gaston, 2006; Pigot, Trisos, & Tobias, 2016). A way to reconcile these two expectations is to study specialization in relation to species richness while taking into account environmental productivity (Belmaker, Sekercioglu, & Jetz, 2012). Under this approach, high specialization is to be expected in assemblages that are particularly species rich for the productivity of environments in which they live, while low specialization can be permissible in assemblages particularly species poor for the productivity of the environment they inhabit.

In this study, we use comprehensive data on five sets of ecological traits in 298 species of Australian songbirds (Passeriformes) to test the specialization-richness and niche-richness relationships in assemblages across three spatial scales. Unlike the previous studies, in addition to regional scales, we incorporate the local spatial scale of assemblages inhabiting small (2-6 ha) areas with species abundance data obtained by repeated censuses in homogeneous habitats. Furthermore, we not only employ commonly used habitat and diet categories to calculate specialization, but we also use detailed data on foraging (stratum, substrate and method used by birds when foraging), which might play a prominent role in fine-scale niche partitioning. We test the following three predictions. First, if niche partitioning is decisive for species coexistence, we expect to find an increasing strength of richness–specialization relationship from regional to local spatial scales (Fig. 1 A). Second, richness–specialization relationship should remain positive even when controlled for environmental conditions, but species in assemblages that are exceptionally rich relative to the available resources should have higher specialization to be able to coexist locally. Thus, the strength of richness–specialization relationship should be stronger in relatively species rich assemblages (Fig. 1 B). Third, specialization and niche overlap should be negatively correlated, because if the species in an assemblage narrowly specialize on a few resources, they should avoid competition by minimizing resource use overlap (Fig. 1 C).

Materials and Methods

Assemblage data

We considered three spatial scales of assemblages: localities of 2-6 ha area, 1 x 1 degree grid cells (longitude x latitude), and bioregions in Australia including the island of Tasmania. We obtained data for localities from Australian Bird Count (ABC; Clarke, 1999), which originally consisted of 1962 localities and 77 383 censuses. We used several criteria to ensure standardization and comprehensive sampling of species on localities. In terms of standardization, we included only censuses with the duration between 20 and 30 min and localities with the area between 2 and 6 ha and at least 20 censuses. We excluded strongly human-modified, urban and rural habitats. Next, in terms of sampling, we applied rarefaction based on sample coverage (Chao & Jost, 2012) using iNEXT (Hsieh, Ma, & Chao, 2016) and included only localities with at least 90% coverage. We also performed a final check on the quality of ABC data by removing observations of species on an ABC locality if they were found more than 100 km away from a border of their range (obtained from BirdLife International & NatureServe, 2014), ending up with 470 localities with 37 250 censuses (median number of censuses per locality was 56). For grid cells, we first created a grid with 1 x 1 degree resolution (longitude x latitude) across Australia and Tasmania in R software (R Core Development Team, 2018) and left only grid cells in which at least one locality was present (n = 87 grid cells). We used IBRA bioregions from the Department of the Environment (2012) and kept only bioregions in which at least one locality was present (n = 49 bioregions). For grid cells and bioregions, we generated lists of species by overlapping each grid cell and bioregion with breeding ranges of bird species obtained from BirdLife International and NatureServe (2014).

Specialization data

We obtained data on specialization of Australian songbirds from the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB; Higgins, Peter, & Steele, 2001; Higgins, Peter, & Cowling, 2006; Higgins & Peter, 2002). We used five ecological traits to compute the specialization indices, separately for each trait. Each trait was divided into several categories and each category of each trait received a value corresponding to proportional use (percentage) of that category by a given species based on information in HANZAB. The sum of all categories of a given trait for a given species was always 100. The traits and their categories were as follows: habitat (ten categories: rainforest, forest, woodland, shrub, grassland, heats, marshes, marine mangrove, bare ground, and human settlements), diet (eight categories: leaves, fruit, nectar and pollen, seeds, insects, other invertebrates, vertebrates, and carrion), foraging method (nine categories: gleaning, hang-gleaning, snatching, hover-snatching, probing, manipulating, pouncing, flycatching, and flush chasing; see Supplement S1 for details on the definition of these categories), foraging stratum (four categories: ground, shrub, sub-canopy, and canopy), and foraging substrate (eight categories: ground, bark, leaves, buds, fruit, flowers, air, other). Due to distinct foraging strategies of swallows (family Hirundinidae) and woodswallows (genus Artamus), we removed these species from our analyses, leaving the final number of 298 species.

There were a few cases of missing data in our dataset (Stratum: one species, Substrate: two species, Method: 25 species; no missing data in Habitat and Diet). To avoid losing species with missing values, we imputed the missing data following Penone et al. (2014) and using the missForest method (Stekhoven & Bühlmann, 2012), which was proved to be a well-performing method for data imputation (Penone et al., 2014; Shah, Bartlett, Carpenter, Nicholas, & Hemingway, 2014). First, we created a phylogenetic distance matrix for all species using the Bayesian maximum clade credibility tree based on 1000 phylogenies obtained from birdtree.org (Hackett constraint; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and using TreeAnnotator software (BEAST2; Bouckaert et al., 2014). Then we performed a principal coordinate analysis (PCoA) on the distance matrix, extracted first ten eigenvectors, added them to the dataset as information on the phylogenetic relationships between species and computed missing data using the 'missForest' package (Stekhoven & Buehlmann, 2012) in R (10 iterations with 100 decision trees). As the imputed data were not integer numbers, we corrected the imputed values by rounding them to the nearest integer and ensuring that their sum was equal to 100.

We calculated specialization as an inversed standardized Levins' index (modification by Belmaker, Sekercioglu, & Jetz, 2012) for each of five ecological traits for every species (j) as:

$$Levins_j = 1 - \frac{\frac{1}{\sum p_i^2} - 1}{n - 1}$$

where p_i is the proportional use of trait category *i* and *n* is the total number of trait categories (e.g. 10 for habitat). Assemblage values of specialization for localities, grid cells, and bioregions were then calculated as arithmetic means of species' specialization across species present in a given assemblage and, in case of localities, weighted by the species' abundances. The Levins' index calculated in this way ranges from 0 (generalists) to 1 (specialists).

Levins' index does not include information on niche partitioning: assemblages where all the species are specialized on the same trait category and assemblages where species are specialized on several different trait categories both show high specialization, i.e. high assemblage-level values of Levins' index (Fig. S1). However, these two types of assemblages might be expected to experience completely different levels of species competitive interactions. Thus, we also calculated niche overlap index (Pianka, 1973), which measures overlap in trait category use between a pair of species, as:

$$Pianka_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} are proportional uses of trait category *i* by species *j* and *k*, respectively, and n is the total number of trait categories. We then calculated assemblage means (only for localities) as a mean of all pairs of species present in a given assemblage weighted by their abundances. Pianka's index values range between 0 (no overlap in trait category use) and 1 (complete overlap). Thus, this index estimates the potential for local competitive interactions between species in the assemblage. R code for calculation of Levins' and Pianka's indices is available in Supplement S2.

We did not compute a single specialization or niche overlap index to study the overall specialization/overlap based on all traits and their categories considered together. The ecological and behavioural traits we used are not mutually exclusive and might show dependencies, so that species specialized on some categories in one trait can probably be constrained to certain categories in other traits (e.g. species eating nectar cannot forage by snatching or flush-chasing). A potential solution would probably be to score species into all combinations of the categories of all five traits and use this scoring to calculate overall specialization/overlap indices. However, this is not possible with our data due to trait dependencies (see above) and the lack of field data on such fine division of the niche for most of the species (see Supplement S3 for more details). We must thus trade-off the scale of this study with the ecological detail. Consequently, we had to keep our analysis based separately on the five traits, as is always the case in studies based on data from the literature. Moreover, analysing specialisation and overlap trait-by-trait can bring interesting insights not obtainable by the analysis of one multidimensional object. For example, we can quantify relative importance of different traits at different spatial scales. Moreover, to account for a possible scenario where species are generalists in one trait, but partition the niche by specializing in another trait, we fit multivariate models controlling for all traits at once (see below).

Environmental predictors

We used moisture and vegetation structure to account for species richness-environment relationships while studying species richness-specialization/niche overlap relationships. Moisture index was expressed as the annual mean of the monthly ratio of precipitation to potential evaporation in 0.2 x 0.2 degree resolution (The Atlas of Living Australia, 2018). We obtained values for localities as a value of the 0.2 x 0.2 degree cell in which a particular locality was present, and for grid cells and bioregions as means from all 0.2 x 0.2 degree cells present in each grid cell or bioregion. Data on vegetation cover and height were already included in the ABC dataset for localities (29 classes based on a combination of the vegetation cover and height), from which we excluded three rural and urban categories (see above). For grid cells and bioregions, we used vegetation height and structure with 17 classes (TERN, 2018). For consistency we merged classes in both datasets according to the vegetation height and cover into the 11 following classes of vegetation complexity: no trees, shrubs and low open woodland, tall open woodland, shrubs and low woodland, tall woodland, very tall woodland, low open forest, tall open forest, very tall open forest, closed forest, and tall closed forest (see Table S1 for full details on category conversion). In the following analyses we used Vegetation complexity as a continuous variable (values ranging from one to 11 according to the classes). Vegetation data were originally in 30 x 30 metres resolution, so we projected them into 0.1 x 0.1 degree resolution (longitude x latitude) and then obtained values for grid cells and bioregions as a class with the highest occurrence in a given grid cell or bioregion. Maps of the spatial distribution of moisture and vegetation complexity for each spatial scale are available in Fig. S2.

Null models

To distinguish whether observed patterns could have originated by random sampling of species or were a result of non-random ecological processes during the assembly of bird communities, we constructed null models in which we randomized the species list in each assemblage. Species in localities, grid cells, and bioregions were randomly drawn from pools consisting of all species present in localities (n = 238), grid cells (n = 281), and bioregions (n = 286), respectively, weighted by the number of assemblages they were present in (i.e. a species found in most assemblages on a respective spatial scale had a higher chance to be picked than a species occurring in just a few assemblages). We thus explicitly omitted any dispersal constraints on species assembly, but we weighted the membership in species pool by overall species occurrence across all sampling units. This model preserves local species richness and, in case of localities, also species abundances in each assemblage (abundances were assigned randomly to species drawn from the localities pool). The explicit aim of this null model was to model species assembly from our species pool while ignoring species traits. By this process, we obtained communities with realistic species richness, abundance, and occurrence, while randomizing ecological specialization across sampling units. We created 1000 random communities for localities, grid cells, and bioregions and computed mean Levins' and Pianka's indices from these replications of each assemblage.

Statistical analyses

We conducted three sets of analyses to investigate relationships between species richness, specialization, niche overlap, and environmental conditions. First, we fit bivariate spatial generalized least-squares (GLS) regressions of species richness (response variable) vs specialization or niche overlap (explanatory variable) for each spatial scale to explore bivariate correlations between richness and specialization/overlap on different spatial scales. On the scale of localities, we used specialization and niche overlap calculated both without and with species' abundances to preserve consistency across all spatial scales (no abundance data were available for grid cells and bioregions) but also to keep the indices with more detailed information (i.e. species abundance) on assemblage composition on the local level.

Second, we tested how specialization/overlap explains richness while accounting for environmental conditions. We fit multi-predictor spatial GLS models with species richness as a dependent variable and specialization/overlap for all five traits (stratum, substrate, method, habitat, and diet), together with two environmental variables (moisture and vegetation complexity), as predictors. In case of localities and bioregions, we also fit the area (ha in localities, km^2 in bioregions) as an additional predictor. We did not include range size or body size as additional predictors. We accounted for range size in the null models where wide-ranging species had a higher probability to be picked than locally occurring ones. Body mass was suggested to be related to specialization (Pineda-Munoz, Evans, & Alroy, 2016), but evidence is missing (Reif, Hořák, Krištín, Kopsová, & Devictor, 2016). We fit these regressions for all three spatial scales, resulting in six models: specialization and niche overlap (both with and without species' abundances) in localities, and specialization in grid cells and bioregions. We used combinations of all specialization/overlap traits and did not perform any model selection. Thus, we checked for collinearity among our predictors by computing variance inflation factors (VIF) which showed that there was very low collinearity present (min. = 1.04, max. = 2.83, median = 1.30).

We use spatial GSL regression model that take spatial autocorrelation into account because assemblages are not distributed randomly in space and nearby assemblages are usually more similar than the distant ones. We incorporated spatial autocorrelation by fitting a spatial structure using the model with the lowest AIC value. Latitudinal and longitudinal values necessary to fit the spatial structure were obtained as geographical coordinates of the localities, as centres of the cells for the grid cells, and as centroids of the bioregions. Residuals of GLS models were tested for remaining spatial autocorrelation by Moran's I. Pseudo R2 for GLS analyses were computed as Cox and Snell pseudo R2 using the function 'nagelkerke' from the 'rcompanion' R package (Mangiafico, 2016).

In addition to these multi-predictor regression models, we also tested the assumption that richness-specialization relationship should be stronger in assemblages, which are exceptionally species rich relative to prevailing environmental conditions using quantile regression. To do this, we calculated residuals from spatial GLS regressions relating species richness to environmental variables (moisture, vegetation complexity and, in case of localities and bioregions, also area). We then fitted a quantile regression relating these residuals to specialization/overlap (R package 'quantreg'; Koenker, 2018) for each trait at all spatial scales (in case of localities we included species' abundances).

Third, we used bivariate spatial GLS analyses to study the relationships between specialization (explanatory variable) and niche overlap (response variable) and therefore the partitioning of the niche within assemblages on the local scale. We expected to find negative relationships between specialization and niche overlap (Fig. 1). Moreover, to assess independent effects of both specialization and niche overlap on species richness we also fitted multi-predictor spatial GLS models with species richness as a dependent variable and both specialization and niche overlap as predictors on the scale of localities. All analyses on the local scale were performed with indices computed using species' abundances to embody more precise information on niche division.

We also repeated all the spatial GLS analyses with means from the null model randomizations to distinguish whether observed patterns were biologically relevant or random (within the constraints of the algorithm of our null models). We subtracted these estimates from the parameter estimates of the models based on observed data and considered this difference significant if it fell outside the 95% confidence intervals (CI) of the null models. CIs were computed as the null model estimate ± 1.96*SE of the null model estimate.

All variables were tested for the normal distribution, transformed if necessary (detailed transformations are in results tables), and all were scaled so that their mean was zero and the standard deviation was one prior to each analysis. All analyses were performed in R version 3.4.3 (R Core Development Team, 2018).

Results

Mean assemblage specialization showed latitudinal gradient at all spatial scales (Fig. S3), even though variability across assemblages was not very distinct, with most of them being relatively specialized in all ecological traits except for stratum (Fig. S4). In grid cells and bioregions, assemblages in the northern and south-eastern Australia and in Tasmania were noticeably more generalist in most of the traits then the rest of the assemblages. Highest specialization in stratum,

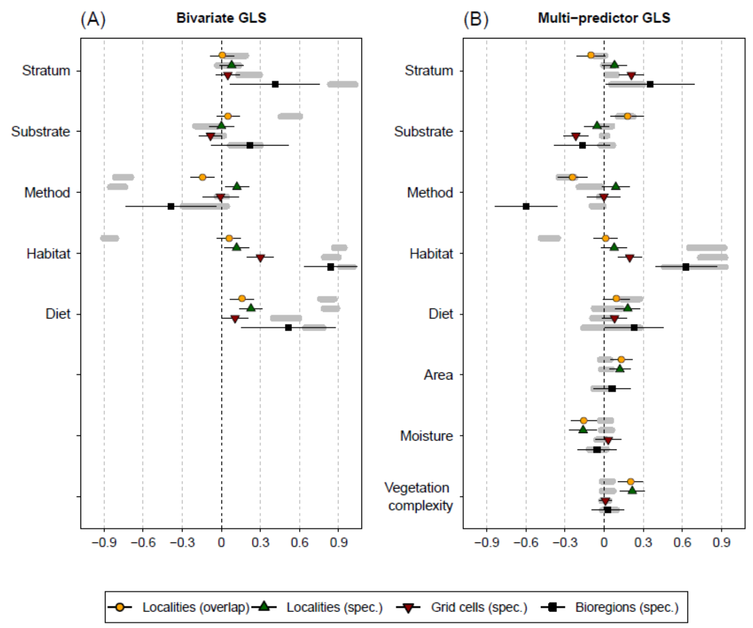

Figure 2. Forest plots of effect sizes with 95% confidence intervals from the relationships between species richness (our response variable) and the predictor variables listed on the left side of both panels. (A) Bivariate spatial generalized least-squares (GLS) analyses between species richness and each predictor fit separately. (B) Multi-predictor GLS analyses between species richness and all predictors fit simultaneously. Results of the local scale are based on indices computed with species' abundances. Colour coding symbolizes different spatial scales. For full results of these analyses see Tables S2 and S3. Grey lines stand for 95% confidence intervals of the null expectations estimated from bivariate and multi-predictor GLS analyses between species richness and the mean from 1000 simulated predictors.

substrate, method, and diet appeared to be mostly located in the south-western Australia and on the eastern coast.

In bivariate analyses, there was a clear positive relationship between species richness and specialization in at least one ecological trait at all spatial scales (Fig. 2, Table S2). Richness increased with increasing specialization for stratum in bioregions, while habitat and diet were positively related to richness at all scales. Foraging method was negatively correlated with richness at scales of localities and bioregions, while foraging substrate showed negative relationship only in localities. However, these relationships at local scales changed when we accounted for species' abundances. While the effect of substrate ceased to be significant, in case of method the relationship was significantly positive (Table S2). The difference between the slopes of the observed and null richness-specialization relationships was positive for foraging substrate and method in localities (both with and without abundances), indicating greater than expected specialization in these two traits. On the other hand, in case of habitat, and diet, the difference between slopes was highly negative at all spatial scales, indicating lower than expected specialization in these traits (Fig. 2, Table S2). Overall, the expectation that the strength of the richness-specialization relationship should increase with decreasing spatial scale was not supported (Fig. 2, Table S2). For example, stratum showed decreasing estimate size towards smaller scales while coefficients of habitat and diet were largest at the scales of both localities and bioregions (Fig. 2, Table S2).

Niche overlap at the finest spatial scale of localities was positively correlated with richness for substrate and diet and negatively for habitat (Fig. 2, Table S2). Diet remained significant even after including species' abundances, but substrate and habitat ceased to be significant and overlap in foraging method was negatively related to richness. Overlap was higher than expected in method and habitat and lower than expected in substrate and diet.

The richness- and overlap-specialization relationships retained similar strength in multi-predictor models which accounted for specialization/overlap in the other ecological traits and for environmental variables. Surprisingly, environmental variables had significant positive (vegetation complexity) or negative (moisture index) effects on species richness, mostly on the finest spatial scale of localities (Fig. 2, Table S3). The expectation that the intensity of the richness-specialization relationship should increase with decreasing spatial scale was not supported even in the multi-predictor spatial GLS analyses (Fig. 2, Table S3).

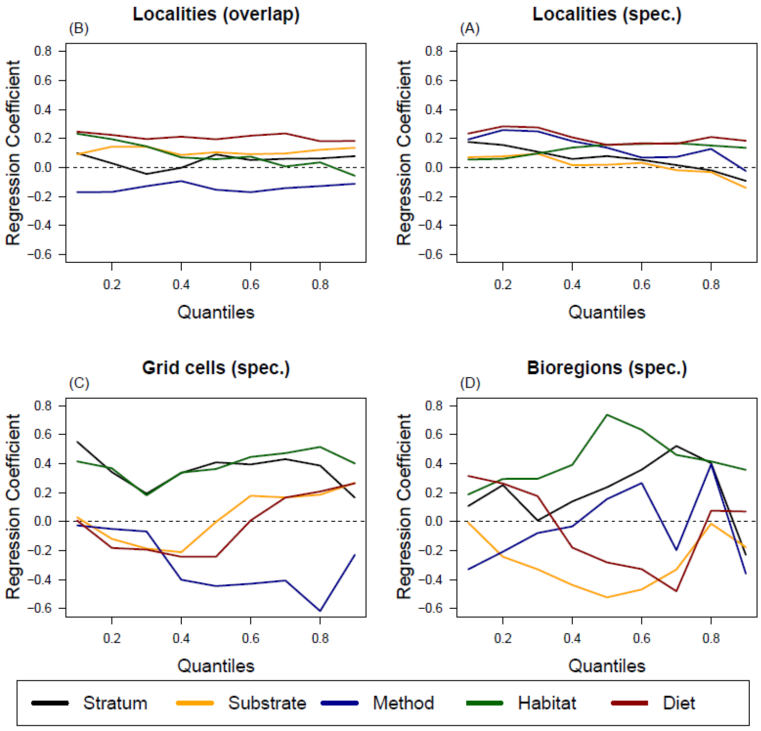

Figure 3. Quantile-specific analyses of the relationships between species richness and specialization or niche overlap (Regression Coefficient on the y axis), divided into quantile cut-offs according to richness-environment residuals. The highest quantiles contain assemblages that are most species rich given their environmental conditions, while the lowest quantile contain assemblages with the least species given the environment. Estimates for localities (specialization, A, and niche overlap, B, computed with species' abundances), grid cells (C), and bioregions (D) are shown separately.

The expectation that the richness-specialization relationship should be steeper in assemblages that are exceptionally species rich for given environmental conditions was not supported by the analyses run separately within quantile cut-offs of the residuals from the regression of species richness on the environmental conditions (Fig. 3, Fig. S5). The positive and negative relationships between specialization and species richness were equally common across our ecological and behavioural traits. Moreover, when positive relationships seemed to prevail (at the scale of grid cells and bioregions), they were equally common across different quantile cut-offs (Fig. 3), i.e. in assemblages both exceptionally species rich and exceptionally depauperate in species for given environmental conditions.

The prediction that specialization and niche overlap should be negatively correlated was supported only in foraging stratum and substrate, which showed the expected strongly negative relationships (Table S4). On the other hand, foraging method, habitat, and diet showed significant positive relationships between specialization and niche overlap, although effect sizes were comparatively smaller than in the negative relationships (Table S4). All traits except for stratum displayed on average high specialization while niche overlap was more variable (Fig. S4). We also expected most assemblages to fall into the lower right quadrant, with high values of specialization and low niche overlap due to niche partitioning. However, this expectation was supported only for foraging substrate (Fig. 4). Assemblages showed both high specialization and high niche overlap in the other three traits (method, habitat, diet), while stratum demonstrated intermediate values of both specialization and overlap with a negative relationship between these two.

In multi-predictor models with both specialization and niche overlap as explanatory variables, specialization was always significantly positively related to species richness except for substrate, while niche overlap was positively related to richness in case of diet and negatively in method (Table S5). These results mirror the bivariate analyses presented above but differ in the effect of stratum specialization on richness, which became significant when controlled for niche overlap. The relationship of species richness to both niche overlap and specialization remained similar after accounting for each other in one model, showing that their relationships with species richness were largely independent of each other.

Discussion

Theory predicts that species in species-rich assemblages should be specialized so that long-term coexistence is facilitated (Hutchinson, 1959; MacArthur, 1972; Eeley & Foley, 1999; Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008; Pigot, Trisos, & Tobias, 2016). Here, we showed that species richness and specialization in Australian songbirds were often positively related, but the relationship changed between individual ecological and behavioural traits and across spatial scales (from local to regional). This was true for both bivariate and multi-predictor models and also when we controlled the analyses for area, available moisture, and vegetation complexity. We expected to find stronger richness-specialization correlations at local spatial scales due to localized species competitive interactions potentially leading to niche partitioning. Surprisingly, our results did not agree with this expectation: richness-specialization relationships were as steep (in terms of positive standardized effects, Fig. 2 and Table S3) and strong (in terms of model R2, Table S3) at regional scales as they were at the local scale. If anything, these effects were most pronounced at the regional scale of bioregions (Fig. 2, Table S3), which is directly opposite to what we expected. This contradicts the idea that richness at the small spatial scales of localities is mainly driven by competition and partitioning of resources (species sorting sensu Leibold & Chase, 2018; Evans, Jackson, Greenwood, & Gaston, 2006; Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008; Pellissier, Barnagaud, Kissling, Sekercioglu, & Svenning, 2018). Therefore, current assemblage structures might not mirror current ecological processes, but might be instead shaped by historical processes (Hawkins, Diniz-Filho, & Soeller, 2005; Remeš & Harmáčková, 2018) that are thought to be more prominent on large spatial scales (Ricklefs, 2006; Ricklefs, 2008), for example faster diversification of clades with specialized species (Belmaker, Sekercioglu, & Jetz, 2012).

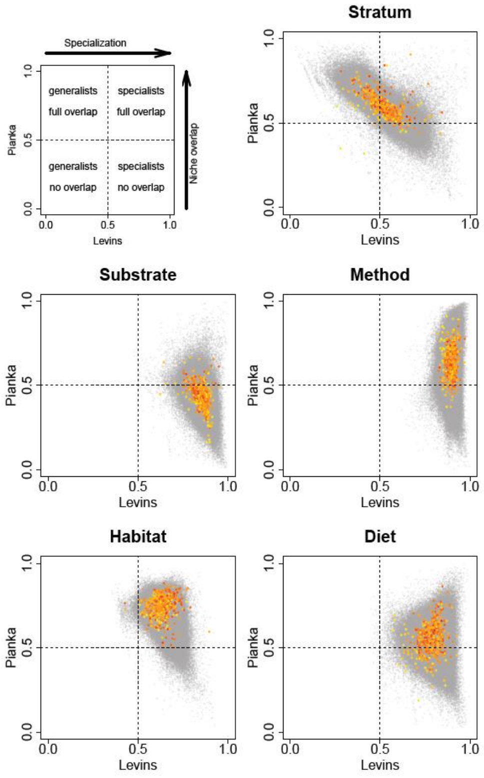

Figure 4. Correlations between Levins' specialization index and Pianka's niche overlap index in local communities (i.e., the scale of localities). The conceptual panel (upper left) shows that if most assemblages contained specialized species with low resource use overlap, they would be concentrated in the lower right quadrant of each panel. Grey points are derived from null model expectations, while coloured points are empirical values for real communities. Their colour represents species richness, ranging from five (yellow) to 71 (red).

We expected the richness-specialization relationship to be particularly steep and strong in assemblages exceptionally rich for the environment that they inhabited. This would show that specialization is particularly important in assemblages with high potential for interspecific competition limiting species coexistence. We accounted for two generally important predictors of species richness and correlates of niche space, namely productivity (via moisture availability) and vegetation complexity (e.g. Hurlbert, 2004; Evans, Jackson, Greenwood, & Gaston, 2006; Remeš & Harmáčková, 2018). Moreover, it is worth stressing that our analyses were weighted by species abundance and thus considered not only species' ecological strategy but also its quantitative importance in structuring the assemblage. However, surprisingly, quantile-based analyses did not support our expectations. In contrast, positive richness-specialization relationships were equally common across different quantile cut-offs, i.e. in assemblages both exceptionally species rich and exceptionally depauperate in species for given environmental conditions. This result again supports the suggestion that species richness is probably not strongly limited by competitive species interactions and partitioning of resources, not even at local spatial scales. Interestingly, strong positive richness-specialization relationships were often found in assemblages that were depauperate in species given the present environment (at least in some ecological traits). This might be caused by the fact that regional avian diversity in Australia is particularly low in arid, low-productive environments (Remeš & Harmáčková, 2018), which might drive species to specialize on scarce resources in these harsh conditions (Wiens, Kozak, & Silva, 2013

We expected the specialization and niche overlap to be negatively correlated across assemblages, because if the species in an assemblage narrowly specialize on a few resources, minimizing resource use overlap might relax competition (see Fig. S1). We found the expected negative relationship only in foraging stratum and substrate, while the rest of the traits showed an unexpected positive relationship (although not so strong; Table S4). The reason for these contrasting results might be that even our detailed trait categories may not still be fine enough to capture actual partitioning of the ecological space. This is apparent especially in habitat and diet, where the categories are quite coarse. For example, several fruit-eating species can coexist in the same place because they differ in the type of fruit they eat, yet in our analyses they represent competing specialists. Unfortunately, information on such a fine division of diet categories is hard to obtain for most of the species. However, we also used fine categories of foraging behaviour to analyse the division of foraging space, which probably plays a prominent role in niche partitioning (MacArthur, 1958; Lack, 1971; Suhonen, Alatalo, & Gustafsson, 1994; Jablonski & Lee, 1998). In this case, results were closer to what we expected. Our assemblages displayed i) the negative relationship between specialization and overlap in foraging stratum and substrate, and ii) the combination of high specialization with low niche overlap in foraging substrate (i.e. the assemblages occupied the lower right quadrant, Fig. 4). Overall, these results suggest that species partition the ecological space in terms of what part of vegetation substrate they forage on, but not in terms of the foraging method they use for obtaining food.

Relationship between species richness and niche overlap was highly inconsistent across traits. We expected to find a negative correlation between niche overlap and species richness, as species in species rich assemblages should have divergent niches to facilitate coexistence. However, this was true only for foraging method and sometimes habitat. This again shows that dividing niche space according to foraging method (see also above) might facilitate species coexistence. On the other hand, we also revealed several positive correlations between overlap and species richness, especially in diet and less so in the foraging substrate. This opposite correlation might be caused by a sampling effect: increasing the number of species in assemblages can lead to higher niche overlap, because there is only a finite number of categories in each ecological trait and thus a limited potential for niche divergence. However, this is probably not the sole explanation, because the effect sizes of these relationships differ significantly from those generated by null models. For example, correlations between overlap and species richness were often positive for diet, but they were almost always smaller than those expected by chance (Tables S2, S3, and S5). Therefore, it appears that even in traits with a positive niche overlap-richness correlation, species sorting processes might have led to lower overlap than expected by chance.

On the local scale, results slightly differed for specialization and niche overlap indices computed with or without species' abundances. The most striking difference was in case of the specialization in foraging method, which showed significantly negative correlation with species richness, yet it changed to positive after accounting for the number of individuals. We included both ways of computing niche overlap indices for the consistency of the analyses carried on various spatial scales as it was not possible to obtain species' abundances for spatial scales of grid cells and bioregions. However, the inclusion of abundances is critical when analysing the composition and evolution of assemblages (Tokeshi & Schmid, 2002). For example, assemblages with the identical number and identity of species might differ in their abundances, which could shift both inter- and intra-specific relationships, the overall biomass of assemblages, and their relation to environment. The analyses carried on local scales that took into account abundances should thus better reflect the actual inter-specific interactions and niche partitioning that potentially take place in local assemblages.

Finally, we conceived our analyses with species richness as a dependent variable and the specialization and niche overlap as explanatory variables. However, this decision was driven by analytical convenience rather than by our intention to imply one-directional causality. Accordingly, we focused on the pattern and strength in richness-specialization and richness-overlap relationships. These relationships can be explained by different mechanisms. For example, high specialization of species can lead to higher packing of species in functional space and thus enable higher richness. However, high specialization of species can also be caused by their need to differentiate niches due to high local/regional species richness that might be e.g. of a historical origin. Similarly, as we point above, specialized clades might generate a large number of species, which might carry-over to local assemblages. Thus, more work is needed to get insight into the drivers and causality of the richness-specialization and richness-overlap relationships, including experiments and theoretical modelling.

Conclusions

Using comprehensive data on habitat, diet, and three foraging characteristics of birds we tested the specialization-richness relationship in Australian songbirds at several spatial scales. We improved on previous studies in four respects, namely by: i) analysing local spatial scales (localities of 2-6 h area) besides the regional ones, ii) using three characteristics of foraging behaviour besides traditionally studied habitats and diets, iii) adding niche overlap index besides the specialization index to better dissect niche partitioning in local assemblages, and iv) using local abundance of species in calculating the specialization and overlap indices. We showed that specialization in Australian songbirds was related to species richness both positively and negatively, depending on the ecological trait under scrutiny, and this was true even after accounting for environmental conditions. At the same time, positive specialization-richness relationships were surprisingly strong at the regional spatial scale. These results do not consistently support the view that inter-specific interactions are decisive for species coexistence and richness. However, on the other hand, species in local communities partitioned ecological space in terms of foraging stratum and substrate, suggesting that coexistence on local scales might actually be facilitated by simultaneous high specialization and low overlap of foraging niches.

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Authors' Contributions

L.H. and V.R. designed the study, E.R. and L.H. collected the data, L.H. performed data analyses with input from V.R., L.H. wrote the manuscript with the contribution of V.R. All authors were acquainted with the final version of the manuscript and gave approval for the publication.

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Specialization and niche overlap across spatial scales: revealing ecological factors shaping species richness and coexistence in Australian songbirds

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Supplementary Material

Supplement S1	Foraging behaviour categories.
Supplement S2	R code for the calculation of the specialization and niche overlap.
Supplement S3	Scoring ecological traits, with consequences for the calculation of ecological specialization.

Table S1	Definitions and conversions of the classes of the vegetation complexity.
Table S2	Results of bivariate analyses of species richness vs specialization or niche overlap.
Table S3	Results of multi-predictor analyses of species richness vs specialization or niche overlap, while controlling for covariates.
Table S4	Results of bivariate analyses of niche overlap vs specialization.
Table S5	Results of multi-predictor analyses of species richness vs specialization and niche overlap.

Figure S1	Conceptual overview of the relationship between Levins' and Pianka's indices.
Figure S2	Spatial distribution of moisture and vegetation complexity.
Figure S3	Geographical distribution of specialization and niche overlap across assemblages.
Figure S4	Distribution of specialization and overlap across species and spatial units.
Figure S5	Full results of the quantile regression analyses of species richness vs specialization or niche overlap.

Supplement S1: Foraging behaviour categories.

We recognized nine types of foraging behaviour that were widely used by previous authors (e.g. Crome 1978, Ford et al. 1986, Franklin 1997, Recher et al. 1985). However, the usage of these behavioural categories was not completely consistent across the authors. Thus, based on previous work, we defined our own categories as follows:

1.	**Gleaning**	Moving on/through the substrate and taking prey from its surface; prey is taken while the bird is on the substrate (e.g. many thornbills, Acanthizidae and honeyeaters, Meliphagidae).
2.	**Hang-gleaning**	Gleaning while the bird is hanging upside-down (e.g. striated thornbill, *Acanthiza lineata* or silvereye, *Zosterops lateralis*).
3.	**Snatching**	Moving on/through the substrate and making short flights to take the prey from nearby spots; prey is taken while the bird is in the air (e.g. rufous whistler, *Pachycephala rufiventris*).
4.	**Hover-snatching**	Snatching while the bird stays in the air for a while when taking the prey (e.g. weebill, *Smicrornis brevirostris*).
5.	**Probing**	Extracting prey from/within thick or deep substrate such as soil, litter or flowers (e.g. flower-feeding honeyeaters).
6.	**Manipulation**	Includes variety of methods such as scratching, digging and tearing to expose the prey (e.g. crested shrike-tit, *Falcunculus frontatus* or Australo-Papuan babblers, Pomatostomidae).
7.	**Pouncing**	Direct flight from a perch to the site where the prey is taken (usually ground), bird lands and takes prey; it may continue flying afterwards (e.g. butcherbirds, Cracticidae or Australasian robins, Petroicidae).
8.	**Flycatching**	Flying from a substrate to take a flying prey, both bird and prey are in the air (e.g. monarch flycatchers, Monarchidae or fantails, Rhipiduridae).
9.	**Flush-chasing**	Rapidly moving on/through substrate, flushing the prey and catching it when it flies off the substrate (e.g. fantails, Rhipidura and some monarchs, Monarchidae).

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Supplement S2: R code for the calculation of specialization and niche overlap.

Levins’ index of specialization:

```
Levins <- function(data, matrix = NULL, community = FALSE, abundance = FALSE) {
      # Function for computation of standardized Levins’ diversity index (Belmaker et al. 2012).
      # A modification for species’ abundance, not only presence/absence data.
      # A modification for specialization of the whole assemblage, not only mean computed from present
        species. The specialization of the whole assemblage sums trait categories of all present species
        and takes their proportion.
      # Sum of trait categories should be the same for all species (e.g. 100 in case of percentage).
      # LH 26.02.2018

      # Input:
      # data = data file where rows = species and columns = categories of one (!) trait, rownames = names
        of species, values = proportion (e.g. in percentage).
      # matrix = community matrix where rows = assemblages and columns = species, values =
        presence/absence (1/0) or abundance. Matrix might be missing if you sought only specialization of
        species and not assemblages. Results for abundance matrix with abundance = FALSE are the same as
        for the presence/absence matrix.
      # community = compute the specialization of the whole assemblage (TRUE), or the mean of
        specialization of species present in the assemblage (FALSE)? Default is FALSE.
      # abundance = to weight specialization by abundance of species (TRUE), or use presence/absence
        (FALSE)? Default is FALSE.

      # Outputs:
      # SR = number of species in an assemblage (species richness).
      # Individuals = number of individuals in assemblages (only when abundance = TRUE).
      # Levins = Levins’ specialization index. Values range from 0 (generalists) to 1 (specialists).

  ##### Species
  # check of input data
if(nrow(data[!complete.cases(data),]) > 0) stop('NAs present in the data file.') # NAs

if(missing(matrix)) { # Species
    d.prop <- data.frame(matrix(ncol = ncol(data), nrow = nrow(data))) # proportion
    for (i in 1:nrow(d.prop)) {d.prop[i, ] <- data[i, ] / rowSums(data[i, ])}
    d.sq <- d.prop^2 # square
    d.ba <- data.frame(Levins = matrix(nrow = nrow(d.sq))) # Levins
    for (i in 1:nrow(d.ba)) {d.ba[i, 1] <- 1 - (1 / sum(d.sq[i, ]) - 1) / (ncol(d.sq) - 1)}
    rownames(d.ba) <- rownames(data)
    invisible(d.ba)
} # Species

##### Assemblages
else { # else Species
# check of input data
    if(nrow(data[!complete.cases(data),]) > 0) stop('NAs present in the data file.') # NAs
    if(nrow(matrix[!complete.cases(matrix),]) > 0) stop('NAs present in the community matrix.') # NAs
    if(nrow(data) != ncol(matrix)) stop('Number of rows in data file does not match number of columns in
    the community matrix.')
    spp <- data.frame(data = rownames(data), matrix = colnames(matrix)) ; spp$F = spp[, 1] == spp[, 2] #
    species order
```

```
if (nrow(spp[spp[, 3] == F, ]) > 0) stop('Order of rownames in data file does not match the order of
colnames in the community matrix, or the names differ.')

matrix.pa <- data.frame(ifelse(matrix == 0, yes = 0, no = 1)) # p/a matrix

### (1) Specialization as a mean of present species
if(community == F) { # 1
    d.prop <- data.frame(matrix(ncol = ncol(data), nrow = nrow(data))) # proportion
    for (i in 1:nrow(d.prop)) {d.prop[i, ] <- data[i, ] / rowSums(data[i, ])}
    d.sq <- d.prop^2 # square
    d.ba <- data.frame(Levins = matrix(nrow = nrow(d.sq))) # Levins
    for (i in 1:nrow(d.ba)) {d.ba[i, 1] <- 1 - (1 / sum(d.sq[i, ]) - 1) / (ncol(d.sq) - 1)}

    pa.sp <- matrix.pa
    for(i in 1:ncol(pa.sp)) {pa.sp[, i] <- ifelse(pa.sp[, i] == 1, yes = d.ba[i, 1], no = NA)}

    # (1a) without abundance
    if (abundance == F) { # 1a
        loc.sp.pa <- data.frame(SR = rowSums(matrix.pa), Levins = rowMeans(pa.sp, na.rm = T)) #
        Levins
        invisible(loc.sp.pa)
    } # 1a
    # (1b) with abundance
    else { # 1b
        loc.sp.ab <- data.frame(SR = rowSums(matrix.pa), Individuals = rowSums(matrix), Levins = NA)
        # empty data frame
        for (i in 1:nrow(loc.sp.ab)) {loc.sp.ab[i, 3] <- weighted.mean(pa.sp[i, ], matrix[i, ], na.rm
        = T)} # Levins
        invisible(loc.sp.ab)
    } # 1b
} # 1

### (2) Specialization of the whole assemblage
else { # 2
    # (2a) without abundance
    if (abundance == F) { # 2a
        locs.pa <- lapply(1:nrow(matrix.pa), function(x) list()) # empty list
        for (i in 1:nrow(matrix.pa)) {
            locs.pa[[i]] <- data[colnames(matrix.pa[i, matrix.pa[i, ] == 1]), ] # for each
            assemblage take data of only the present species
            locs.pa[[i]] <- colSums(locs.pa[[i]])} # sum of categories of all species present in an
            assemblage

        loc <- data.frame(matrix(unlist(locs.pa), nrow = nrow(matrix.pa), byrow = T))
        colnames(loc) <- colnames(data) ; rownames(loc) <- rownames(matrix.pa)

        loc.prop <- loc # proporce
        for (i in 1:nrow(loc.prop)) {loc.prop[i, ] <- loc[i, ] / rowSums(loc[i, ])}
        loc.sq <- loc.prop^2 # square

        loc.com.pa <- data.frame(SR = rowSums(matrix.pa), Levins = NA) # empty data frame
        for (i in 1:nrow(loc.com.pa)) {loc.com.pa[i, 2] <- 1 - (1 / sum(loc.sq[i, ]) - 1) /
        (ncol(loc.sq) - 1)} # Levins
        invisible(loc.com.pa)
```

```
        } # 2a
        # (2b) with abundance
        else { # 2b
            locs.ab <- lapply(1:nrow(matrix), function(x) list()) # list
            for (i in 1:nrow(matrix)) {
                locs.ab[[i]] <- data[colnames(matrix[i, matrix[i, ] > 0]), ] # for each assemblage take
                data of only the present species
                ab <- matrix[i, colnames(matrix[i, matrix[i, ] > 0])] # species abundance for each
                assemblage
                for (j in 1:nrow(locs.ab[[i]])) {locs.ab[[i]][j, ] <- locs.ab[[i]][j, ] * ab[, j]} #
                multiply kategories with abundance
                locs.ab[[i]] <- colSums(locs.ab[[i]]) # sum of all species in every category for each
                locality
            }
            loc <- data.frame(matrix(unlist(locs.ab), nrow = nrow(matrix), byrow = T))
            colnames(loc) <- colnames(data) ; rownames(loc) <- rownames(matrix)

            loc.prop <- loc # proportion
            for (i in 1:nrow(loc.prop)) {loc.prop[i, ] <- loc[i, ] / rowSums(loc[i, ])}
            loc.sq <- loc.prop^2 # square

            loc.com.ab <- data.frame(SR = rowSums(matrix.pa), Individuals = rowSums(matrix), Levins = NA)
            # prazdny data frame
            for (i in 1:nrow(loc.com.ab)) {loc.com.ab[i, 3] <- 1 - (1 / sum(loc.sq[i, ]) - 1) /
            (ncol(loc.sq) - 1)} # Levins
            invisible(loc.com.ab)
        } # 2b
    } # 2
} # else Species
} # Levins

##### Examples:
d <- data.frame(A1 = c(20,20,20,30, 90,100,90,90, 10,100,0,0), A2 = c(20,30,30,30, 10,0,10,5, 0,0,90,5),
A3 = c(30,20,30,20, 0,0,0,5, 0,0,10,90), A4 = c(30,30,20,20, 0,0,0,0, 90,0,0,5), B1 = c(30,30,40,40,
60,10,30,30, 10,50,40,50), B2 = c(30,40,30,20, 10,50,10,20, 70,20,0,0), B3 = c(40,30,30,40, 30,40,60,50,
20,30,60,50)) ; rownames(d) <- c('Sp01','Sp02','Sp03','Sp04', 'Sp05','Sp06','Sp07','Sp08',
'Sp09','Sp10','Sp11','Sp12') # data
rowSums(d[, 1:4]) ; rowSums(d[, 5:7])

m <- data.frame(Sp01 = c(6,0,0), Sp02 = c(10,0,0), Sp03 = c(1,0,0), Sp04 = c(2,0,0), Sp05 = c(0,2,0), Sp06
= c(0,4,0), Sp07 = c(0,12,0), Sp08 = c(0,3,0), Sp09 = c(0,0,1), Sp10 = c(0,0,5), Sp11 = c(0,0,10), Sp12 =
c(0,0,15)) ; rownames(m) <- c('Loc1', 'Loc2', 'Loc3') # community matrix with number of individuals

spp <- Levins(d[, 1:4]) # specialization of species

comm <- data.frame(Levins(d[, 1:4], m)) # assemblage mean (original from Belmaker et al. 2012)
Levins.abund <- Levins(d[, 1:4], m, abundance = T)[, 3] # assemblage mean with abundance
Levins.community <- Levins(d[, 1:4], m, community = T)[, 2] # specialization of assemblages
Levins.community.abund <- Levins(d[, 1:4], m, community = T, abundance = T)[, 3] # specialization of
assemblages with abundance
Levins.B <- Levins(d[, 5:7], m)[, 2] # trait B
```

Pianka’s index of niche overlap:

```
Pianka <- function(data, matrix) {
    # Function for computation of Pianka’s niche overlap (Pianka 1973) for assemblages.
    # Computed as a mean niche overlap of species present in an assemblage.
    # Takes into account the abundance of species.
    # Inputs same as in the Levins’ function.
    # LH 19.03.2018

res <- matrix(nrow = nrow(matrix))
for (i in 1:nrow(matrix)){
    loc <- matrix[i, ] # one community
    loc <- t(loc[, loc > 0]) # species and their abundances in one community transponed into a column
    dat <- data[rownames(loc), ]
    dat <- dat/rowSums(dat) # proportions
    pairwise <- cbind(t(combn(nrow(dat), 2)), 0, 0) # all combinations of species + 2 empty columns for
    abundances and Pianka pairs
    for(j in 1:nrow(pairwise)) pairwise[j, 3] <- loc[pairwise[j, 1], ] * loc[pairwise[j, 2], ]
    for (k in 1:nrow(pairwise)) pairwise[k, 4] <- sum(dat[pairwise[k, 1], ] * dat[pairwise[k, 2],
    ])/sqrt(sum(dat[pairwise[k, 1], ]^2) * sum(dat[pairwise[k, 2], ]^2))
    res[i] <- weighted.mean(pairwise[, 4], pairwise[, 3])
    }
invisible(res)
}

##### Examples:
overlap <- Pianka(d, m)
```

References:

Belmaker J., Sekercioglu C. H. and Jetz W. (2012) Global patterns of specialization and coexistence in bird assemblages. J. Biogeogr. 39: 193-203.

Pianka, E. R. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4: 53-74.

Supplement S3: Scoring ecological traits, with consequences for the calculation of ecological specialization.

(A)

		Method			
		Flycatching	**Gleaning**	**Probing**	**Σ**
Substrate	**Air**	20	0	0	**20**
	Leaf	0	35	5	**40**
	Flower	0	5	35	**40**
	Σ	**20**	**40**	**40**	**100**

(B)

		Method			
		Flycatching	**Gleaning**	**Probing**	**Σ**
Substrate	**Air**	**4**	**8**	**8**	20
	Leaf	**8**	**16**	**16**	40
	Flower	**8**	**16**	**16**	40
	Σ	20	40	40	100

(C)

		Method		
		Flycatching	**Gleaning**	**Probing**
Substrate	**Air**	**-16**	**8**	**8**
	Leaf	**8**	**-19**	**11**
	Flower	**8**	**11**	**-19**

Here we illustrate problems with the calculation of ecological specialization based on traits scored from the literature: In table **A**), we see hypothetical empirical observations in the field, where we obtain directly individual foraging behaviours for individual birds (grey numbers in table **A**), which enables us to calculate ecological specialization directly on these observations (i.e. always a combination of Method and Substrate in the inner table cells). If needed, we can calculate marginal sums for foraging Method and Substrate (black numbers in table **A**). In the literature, foraging Methods and Substrates for each species are given separately, NOT their combinations – as illustrated in table **B**) by grey numbers. We can thus calculate ecological specialization ONLY separately for Method and Substrate. If we used these marginal sums (grey numbers in table **B**) to calculate combinations of Method and Substrate (expected frequencies for inner table cells, black numbers in table **B**), we would get very misleading results (see table **C**, that gives the difference of inner cells between table **B** and table **A**). Obviously, if we based our calculation of ecological specialization on the expected frequencies in the inner cells of table **B**, we would get very misleading estimates. The reason is that birds do not use Methods randomly in relation to Substrates. For example, Flycatching cannot be done on Leaves or Flowers (by definition), Gleaning is used most often on Leaves, while Probing is used most often on Flowers (grey numbers in table **A**). This problem also disallows the calculation of multivariate Functional Richness indices (convex hull and its equivalents), because we do not have empirical trait combinations (grey numbers in table **A**).

Table S1: Definitions of ABC and TERN classes of vegetation height and cover and their conversion to a common scale of vegetation complexity.

(A) Definitions of ABC and TERN classes:

ABC classes				TERN classes			
Code	Name	Height (m)	Cover (%)	Code	Name	Height (m)	Cover (%)
A01	Tall closed forest	>30	70-100	10	No trees	0	0
A02	Closed forest	10-30	70-100	21	Low scattered trees	<9	0-6
A03	Low closed forest	5-10	70-100	22	Medium scattered trees	9-17	0-6
A04	Closed scrub	2-8	70-100	31	Low open woodland	<9	6-11
A05	Closed heathland	0-2	70-100	32	Medium open woodland	9-17	6-11
A06	Closed mossland, fernland, sedgeland	-	70-100	33	Tall open woodland	17-27	6-11
B01	Tall open forest	>30	30-70	41	Low woodland	<9	11-30
B02	Open forest	10-30	30-70	42	Medium woodland	9-17	11-30
B03	Low open forest	5-10	30-70	43	Tall woodland	17-27	11-30
B04	Open scrub	2-8	30-70	44	Very tall woodland	27-57	11-30
B05	Open heath	0-2	30-70	51	Low open forest	<9	30-70
B06	Tussock, grassland, mossland, fernland	-	30-70	52	Medium open forest	9-17	30-70
C01	Tall woodland	>30	10-30	53	Tall open forest	17-27	30-70
C02	Woodland	10-30	10-30	54	Very tall open forest	27-57	30-70
C03	Low woodland	5-10	10-30	55	Extremely tall open forest	>57	30-70
C04	Tall shrubland	2-8	10-30	63	Tall closed forest	17-27	>70
C05	Low shrubland	0-2	10-30	64	Very tall closed forest	27-57	>70
C06	Hummock grassland	<2	10-30				
C07	Open tussock, open grassland, mosses, etc	-	10-30				
D01	Tall open woodland	>30	<10				
D02	Open woodland	10-30	<10				
D03	Low open woodland	5-10	<10				

D04	Tall open shrubland	2-8	<10
D05	Low open shrubland	0-2	<10
D06	Open hummock grassland	0-2	<10
E01	Cleared rural landscape	-	-
E02	Urban parkland	-	-
E03	Urban garden	-	-
F01	Wetland (swamps, ponds, lakes, marshes, reed banks)	-	-

(B) Conversion of ABC and TERN classes to a common scale of vegetation complexity (Value):

Value	Name	Height (m)	Cover (%)	ABC codes	TERN codes
1	No trees	<2	-	A05, A06, B06, C06, C07, D06, F01	10
2	Shrubs and low open woodland	2-10	<10	D03, D04, D05	21, 31
3	Tall open woodland	>10	<10	D01, D02	22, 32, 33
4	Shrubs and low woodland	2-10	10-30	C03, C04, C05	41
5	Tall woodland	10-30	10-30	C02	42, 43
6	Very tall woodland	>30	10-30	C01	44
7	Low open forest	2-10	>30	A04, B03, B04, B05	51
8	Tall open forest	10-30	30-70	B02	52, 53
9	Very tall open forest	>30	30-70	B01	54, 55
10	Closed forest	<30	>70	A02, A03	63
11	Tall closed forest	>30	>70	A01	64

Note: ABC codes E01, E02, and E03 were not used.

Table S2: Results of bivariate spatial GLS analyses of species richness vs specialization or niche overlap. Response variable is always SPECIES RICHNESS.

	Obs.		Null.		Obs. – Null.
	Est. ± SE	t-value	Est. ± SE	t-value	Est.
With species' abundances					
Localities (niche overlap)					
Stratum	0.01 ± 0.04	0.2	0.11 ± 0.04	2.6 *	-0.10 †
Substrate	0.05 ± 0.04	1.2	0.53 ± 0.04	14.5 ***	-0.48 †
Method	-0.14 ± 0.04	-3.3 **	-0.75 ± 0.03	-24.7 ***	0.61 †
Habitat	0.06 ± 0.04	1.4	-0.85 ± 0.02	-35.7 ***	0.92 †
Diet	0.16 ± 0.04	3.6 ***	0.81 ± 0.03	30.6 ***	-0.66 †
Localities (specialization)					
Stratum	0.08 ± 0.04	1.8	0.05 ± 0.04	1.3	0.03
Substrate	0.00 ± 0.05	0.0	-0.11 ± 0.04	-2.6 *	0.11 †
Method	0.12 ± 0.05	2.7 **	-0.80 ± 0.03	-28.3 ***	0.92 †
Habitat	0.12 ± 0.05	2.6 *	0.90 ± 0.02	46.0 ***	-0.79 †
Diet	0.23 ± 0.04	5.3 ***	0.84 ± 0.03	33.0 ***	-0.61 †
Without species' abundances					
Localities (niche overlap)					
Stratum	-0.01 ± 0.05	-0.2	0.41 ± 0.04	10.0 ***	-0.42 †
Substrate	0.13 ± 0.04	3.1 **	0.82 ± 0.03	31.6 ***	-0.69 †
Method	-0.01 ± 0.04	-0.3	-0.93 ± 0.02	-53.0 ***	0.91 †
Habitat	-0.13 ± 0.05	-2.9 **	-0.96 ± 0.01	-77.8 ***	0.83 †
Diet	0.26 ± 0.04	6.1 ***	0.94 ± 0.02	62.1 ***	-0.68 †
Localities (specialization)					
Stratum	-0.04 ± 0.04	-1.0	-0.08 ± 0.04	-1.7	0.03 †
Substrate	-0.13 ± 0.04	-2.9 **	-0.18 ± 0.04	-4.3 ***	0.05 †
Method	-0.14 ± 0.05	-3.1 **	-0.95 ± 0.01	-68.3 ***	0.81 †
Habitat	0.58 ± 0.04	15.2 ***	1.00 ± 0.00	304.7 ***	-0.42 †
Diet	0.46 ± 0.04	11.7 ***	0.98 ± 0.01	107.3 ***	-0.52 †
Cell grids (specialization)					
Stratum^10	0.05 ± 0.04	1.1	0.21 ± 0.04	5.2 ***	-0.16 †
Substrate	-0.08 ± 0.04	-1.9	-0.02 ± 0.02	-1.0	-0.06
Method	-0.01 ± 0.07	-0.1	0.01 ± 0.02	0.3	-0.01
Habitat	0.30 ± 0.05	5.9 ***	0.84 ± 0.03	30.9 ***	-0.54 †
Diet	0.11 ± 0.05	2.2 *	0.50 ± 0.05	10.0 ***	-0.39 †
Bioregions (specialization)					
Stratum	0.41 ± 0.17	2.4 *	0.93 ± 0.05	19.4 ***	-0.52 †
Substrate	0.22 ± 0.15	1.5	0.19 ± 0.06	3.2 **	0.03 †
Method	-0.39 ± 0.17	-2.2 *	-0.13 ± 0.08	-1.5	-0.26
Habitat	0.84 ± 0.10	8.2 ***	0.96 ± 0.02	38.9 ***	-0.12 †
Diet	0.51 ± 0.18	2.9 **	0.71 ± 0.03	21.0 ***	-0.20 †

* Significance: P < 0.05, ** P < 0.01, *** P < 0.001.

† Significance against the null model expectations.

Table S3: Results of multi-predictor GLS analyses of species richness in relation to specialization or niche overlap while accounting for moisture and vegetation complexity (and area in case of localities and bioregions). Response variable is always SPECIES RICHNESS.

	Obs.			Null.			Obs. – Null.	
	Est. ± SE	t-value		Est. ± SE	t-value		Est.	
With species' abundances								
Localities (niche overlap)		Pseudo R^2 = 0.12			Pseudo R^2 = 0.83			
Stratum	-0.10 ± 0.05	-1.9		-0.03 ± 0.02	-1.6		-0.07	
Substrate	0.18 ± 0.06	2.8	**	0.17 ± 0.03	5.8	***	0.01	†
Method	-0.24 ± 0.06	-4.4	***	-0.29 ± 0.03	-9.2	***	0.04	†
Habitat	0.01 ± 0.05	0.3		-0.42 ± 0.03	-13.0	***	0.43	†
Diet	0.09 ± 0.05	1.9		0.20 ± 0.04	5.6	***	-0.11	†
Log10 Area	0.13 ± 0.04	3.2	**	0.01 ± 0.02	0.4		0.12	†
Sqrt Moisture	-0.16 ± 0.05	-3.3	**	0.01 ± 0.02	0.6		-0.17	†
Vegetation complexity	0.20 ± 0.05	4.3	***	0.02 ± 0.02	1.2		0.18	†
Localities (specialization)		Pseudo R^2 = 0.13			Pseudo R^2 = 0.82			
Stratum	0.08 ± 0.05	1.7		0.04 ± 0.02	1.7		0.04	
Substrate	-0.05 ± 0.05	-1.2		0.02 ± 0.02	0.7		-0.07	†
Method	0.09 ± 0.05	1.7		-0.11 ± 0.04	-2.4	*	0.19	†
Habitat	0.08 ± 0.05	1.6		0.79 ± 0.07	11.8	***	-0.71	†
Diet	0.18 ± 0.05	3.9	***	0.03 ± 0.05	0.5		0.15	†
Log10 Area	0.12 ± 0.04	3.0	**	0.02 ± 0.02	0.9		0.10	†
Sqrt Moisture	-0.16 ± 0.05	-3.2	**	0.02 ± 0.02	0.9		-0.18	†
Vegetation complexity	0.22 ± 0.05	4.7	***	0.03 ± 0.02	1.3		0.19	†
Without species' abundances								
Localities (niche overlap)		Pseudo R^2 = 0.17			Pseudo R^2 = 0.97			
Stratum	-0.08 ± 0.05	-1.8		0.03 ± 0.01	3.2	**	-0.11	†
Substrate	0.08 ± 0.05	1.6		0.05 ± 0.02	2.6	**	0.03	
Method	-0.04 ± 0.05	-0.8		-0.28 ± 0.02	-13.3	***	0.24	†
Habitat	-0.21 ± 0.04	-4.7	***	-0.48 ± 0.03	-18.6	***	0.27	†
Diet	0.25 ± 0.05	5.4	***	0.21 ± 0.03	7.6	***	0.05	†
Log10 Area	0.11 ± 0.04	2.7	**	0.00 ± 0.01	-0.1		0.11	†
Sqrt Moisture	-0.15 ± 0.05	-3.1	**	0.00 ± 0.01	-0.2		-0.15	†
Vegetation complexity	0.19 ± 0.05	4.2	***	0.00 ± 0.01	-0.5		0.20	†
Localities (specialization)		Pseudo R^2 = 0.40			Pseudo R^2 = 0.99			
Stratum	0.07 ± 0.04	1.6		0.01 ± 0.00	2.2	*	0.06	†
Substrate	0.00 ± 0.04	0.1		0.00 ± 0.00	0.1		0.00	
Method	-0.11 ± 0.04	-2.4	*	0.00 ± 0.01	-0.3		-0.10	†
Habitat	0.41 ± 0.04	9.6	***	1.01 ± 0.02	42.7	***	-0.60	†
Diet	0.24 ± 0.04	5.9	***	-0.01 ± 0.02	-0.5		0.25	†
Log10 Area	0.09 ± 0.03	2.7	**	-0.01 ± 0.00	-1.5		0.09	†
Sqrt Moisture	-0.08 ± 0.04	-1.8		0.00 ± 0.00	0.5		-0.08	†
Vegetation complexity	0.12 ± 0.04	3.0	**	-0.01 ± 0.00	-2.5	*	0.13	†
Cell grids (specialization)		Pseudo R^2 = 0.32			Pseudo R^2 = 0.91			
Stratum^10	0.21 ± 0.05	4.5	***	0.06 ± 0.02	3.1	**	0.15	†
Substrate	-0.22 ± 0.05	-4.7	***	0.00 ± 0.01	0.3		-0.22	†
Method	0.00 ± 0.06	0.0		-0.02 ± 0.01	-2.2	*	0.02	†
Habitat	0.20 ± 0.04	4.4	***	0.83 ± 0.05	17.5	***	-0.64	†
Diet	0.08 ± 0.05	1.7		-0.02 ± 0.04	-0.5		0.10	
Sqrt Moisture	0.03 ± 0.05	0.6		-0.02 ± 0.02	-0.8		0.05	†
Vegetation complexity	0.01 ± 0.02	0.4		0.01 ± 0.01	0.6		0.00	

Bioregions (specialization)	Pseudo R^2 = 0.73			Pseudo R^2 = 0.96				
Stratum	0.35 ± 0.17	2.1	*	0.18 ± 0.06	2.9	**	0.18	
Substrate	-0.17 ± 0.11	-1.6		0.02 ± 0.02	0.9		-0.19	†
Method	-0.60 ± 0.12	-5.0	***	-0.05 ± 0.02	-2.2	*	-0.55	†
Habitat	0.63 ± 0.12	5.4	***	0.69 ± 0.12	5.9	***	-0.06	†
Diet	0.23 ± 0.11	2.1	*	0.06 ± 0.11	0.5		0.17	
Log 10 Area	0.06 ± 0.07	0.9		-0.02 ± 0.03	-0.8		0.08	†
Sqrt Moisture	-0.05 ± 0.07	-0.8		-0.05 ± 0.03	-1.4		-0.01	
Vegetation complexity	0.03 ± 0.06	0.4		0.04 ± 0.03	1.4		-0.01	

* Significance: $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Significance against the null model expectations.

Table S4: Results of bivariate spatial GLS analyses of niche overlap vs specialization. Results are for the scale of localities and include species' abundances. Response variable is always NICHE OVERLAP.

	Obs.		Null.		Obs. – Null.
	Est. ± SE	t-value	Est. ± SE	t-value	Est.
Stratum	-0.56 ± 0.04	-14.6 ***	-0.79 ± 0.03	-27.8 ***	0.23 †
Substrate	-0.41 ± 0.04	-9.7 ***	-0.45 ± 0.04	-10.9 ***	0.04
Method	0.10 ± 0.05	2.1 *	0.65 ± 0.04	18.5 ***	-0.55 †
Habitat	0.10 ± 0.05	2.2 *	-0.92 ± 0.02	-50.2 ***	1.02 †
Diet	0.19 ± 0.05	4.1 ***	0.78 ± 0.03	26.4 ***	-0.59 †

* Significance: P < 0.05, ** P < 0.01, *** P < 0.001.

† Significance against the null model expectations.

Table S5: Results of multi-predictor spatial GLS analyses of species richness in relation to both specialization and niche overlap. Results are for the scale of localities and include species' abundances. Response variable is always SPECIES RICHNESS.

	Obs.		Null.		Obs. – Null.
	Est. ± SE	t-value	Est. ± SE	t-value	Est.
Stratum					
Specialization	0.12 ± 0.05	2.2 *	0.33 ± 0.06	5.2 ***	-0.22 †
Niche overlap	0.07 ± 0.05	1.3	0.35 ± 0.06	5.7 ***	-0.28 †
Substrate					
Specialization	0.03 ± 0.05	0.5	0.13 ± 0.04	3.1 **	-0.10 †
Niche overlap	0.06 ± 0.05	1.3	0.59 ± 0.04	14.7 ***	-0.53 †
Method					
Specialization	0.13 ± 0.04	3.0 **	-0.53 ± 0.03	-16.7 ***	0.67 †
Niche overlap	-0.16 ± 0.04	-3.5 ***	-0.40 ± 0.03	-12.6 ***	0.25 †
Habitat					
Specialization	0.11 ± 0.05	2.4 *	0.77 ± 0.05	15.9 ***	-0.66 †
Niche overlap	0.05 ± 0.04	1.1	-0.15 ± 0.05	-3.1 **	0.20 †
Diet					
Specialization	0.22 ± 0.04	5.0 ***	0.51 ± 0.03	14.8 ***	-0.30 †
Niche overlap	0.12 ± 0.04	2.9 **	0.42 ± 0.03	12.1 ***	-0.30 †

* Significance: $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Significance against the null model expectations.

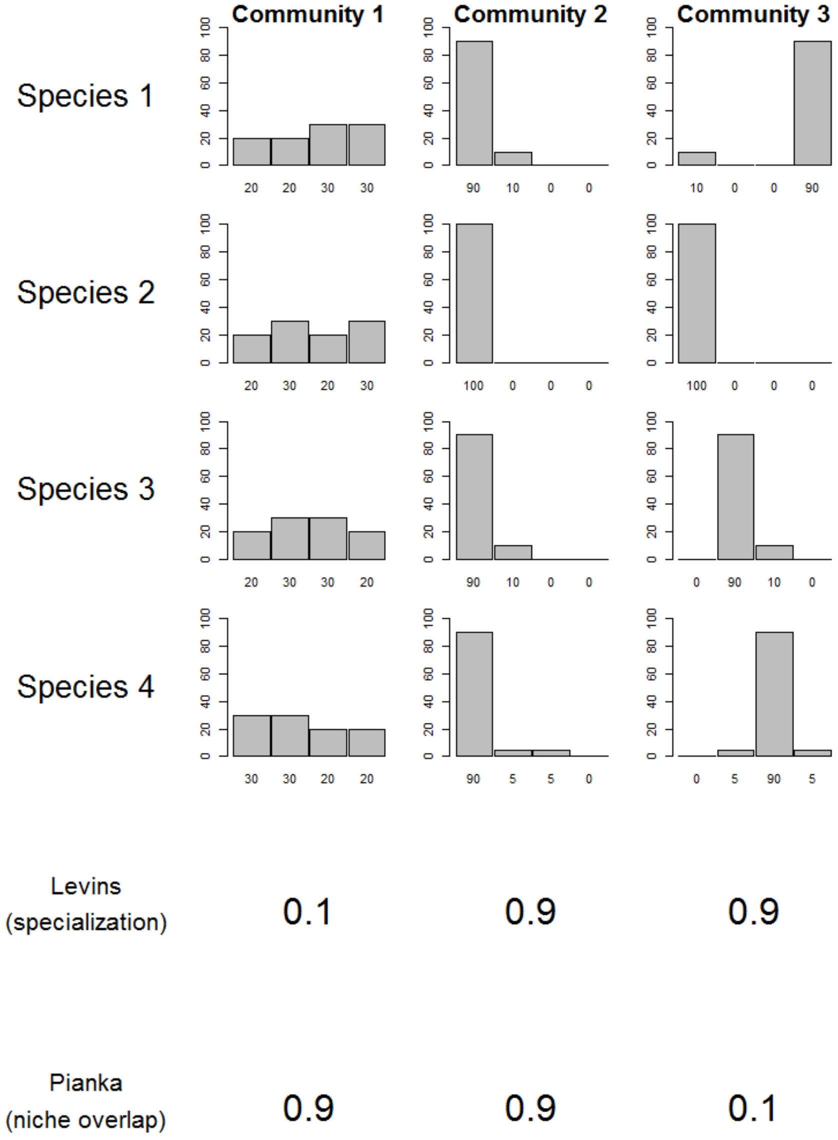

Figure S1. Conceptual overview of the relationship between Levins' and Pianka's indices. Increasing index value means higher specialization (Levins) and overlap (Pianka). Imagine three assemblages (community 1-3) with four species each (species 1-4) and a trait with four categories (bars). Sum of all categories for the trait in each species is always 100. Species in community 1 show even distribution of trait categories and are therefore generalists (low Levins' index), while species in communities 2 and 3 are specialized on one category and therefore represent specialists (high Levins' index). However, species in community 2 are specialized on the same category, while species in community 3 differ in their category use. Even though both assemblages show high Levins' index and thus specialization, they differ in their niche overlap, which is high in community 2 (high Pianka's index) and low in community 3 (low Pianka's index).

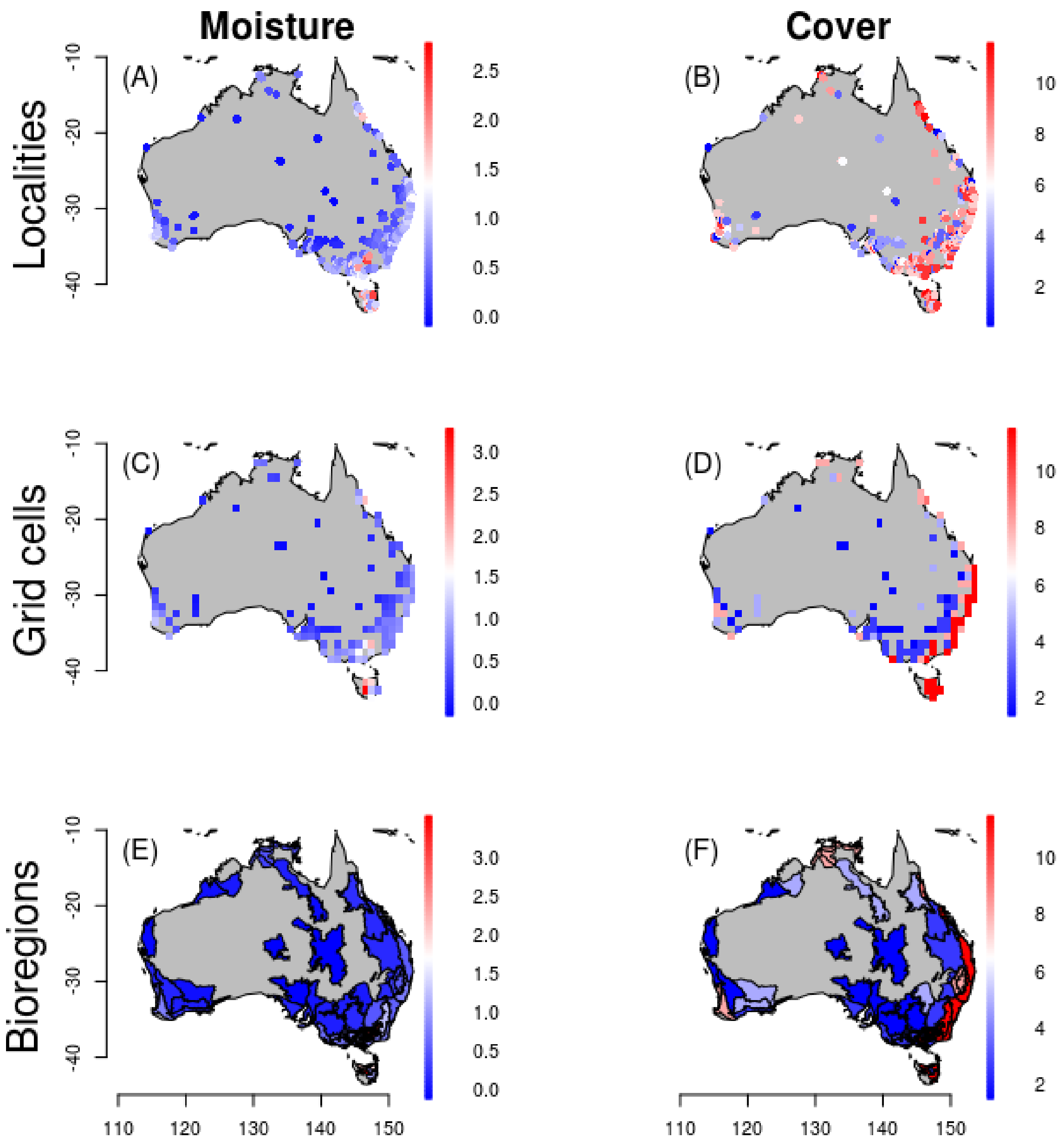

Figure S2. Spatial distribution of moisture (A, C, E) and vegetation complexity (B, D, F) across localities (A, B), grid cells (C, D), and bioregions (E, F). Moisture is expressed as the annual mean of the monthly ratio of precipitation to potential evaporation and vegetation complexity is represented by categories as described in Table S1 (part B) from the lowest vegetation height and cover (category 1) to the highest vegetation height and cover (category 11)

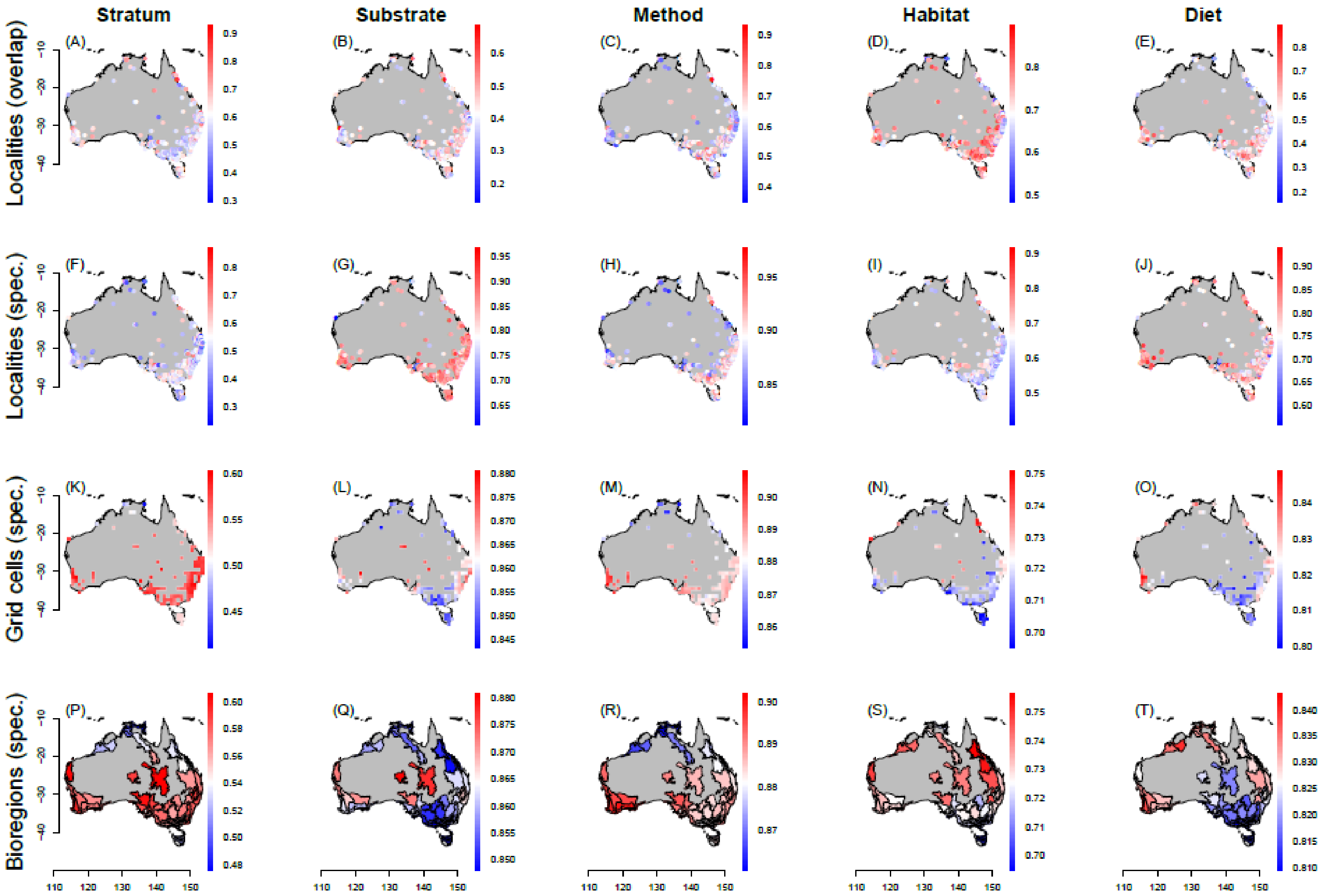

Figure S3. Geographical distribution of mean specialization (Levins' index) and niche overlap (Pianka's index) for localities (A-E niche overlap, F-J specialization; computed with species' abundances), squares (K-O specialization), and bioregions (P-T specialization). High values (red colour) mean high specialization and high niche overlap, while low values (blue colour) mean the opposite.

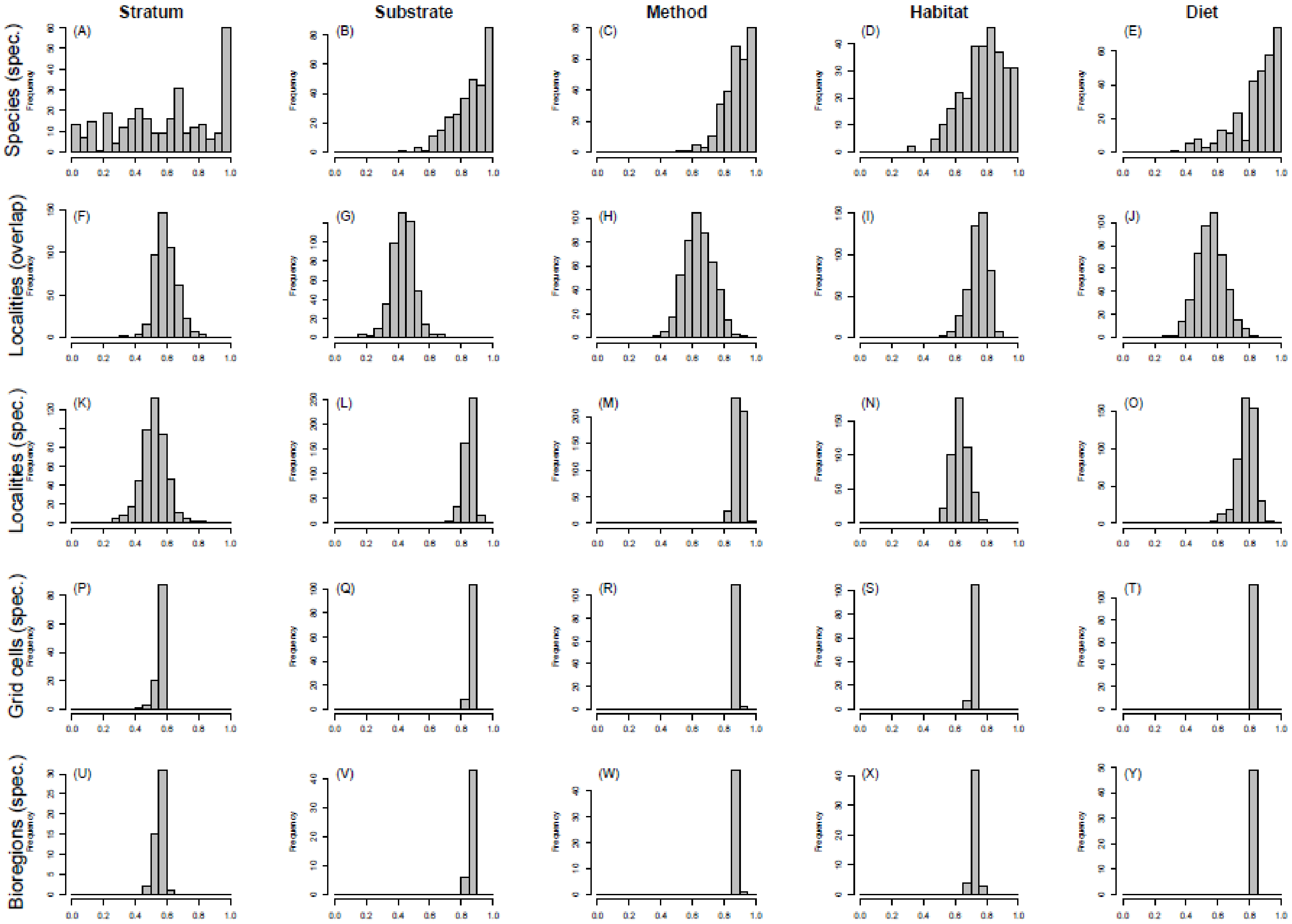

Figure S4. Distribution of specialization and overlap indices for all five environmental traits (individual panel columns) across species (A-E top panel row) and spatial units (remaining panel rows, from top to bottom: F-J niche overlap in localities, K-O specialization in localities, P-T specialization in squares, and U-Y specialization in bioregions). Specialization and niche overlap in localities are computed with species' abundances.

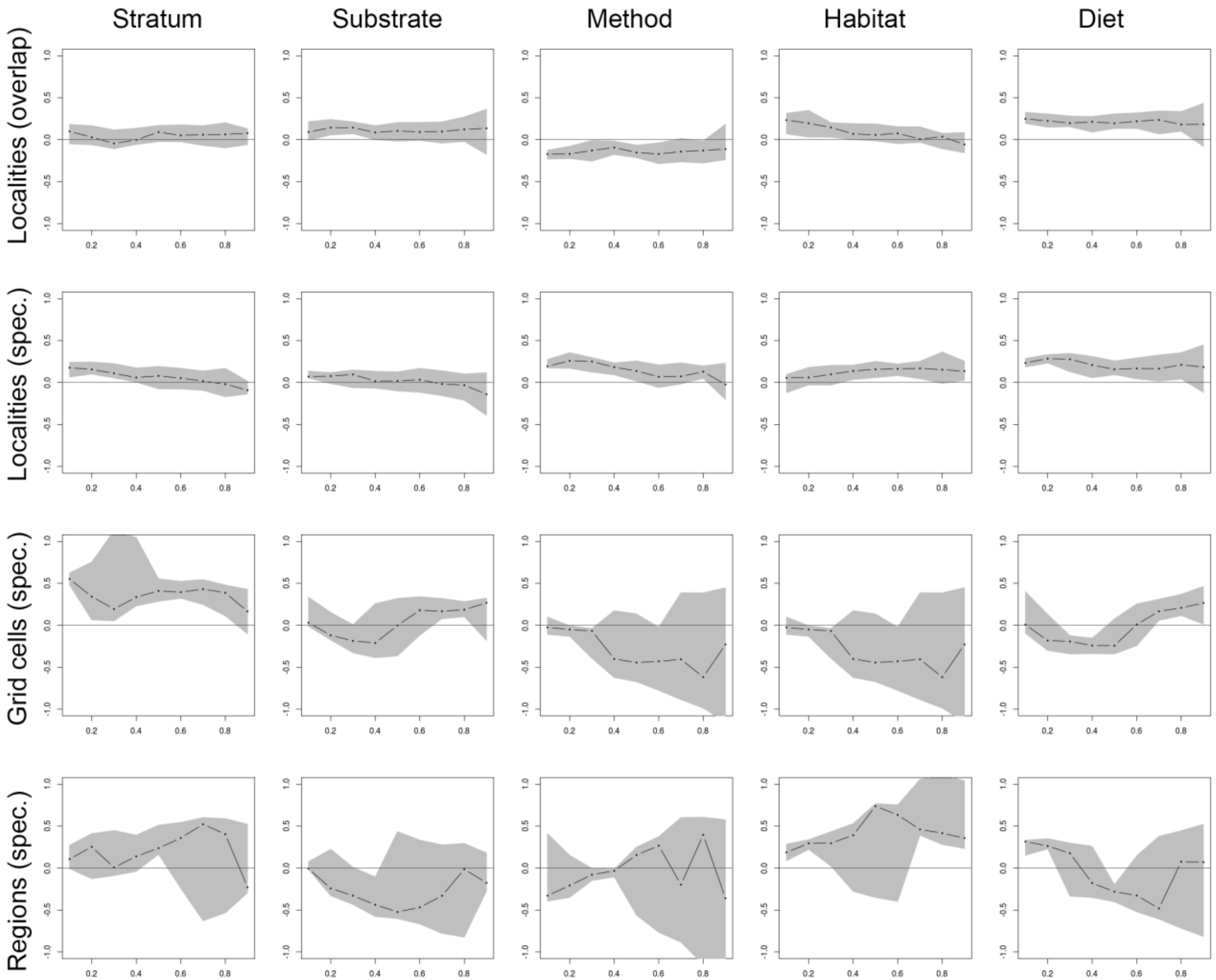

Figure S5. Full results of the quantile regression analyses of species richness vs specialization and niche overlap. Quantile-specific analyses of the relationships between species richness and specialization (Regression Coefficient on the y axis), divided into quantile cut-offs according to richness-environment residuals. The highest quantiles contain assemblages that are most species rich given their environmental conditions, while the lowest quantiles contain assemblages with the least species given the environment. Specialization and niche overlap in localities are computed with species' abundances. Grey bands represent confidence intervals.

Palacký University in Olomouc

Faculty of Science

Department of Zoology and Laboratory of Ornithology

Macroecology, life histories, and diversity of Australian birds

Makroekologie, životní strategie a diverzita ptáků Austrálie

Summary of the Ph.D. thesis

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Supervisor: doc. Mgr. Vladimír Remeš, Ph.D.

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Abstract (in English)

Macroecology seeks to study relationships between organisms and their environment on large spatial, temporal, and taxonomical scales. Environment can affect the evolution of traits important for reproduction and survival, so-called life history traits. Among these traits belongs for example clutch size, i.e. number of eggs per one breeding attempt. Many theories were proposed to explain variability and evolution of clutch size, focusing for instance on the productivity of environment, predation, or nestling development. One of the life history traits is also beak size, which is thought to be driven mainly by diet, but can also be tied to thermoregulation and climate. Life history traits can affect species' diversity patterns. Diversity can be affected by evolutionary processes, history, or abiotic and biotic conditions. Effects can be direct or indirect and can differ across spatial scales. In this thesis I applied macroecological approaches to study variability and evolution of life history traits and diversity of Australian avifauna. I found that (i) clutch size of Australian songbirds was probably influenced by different factors than in Northern Hemisphere species, as it showed no relation to environmental productivity or nest predation, but instead was related to the nestling development. (ii) Beak size of Australasian honeyeaters and allies was shaped by winter, not summer temperatures. It thus appears that while diet affects beak shape, its size is driven by thermoregulation. (iii) While the gradient in species richness in Australian birds was driven by water availability both directly (physiology) an indirectly (vegetation complexity and niche availability), phylogenetic and functional diversity appeared to be more strongly related to the age of biomes and evolutionary history. (iv) Species richness and specialization were closely related across several ecological traits and spatial scales. However, abiotic factors, not interspecific interactions, were probably major drivers shaping assemblage composition of Australian songbirds. Thus, the evolution of avian life history traits appears to be under the influence of different factors in Australia than in other regions of the world. The diversity patterns and assemblage composition are mostly driven by the historic effects rather than by current ecological conditions.

Abstrakt (in Czech)

Makroekologie studuje vztahy mezi organismy a jejich prostředím na velkých prostorových, časových a taxonomických škálách. Prostředí může ovlivnit evoluci znaků důležitých pro reprodukci a rozmnožování, tzv. life-history (životní historie) znaků. Mezi tyto znaky patří třeba velikost snůšky, tedy počet vajec snesených v jednom reprodukčním pokusu. Byl navrhnut nespočet teorií snažících se vysvětlit variabilitu a evoluci velikosti snůšky, které se soustředily třeba na produktivitu prostředí, predaci nebo gradient ve vývoji mláďat. Jedním z life-history znaků je také velikost zobáků, která je údajně závislá na potravě, ale může být také svázána s termoregulací a klimatem. Life-history znaky mohou také ovlivnit patrnosti v druhové diverzitě. Diverzita může být ovlivněna evolučními procesy, historií nebo abiotickými a biotickými podmínkami. Vlivy mohou být přímé nebo nepřímé a mohou se lišit napříč prostorovými škálami. V této práci jsem aplikovala makroekologické přístupy na studium variability a evoluce patrností v life-history znacích a diverzitě australské avifauny. Zjistila jsem, že (i) velikost snůšky australských pěvců je pravděpodobně ovlivněna jinými faktory, než jak je tomu u druhů ze severní polokoule, neboť neukázala žádný vztah k produktivitě prostředí či hnízdní predaci, ale k vývinu mláďat. (ii) Velikost zobáku australských medosavek je řízena zimními, a ne letními teplotami. Zdá se proto, že zatímco potrava ovlivňuje tvar zobáku, jeho velikost je řízena termoregulací. (iii) Zatímco je gradient v druhové bohatosti australských ptáků řízen dostupností vody, a to jak přímo (fyziologicky), tak nepřímo (komplexnost vegetace a dostupnost nik), fylogenetická a funkční diverzita se zdá být spíše spjata se stářím biomů a evoluční historii. (iv) Druhová bohatost a specializace jsou úzce spjaté s množstvím ekologických znaků a napříč prostorovými škálami. Nicméně, abiotické faktory, a ne mezidruhové interakce zřejmě hrají prim v utváření složení společenstev australských pěvců. Evoluce ptačích life-history znaků se tedy zdá býti v Austrálii ovlivněna rozdílnými podmínkami, než je tomu v jiných oblastech světa. Diverzita a složení společenstev jsou řízeny především historickými vlivy spíše než současnými ekologickými podmínkami.

Introduction

Macroecology

Macroecology is a rather new scientific field that investigates relationships between organisms and their environment on large spatial, temporal, and taxonomical scales (Brown 1995, McGill 2019). It rose to utilize results of many small-scale studies and integrate them into a single framework that is able to analyse large-scale patterns (Brown & Maurer 1989, Brown 1995, McGill 2019). Macroecological studies focus mostly on latitudinal gradients of diversity and variability in species richness, species abundance, body size, and range size (Brown & Maurer 1989, Gaston & Blackburn 2000, Storch & Reif 2002). Many of these works used birds in their research. Birds represent a very suitable group of organisms used in macroecological studies because they are quite well studied and large databases with their functional traits, phylogeny, and geographic distribution exist.

Life history

Species show a great intra- and interspecific variability in their life-history traits. This variability is in the focus of the life history theory that seeks to explain how the environment drives natural selection and shapes organisms so that they optimize their fitness via reproductive effort and survival (Stearns 2000). Many of the life history traits were studied extensively in the past, for example body size, egg size, lengths of the incubation and fledging periods, or life span (Western & Ssemakula 1982). Here, I focus on two aspects of avian life histories discussed in this thesis – reproductive effort and morphology, particularly on clutch size and beak size.

First, one of the most studied aspects of life history traits in birds is clutch size. Birds show high interspecific variability in clutch sizes where some species lay only one egg, while others up to fourteen eggs. Clutch size appears to be related to latitude and species with largest clutches inhabit mostly temperate regions on the Northern Hemisphere (Moreau 1944, Cardillo 2002, Jetz et al. 2008). Many theories were suggested to explain interspecific variation in avian clutch size and its relationship to latitude. Briefly, according to Lack (1947, 1948), birds are limited by available resources, specifically by the amount of food they can provide to their offspring, which is tied to the day length. Ashmole (1963) proposed that the seasonality in resources could drive clutch size via the variation in population densities and per-capita food availability. Skutch (1949) focused on the effect of predation and expected that in areas with high number of predators it is more effective to have smaller clutches. Recently, Martin (2014, 2015) proposed a new theory that focuses on a gradient in nestling development and is tied to the nest predation rates. However, the evidence for the diverse theories is mixed. Most of the hypotheses were not tested simultaneously and the research on clutch size was mostly carried on Northern Hemisphere species. Tropical and Southern Hemisphere species have considerably longer nesting periods, smaller clutches, and the latitudinal gradient in clutch size is not so pronounced in the Southern Hemisphere (Jetz et al. 2008). Thus, it is important to focus research effort on life history traits of tropical and Southern Hemisphere species.

Second, avian morphology plays an important role in life histories as well. For example, larger species inhabit colder climates (Olson et al. 2009), the shape of wings is vital for movement and migration (Mönkkönen 1995), and avian morphology is also related to species' ecology, habitat occupation, and foraging and diet preferences (Miles & Ricklefs 1984, Ricklefs 2012, Pigot et al. 2016). One of the most specific avian structures is beak. Beaks show a great range of shapes and sizes and have an important role in foraging. However, beaks probably have thermoregulatory functions as well and can affect the dissipation of body heat (Tattersall et al. 2009, Greenberg et al. 2012). Studies concerning the relationship between beak size and thermoregulation are scarce. It is also still not clear whether thermal effects are really important and if so, whether hot temperatures which could drive the increase in beak sizes to dissipate heat, or cold temperatures driving smaller beaks because of the heat retention are more important.

Diversity

Environment can affect not only life history traits of species, but also interact with their ecological niche to affect diversity. Niche is seen as an ecological space available for species to divide it between them. Specialization on a limited range of resources can help partition the niche and thus enhance coexistence of species and promote diversity (Hutchinson 1959, MacArthur 1972, Eeley & Foley 1999, Mason et al. 2008, Pigot et al. 2016). Most of the studies focused on the specialization on habitat utilization and diet preferences, yet niche partitioning can take place also in foraging behaviour. The packing of species in ecological space and their specialization can therefore play an important role in interspecific interactions, shaping community composition, as well as affecting diversity.

Countless number of definitions exists of what diversity is and how to express it. The most simple is the number of species present (species richness), which can be improved by taking species' abundances into account (Tokeshi & Schmid 2002). Phylogenetic diversity increases the information value by including species' evolutionary history (Tucker et al. 2016), while functional diversity focuses on ecological differences between species and assemblages and employs functional traits (e.g. morphological or ecological characteristics, including life history traits; Petchey & Gaston 2006).

Out of several climatic variables it appears that energy (e.g. environmental productivity, solar radiation) and water (e.g. rainfall, PET) are the major drivers of biodiversity worldwide (Hawkins et al. 2003). The effect of these variables can be either direct (physiological tolerances; Buckley et al. 2012) or indirect, e.g. environmental productivity can facilitate more complex vegetation and thus create 'larger' ecological space (Hurlbert 2004, Tews 2004). Patterns in species richness of various groups of organisms in relation to environment were studied widely (e.g. Hawkins et al. 2003, Kissling et al. 2008, Jiménez-Alfaro et al. 2016), but less attention was paid to phylogenetic and functional diversity (e.g. Graham et al. 2009, Schleuter et al. 2012, Lanier et al. 2013). Moreover, the effect of environment on diversity is thought to be most prominent on large spatial scales (in terms of bioregions and larger), while on finer scales assemblage composition should be shaped more by interspecies interactions, such as competition for resources and niche partitioning (Whittaker et al. 2001, Belmaker & Jetz 2011, Ferger et al. 2014, Fergnani & Ruggiero 2017). Yet, most of the studies fail to incorporate various spatial scales to differentiate between these processes (Belmaker et al. 2012).

Australia

Australia represents a unique system for studying geographical patterns and evolution of diversity and variation in life history traits in local avifauna. Even in these times, studies performed on Northern Hemisphere temperate species still make a majority of scientific work and we still lack sufficient knowledge about variables shaping diversity and life histories of species on the Southern hemisphere and in the tropics.

Even though the climatic and environmental conditions, as well as fauna in Australia are highly diverse, most of the continent (around 70%; Byrne et al. 2008) is arid with the presence of several deserts in the central plateau. Remnants of the historic mesic environments can be found along the eastern coastline, which is covered by tropical and temperate rainforests with high and non-seasonal patterns in rainfall. While in the north, a monsoon region with high temperatures and fluctuations in rainfall is present, south of the continent and the island of Tasmania fall to the temperate zone with variation in temperature, but not in rainfall. Most of the Australian environment therefore consists of arid and semi-arid habitats (Byrne et al. 2011), such as open forests, woodlands and shrublands. In such arid environment, water availability is thus thought to play the most prominent role in shaping avian diversity in Australia (Hawkins et al. 2005).

Nearly 900 species of birds are now recognized to reside in Australia and Tasmania, from which 45% are local endemics (Chapman 2009). Distribution of avian species richness is highly uneven, with the lowest number of species in central arid plains and the highest along the mesic eastern coast. This does not agree with the usual north-south gradient in species richness observed in the Northern Hemisphere (Hurlbert & Jetz 2007). It also appears that Australian birds have low diversification rates (Jetz et al. 2012) and only few clades were able to invade newly arisen arid environments (Brooker et al. 1979). In comparison to species from other Southern hemisphere continents, Australian avifauna is quite well studied and therefore suitable for macroecological studies.

Thesis focus

Aims of this thesis are to apply macroecological approach to study patterns in diversity and life history traits of Australian birds. More specifically, **Chapter I** concerns interspecific variability in clutch size of Australian songbirds (order Passeriformes). We focused on three sets of hypotheses involving (i) resource availability, (ii) nest predation, and (iii) development of fledglings. For the first time we tested these hypotheses simultaneously while focusing on less explored Southern Hemisphere species.

Chapter II shifts the attention from clutch size to the evolution of beak size. The role of beak shape in foraging is well known, but the evolution of its size might have been caused by the need for thermoregulation; either to dissipate excess body heat or for heat retention in cold ambient temperatures. We tested this assumption on three families of Australian and New Guinean songbirds.

In **Chapter III** we tried to disentangle direct and indirect effects of environment on shaping diversity of Australian birds. Climate can affect patterns in diversity either directly via physiological tolerances of species, or indirectly via facilitation of vegetation complexity and resource availability. We computed several diversity indices based on the number of species, their phylogenetic relations and variability in functional traits, and quantified to which extent their spatial patterns were affected directly or indirectly by climate.

Finally, **Chapter IV** focuses in more detail on the coexistence of species and how foraging specialization enables partitioning of resources and increase in SR. It is to be expected that more species can coexist if they are specialized and thus the competition between them is relaxed, and that this relationship should be more pronounced on local spatial scales than on the large ones. We tested this concept on Australian songbirds while using detailed data on their habitat, diet and foraging preferences. We worked across three spatial scales ranging from small localities to bioregions.

Conclusions

In this thesis I focused on studying interspecific variability, evolution, and geographical patterns in life history traits, morphology, and diversity of Australian birds. I showed that the evolution of clutch size and beak size were under the influence of different factors in Australia compared to other regions of the world. Moreover, diversity patterns and assemblage composition were probably mostly driven by historical effects rather than by current ecological conditions and interspecific interactions. The main conclusions of this work are as follows:

I. Clutch size of Australian songbirds showed low interspecific and spatial variability, but still increased away from the equator. Out of the three hypotheses tested, the role of nestling development in shaping the evolution of clutch size of Australian songbirds was most prominent. In contrast to many Northern Hemisphere studies, we found no relation between resource availability or nest predation and clutch size.

II. Winter, not summer, temperatures explained most of the variation in beak size in honeyeaters and allies across Australia and New Guinea. It appears that the need for heat retention in cold months affects the evolution of beak size in this group of Australasian songbirds.

III. Water availability had positive direct as well as indirect (via vegetation complexity) effects on species richness of Australian birds. However, phylogenetic and functional diversity were only poorly predicted by environmental conditions and were possibly more affected by the age of biomes and evolutionary history of the studied clades.

IV. Species richness and specialization of Australian songbirds showed both positive and negative mutual relationships depending on the ecological trait used (habitat selection, dietary preferences, or several types of foraging behaviour). The richness-specialization relationship was strongest at the regional scales, which is in contrast to the expectations that interspecific interactions should be most prominent on local spatial scales and shape the assemblage composition. However, it still appears that species partition their ecological space via the foraging on a particular vegetation stratum and substrate.

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List of chapters

Chapter I	**Harmáčková L.** & Remeš V. (2017) *The evolution of clutch size in Australian songbirds in relation to climate, predation, and nestling development.* Emu – Austral Ornithology 117: 333–343.
Chapter II	Friedman N.R., **Harmáčková L.**, Economo E.P. & Remeš V. (2017) *Smaller beaks for older winters: Thermoregulation drives beak size evolution in Australasian songbirds*. Evolution 71: 2120–2129.
Chapter III	Remeš V. & **Harmáčková L.** (2018) *Disentangling direct and indirect effects of water availability, vegetation, and topography on avian diversity*. Scientific Reports 8: 15475.
Chapter IV	**Harmáčková L.**, Remešová E. & Remeš V. (manuscript) *Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds.*

Chapter abstracts

Chapter I

The study of clutch size has been a productive approach to gaining better understanding of life-history evolution, especially in Northern Hemisphere birds. Factors driving life-history evolution in Southern Hemisphere species are less well understood. Moreover, studies often focus on single hypotheses for clutch size evolution and rarely test several hypotheses simultaneously. This severely limits more general conclusions of life-history evolution. We assembled an extensive dataset on 313 species (ca.98%) of Australian songbirds (Passeriformes) and tested three hypotheses for the evolution of clutch size in birds: (1) resource availability and their seasonality (Lack's and Ashmole's hypotheses), (2) nestling mortality (age-specific mortality and Skutch's hypotheses), and (3) fledgling developmental gradient (Martin's hypothesis). The mean clutch size of Australian songbirds was 2.69 eggs and increased in higher latitudes. Clutch size was positively related to the length of the nestling period and in species with short nestling periods offspring left the nest with lower body mass, consistent with Martin's hypothesis. In contrast to many Northern Hemisphere studies we did not detect any direct effect of the productivity of environment, its seasonality or nest predation rate. Our work provides one of only a handful of comprehensive tests of clutch size evolution in Southern Hemisphere birds. Its findings stress the importance of breaking the Northern temperate bias of life-history studies.

Chapter II

Birds' beaks play a key role in foraging, and most research on their size and shape has focused on this function. Recent findings suggest that beaks may also be important for thermoregulation, and this may drive morphological evolution as predicted by Allen's rule. However, the role of thermoregulation in the evolution of beak size across species remains largely unexplored. In particular, it remains unclear whether the need for retaining heat in the winter or dissipating heat in the summer plays the greater role in selection for beak size. Comparative studies are needed to evaluate the relative importance of these functions in beak size evolution. We addressed this question in a clade of birds exhibiting wide variation in their climatic niche: the Australasian honeyeaters and allies (Meliphagoidea). Across 158 species, we compared species' climatic conditions extracted from their ranges to beak size measurements in a combined spatial-phylogenetic framework. We found that winter minimum temperature was positively correlated with beak size, while summer maximum temperature was not. This suggests that while diet and foraging behavior may drive evolutionary changes in beak shape, changes in beak size can also be explained by the beak's role in thermoregulation, and winter heat retention in particular.

Chapter III

Climate is a major driver of species diversity. However, its effect can be either direct due to species physiological tolerances or indirect, whereby wetter climates facilitate more complex vegetation and consequently higher diversity due to greater resource availability. Yet, studies quantifying both direct and indirect effects of climate on multiple dimensions of diversity are rare. We used extensive data on species distributions, morphological and ecological traits, and vegetation across Australia to quantify both direct (water availability) and indirect (habitat diversity and canopy height) effects of climate on the species richness (SR), phylogenetic diversity (PD), and functional diversity (FD) of 536 species of birds. Path analyses revealed that SR increased with wetter climates through both direct and indirect effects, lending support for the influence of both physiological tolerance and vegetation complexity. However, residual PD and residual FD (adjusted for SR by null models) were poorly predicted by environmental conditions. Thus, the FD and PD of Australian birds mostly evolved in concert with SR, with the possible exception of the higher-than-expected accumulation of avian lineages in wetter and more productive areas in northern and eastern Australia (with high residual PD), permitted probably by older biome age.

Chapter IV

Ecological specialization enables the partitioning of resources and thus can facilitate the coexistence of species and promote higher species richness. Specialization and niche partitioning are expected to exert a decisive influence on local spatial scales, while species richness at regional scales should be shaped mostly by historical factors and abiotic conditions. Moreover, specialization is expected to be particularly important in communities that are exceptionally species rich for their environmental conditions. At the same time, niche overlap in these communities should be minimized to enable species coexistence. We tested these hypotheses by studying specialization-richness relationship and niche overlap in assemblages of 298 species of songbirds (Passeriformes) across Australia. We improved on previous studies by studying scales from truly local (2-6 ha) to regional (bioregions), and by using detailed data on habitats, diet, and especially foraging behaviour (method, substrate, and stratum), which might be particularly important in fine niche partitioning. We expected the richness-specialization relationship to be particularly strong on local spatial scales and in communities exceptionally species rich for given environmental conditions (approximated by moisture and vegetation complexity). We also expected low niche overlap in assemblages with specialized species. While the specialization and species richness were often positively related, the strength (and even the direction) of the relationship changed between traits and across spatial scales. Moreover, the strength of specialization-richness relationship was actually as strong, or even stronger, on regional scales as on local scales. On the other hand, we found the expected negative relationship between specialization and overlap in foraging stratum and substrate (in local communities), suggesting that species partition ecological space in terms of where they find food. Overall, our results suggest that ecological processes related to obtaining resources (foraging behaviour) are important in structuring avian communities across spatial scales.

Curriculum Vitae

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Research interest Spatial patterns of biodiversity, mainly the evolution and geographic variability in functional traits of Australian birds, gradients of species richness, mapping phylogenetic and functional diversity, and analysing community structure and species co-existence at different spatial scales.

Education

Since 2013	Ph.D. in Zoology, Palacký University in Olomouc Thesis topic: Macroecology, life histories, and diversity of Australian birds Supervisor: doc. Mgr. Vladimír Remeš, Ph.D.
2011–2013	Master's degree in Zoology, Palacký University in Olomouc Thesis topic: Geographical variability in functional traits of Australian birds Supervisor: doc. Mgr. Vladimír Remeš, Ph.D.
2008–2011	Bachelor's degree in Biology, Jan Evangelista Purkyně University in Ústí nad Labem Thesis topic: Avifauna of Chabařovice ponds, Ústí nad Labem district Supervisor: doc. RNDr. Jaromír Hajer, Csc.

Foreign experiences

Since September 2018	Senckenberg Biodiversity and Climate Research Centre (SBiK-F) Frankfurt am Main, Germany Supervisor: Dr. Susanne Fritz Support of Academic mobility at Palacký University in Olomouc
May – August 2016	Senckenberg Biodiversity and Climate Research Centre (SBiK-F) Frankfurt am Main, Germany Supervisor: Dr. Christian Hof Erasmus+ internship

Publications

Remeš V. & Harmáčková L. (2018) Disentangling direct and indirect effects of water availability, vegetation, and topography on avian diversity. Scientific Reports 8: 15475.

Harmáčková L. & Remeš V. (2017) The evolution of clutch size in Australian songbirds in relation to climate, predation, and nestling development. Emu – Austral Ornithology 117: 333–343.

Friedman N.R., Harmáčková L., Economo E.P. & Remeš V. (2017) Smaller beaks for older winters: Thermoregulation drives beak size evolution in Australasian songbirds. Evolution 71: 2120–2129.

Harmáčková L., Remešová E. & Remeš V. (manuscript) Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds.

Harmáčková L., Remeš V., Khaliq I. & Hof C. (manuscript) The global variation of evaporative water loss in birds in relation to climate and diet.

Selected conference attendance

Harmáčková L., Remešová E. & Remeš V. (2019): *Foraging specialization and niche overlap in Australian songbirds*. In: International Biogeography Society 9th Biennial Meeting, 8.–12. January 2019, Málaga, Spain. (*poster*)

Remeš V. & Harmáčková L. (2018): *Srážky, vegetace a diverzita ptáků Austrálie*. In: Bryja J. & Solský M. (Eds.): Zoologické dny, Sborník abstraktů z konference, 8.-9. February 2018, Praha, Czechia. (*poster*)

Harmáčková L. & Remeš V. (2017): *Phylogenetic and functional diversity of Australian birds is shaped by geographic and climatic history, not environmental diversity*. In: Macroecology in Space and Time, 10th Annual Meeting of the Specialist Group on Macroecology of the Ecological Society of Germany, Austria and Switzerland, 19.-21. April 2017, Wien, Austria. (*talk*)

Harmáčková L., Remeš V. & Hof C. (2017): *Evaporative water loss in birds in relation to body mass, climate, and diet*. In: Bryja J., Horsák M., Horsáková V., Řehák Z. & Zukal J. (Eds.): Zoologické dny, Sborník abstraktů z konference, 9.-10. February 2017, Brno, Czechia. (*poster*)

Harmáčková L. & Remeš V. (2016): *Vývin mláďat hraje v evoluci velikosti snůšky australských pěvců důležitější roli než klima a predace*. In: Bryja J., Sedláček F. & Fuchs R. (Eds.): Zoologické dny, Sborník abstraktů z konference, 11.-12. February 2016, České Budějovice, Czechia. (*talk*)

Harmáčková L. & Remeš V. (2015): *Species diversity, habitat and food specialisation in Australian birds*. In: Gavin D., Beierkuhnlein C., Holzheu S., Thies B., Faller K., Gillespie R. et al. (Eds.): Conference program and abstracts. International Biogeography Society 7th Biennial Meeting, 8.-12. January 2015, Bayreuth, Germany. Frontiers of Biogeography Vol. 6, suppl. 1. International Biogeography Society. (*poster*)

Teaching experiences

Phylogeny and classification of Czech species of vertebrates (mainly focused on birds and mammals).
Reading, understanding, and discussion of scientific articles.
Zoological field trips (focused on birds).

Other activities

Member of the Czech society for Ornithology.
Organisation and participation in educational programmes for public concerning birds, their research and protection.
Holder of the Czech bird-ringing license.
Participation in in the Qarry Life Award 2018 (Hrabůvka quarry: A potential refuge of rare species) – ornithological survey.

Geophaps plumifera