The island syndrome in birds

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Declaration

I declare that this thesis was composed by myself and that the work contained in it is my own except where attributed in the text. The work has not been submitted for any degree or professional qualification except as specified.

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Publications and contributions

Parts of this thesis have already been published, or are under consideration in peer-reviewed journals. Appropriate statements on that, together with attribution of my co-authors, and work-specific acknowledgements, precede the specific chapters in form of a title page.

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Abstract

Islands are home to some of the most unique and threatened groups of organisms in the world. The distinctiveness and vulnerability of island species stems from their adaptations to insular environments. Meanwhile, the similarity of different island environments can lead to the repeated evolution of similar forms on different islands, despite taxonomic differences and distinct community compositions. This pattern of independent acquisition of similar morphological, ecological, and behavioural characteristics in island taxa is known as the 'island syndrome'. The island syndrome is thought to evolve due to the dual limitations of area and isolation, creating communities with low predation and interspecific competition, leading to the evolution of, among other traits, 'slow' life histories, generalist strategies, and intermediate body sizes. Although the island syndrome is considered a global phenomenon, evidence for its taxonomic, morphological, and geographical generality is lacking. Here, I summarise the scope of the island syndrome focusing on a particular taxonomic group – birds (**Chapter 1**). I review the level of support for the island syndrome, and the extent of biological traits involved, showing that, beyond body size, most island adaptations are poorly understood, particularly with respect to behavioural and life history traits. Furthermore, I find that most studies are focused on small sample sizes, and do not utilise phylogenetic comparative methods, which are critical to accurately study trait evolution across hundreds of species. Following these findings, my empirical work focuses on investigating two reproductive traits in birds – clutch size and nest architecture. Clutch size has been at the forefront of avian life history research since David Lack's studies, and its variation has significant consequences for animal fitness. I explored variation in clutch

size for some 4,500 bird species, to examine whether average clutch size differs between island and continental species (**Chapter 2**). I found that clutches on islands tend to be smaller, which is consistent with the 'slowing down' of life histories, and that this effect persists across both land birds and seabirds. The latter have traditionally been ignored in island syndrome studies, but my work demonstrates they undergo the same changes as land birds. Nest architecture has also been poorly explored in a macro-evolutionary context. As a result, it is unclear which aspects of the environment shape nest architecture, with a long-standing debate on the importance of abiotic versus biotic factors. I have collected nest architecture data for all bird species in the world, and I show that biotic interactions (approximated by predator diversity) are the predominant drivers of nest variation (**Chapter 3**). Island endemicity is also a significant predictor of nest architecture, resulting in the evolution of 'simpler' nests. Finally (**Chapter 4**), I explore the island diversification of Eurasian Wrens (*Troglodytes troglodytes*) in the British Isles. This study focusses on a particular set of populations to i) characterise the phylogenetic relationships between geographically distinct populations; ii) characterise the evolution of Wrens with respect to morphology and song; and iii) explore the genomic patterns of divergence between island populations. To this end, I have collected morphological, song, and genetic data for the five subspecies of British wrens: *Troglodytes troglodytes troglodytes indigenus* (most of the British Isles), *hebridensis* (Outer Hebrides), *hirtensis* (St Kilda), *zetlandicus* (Shetland) and *fridariensis* (Fair Isle). I show that the British Isles contain three distinct lineages of Wrens: one in Shetland, one of the British and Hebridean subspecies, and within that, the strongly divergent St Kilda Wrens. The Shetland and St Kilda Wrens show considerable morphological

convergence, despite vocal and genetic divergence. I show they share patterns of genetic evolution, including apparent differentiation in a genomic region containing the same gene. Overall, my work provides a thorough description of the avian island syndrome, and highlights research gaps which will help to delineate its drivers.

Introduction

Biologically, an ‘island’ can be any environment surrounded by an inhospitable matrix (Matthews & Triantis, 2021). This definition includes a diverse range of habitats, including lakes (Browne, 1981), caves (Culver, 1976), or even water bodies accumulating in cavities within plants (Kitching, 2001). The ‘true islands’ (Matthews & Triantis, 2021), which are emergent subcontinental land masses surrounded by the sea, are the focus of this thesis. Such islands can be found in both shallow seas and open oceans, and constitute about 7% of the world’s emergent land mass. Islands have been at the centre of many developments in the biological sciences (Whittaker et al., 2017), including the development of early evolutionary theories (Darwin, 1859; Wallace, 1880).

Together, the limited area and isolation of islands determine the rates of extinction and speciation of the organisms that inhabit them (MacArthur & Wilson, 1967; Valente et al., 2020). Although islands are diverse environments (Ali, 2017), spanning multiple climate zones and differing widely in their geology (Steadman, 2006; Ali, 2017), many aspects of their ecology can be approximated using a set of (fairly) simple equations (MacArthur & Wilson, 1963, 1967). These equations incorporate area and isolation, which have been shown to accurately predict the diversity of species on islands. The relative paucity of species on islands compared to continents can mean that the former lack entire ecological groups (Simberloff, 1995). The presence or absence of different groups of species is often predictable (Kadmon & Pulliam, 1993), for example abiotically pollinated (König et al., 2021)

and bird-dispersed (flesh-fruited) (Burns & Pugnaire, 2005) plants are overrepresented on islands.

The diversity, uniqueness, and peril of island species

Despite occupying a small fraction of the world's land surface (Fernández-Palacios et al., 2021), island species constitute up to 20% of all species for groups such as birds and flowering plants (Tershy et al., 2015). In addition to high species richness, island regions are associated with very high rates of endemism, with an average of 9.5x and 8.1x higher richness of endemic species among plants and vertebrates, respectively (Kier et al., 2009). At the same time, island species are disproportionally threatened, with 41% of the most threatened vertebrates in the world being island endemics (Spatz et al., 2017). In birds, 8% of all island endemics are extinct (cf. to 0.002% overall) (Matthews et al., 2022). Furthermore, the proclivity towards endemism has made island species central to studies of speciation (Gillespie & Roderick, 2002; Price, 2008), whilst the tractability of smaller ecosystems and multiple, semi-independent colonisation events make islands important in the study of evolutionary and ecological principles (Whittaker et al., 2017; Losos & Ricklefs, 2009). One particular aspect of ecology and evolution on islands underpins both their endemism and vulnerability, and describes how island species differ from their continental relatives.

The island syndrome

Decades of research focussed on island species have revealed an incredibly consistent pattern - that of similarity in morphology, behaviour, and life history traits among island species globally (Sandvig et al., 2019; Whittaker et al., 2023a). This pattern, referred to as the 'island syndrome', manifests as consistent directional change in traits such as body size (Benítez-López et al., 2021), growth rate (Sandvig et al., 2019) or number of offspring for island species (Covas, 2012). The island syndrome was first noted in island mammals with respect to body size (Foster, 1964; Van Valen, 1973). Since then, studies of other phylogenetic groups (Clegg & Owens, 2002) and traits (Adler & Levins, 1994) have shown the island syndrome to be a more widespread pattern. Today, it is recognised that the island syndrome may affect all island taxa to some extent (Wright et al., 2016), but that not all species reach the extreme trait values (Burns, 2022) that characterise famous island species, such as the Dodo (*Raphus cucullatus*) (Hume & Walters, 2017).

It has proven difficult to confidently identify and disentangle the drivers of the island syndrome (Whittaker et al., 2023a). The repeated similarity of abiotic and biotic conditions on islands is often argued as a key driver of the pattern. Island communities are usually species-depauperate and disharmonic in terms of occupied ecological niches (Simberloff, 1995; Lomolino et al., 2012). In addition, the diverse geological properties of islands (Ali, 2017; Whittaker et al., 2017), coupled with their limited size, are thought to result in limited resources and less seasonal conditions (Covas, 2012; Lomolino et al., 2012). These repeated properties, in spite of the overall geological diversity of islands, result in a selective

landscape that is repeated globally, wherein species experience limited abiotic resources, lower predation, and lower interspecific competition (Lomolino et al., 2012), whilst facing increased intraspecific competition (MacArthur et al., 1972). This proposed explanation for the similar trait distributions of species on islands invokes evolutionary change. Supporting this, patterns of trait evolution have been linked to patterns of predator and competitor richness on islands (Wright et al., 2016; Ponti et al., 2023). However, neutral explanations for the island syndrome also exist. These hypotheses include filters regarding colonisation, such as ability to cross dispersal barriers or establish in species impoverished island environments (Burns & Pugnaire, 2005; Lomolino et al., 2012; König et al., 2021), as well as random evolutionary drift towards some physiologically-defined optimum, in the absence of selection (Biddick & Burns, 2021). However, the relative contributions of these non-adaptive drivers remain unclear (Whittaker et al., 2023a) and have received limited study. Although parts of the island syndrome must involve evolutionary change (e.g. the evolution of bird flightlessness (Livezey, 2003)), studies of the island syndrome often fail to conclusively demonstrate this.

The problem of the island syndrome

The island syndrome represents one of the most widespread examples of trait similarity on the planet, potentially involving convergent evolution caused by similar ecological conditions on islands. Despite significant scientific interest in body size (Clegg & Owens, 2002; Biddick et al., 2019; Benítez-López et al., 2021) and life history evolution (Covas, 2012; Sandvig et al., 2019; Cooney et al., 2020), the island syndrome literature suffers from multiple problems.

Firstly, the island syndrome is supported by a methodologically diverse array of tests that have mostly used small sample sizes or examined different traits across disparate taxonomic groups (Whittaker et al., 2023b). The results of these studies are therefore difficult to compare. In particular, the extent to which taxonomic focus affects the evidence for the island syndrome is unclear. Furthermore, the biological extent of the island syndrome (i.e., which traits are affected) is not known for any single taxonomic group (Whittaker et al., 2023b).

Second, the diverse methodologies used to study the island syndrome tend to compare island species with their nearest mainland relative (e.g. Livezey, 2003; Biddick et al., 2019; Benítez-López et al., 2021), but often fail to include explicit phylogenetic methods (Whittaker et al., 2023a). Therefore, whilst evolutionary change is invoked as a key mechanism driving the island syndrome, the evidence for this is scant and restricted to certain traits (e.g. flightlessness (Wright et al., 2016; Sayol et al., 2020) or development (Sandvig et al., 2019;

Cooney et al., 2020) in birds). The island syndrome literature (with a particular focus on body size) has been criticised (Meiri et al., 2008). Specifically, it has been argued that observed patterns in body size 'evolution' on islands may represent an artefact, due to influential clades (e.g. giant bird groups such as elephant birds or moas). Explicit use of phylogenetic comparative methods can partially alleviate this problem by modelling the evolution of body mass alongside evolutionary history, together with other traits of interest.

The purpose of this thesis

In this thesis, I aim to review and expand our understanding of the biological extent of the island syndrome. In particular, I focus on studying this biological phenomenon in an explicitly evolutionary framework. The work presented here focuses on birds, the most speciose land vertebrates, with some 11,000 described species (del Hoyo & Allen, 2020). Birds are prime island colonisers, with 2,000 species endemic to islands (Tershy et al., 2015). They represent some of the best-studied organisms in the world, resulting in the widespread availability of data on their biology (Billerman et al., 2020; Tobias et al., 2022), distributions (BirdLife International and Handbook of the Birds of the World, 2020), and evolutionary history (Jetz et al., 2012). These data make it possible to examine patterns of evolution in island birds across thousands of species, whilst interest in the comparative genomics of birds (Feng et al., 2020) and knowledge of their natural history (Shirihai & Svensson, 2018) makes it possible to study micro-evolutionary changes in non-model species.

The following thesis is composed of four chapters:

Chapter 1 is a literature review that examines pattern of trait occurrence, and presumed adaptation, among island birds. This review, for the first time, synthesises all available evidence for the island syndrome and island adaptations in a major group of organisms. The chapter broadly spans morphology, behaviour, life history, and physiology, reviewing the evidence for the island syndrome, understood as a comparative pattern between mainland and island populations. The review is meant to serve as an authoritative introduction to the island syndrome, and recommends methodological improvements for further study of the island syndrome.

Chapter 2 is a biogeographical study of clutch size evolution in island birds. Clutch size is an important fitness-related trait. Using the largest sample size to investigate the island syndrome in any trait to date, I show that across 4,500+ species of birds, island breeding species have smaller clutches. This pattern is associated with breeding area of island birds, consistent with the expectation that island biogeographic patterns are an important driver. Additionally, I show this effect to be highly general across the avian tree of life, including unique groups such as seabirds, which have hitherto not been included in many island syndrome investigations.

Chapter 3 is a global study of an extended phenotype – the avian nest. This study presents data on five nest traits for all bird species in the world, supporting recent advances in our understanding of global nest traits. I use a subsample of 2,996 species (those for which complete data is available) to derive a multivariate description of nest architecture, spanning the entire diversity of birds for the first time. This 'morphospace' is then used to investigate patterns of biogeographic variation in nest architecture in relation to climate, predator diversity, and island endemicity.

Chapter 4 is an investigation attempting to clarify the relationships between, and the evolution of, the Eurasian Wrens (*Troglodytes troglodytes*) of the British Isles. This chapter uses genomics, sound recordings, and morphological measurements to explore: i) genetic divergence and population structure amongst the currently accepted Wren subspecies; ii) whether the Wrens show phenotypic patterns consistent with the island syndrome; and iii) characterise genomic patterns of evolution in different Wren populations to tentatively link divergent regions to observed phenotypic variation. This represents one of the few studies which link genomic variation and phenotypic similarity in island species, offering a glimpse into the micro-evolutionary patterns associated with the island syndrome.

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Chapter 1 – The island syndrome in birds

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Madeiran Chaffinch (*Fringilla madeirensis*), an endemic, recently recognised species that has evolved seemingly darker colouration on islands. © Michał T. Jezierski.

Abstract

The island syndrome is a widespread biological phenomenon that describes a suite of morphological, behavioural, demographic, and life history changes associated with island dwelling. These similar evolutionary responses among disparate groups of animals and plants represent a remarkable case of convergent evolution. Among animals, birds are a highly suitable group to study the island syndrome; they are a comparatively data-rich taxon, are frequent island colonisers, and sometimes display extreme adaptations such as the loss of flight. However, the avian island syndrome literature is fragmented, and multiple components are rarely considered together even though many are inextricably linked. We reviewed multi-species comparative studies, single-species or population-level studies, and anecdotal accounts, to summarise and assess the support for individual components of the island syndrome for birds, and to identify suites of traits that should be considered together. The weight of evidence for island syndrome patterns in morphology is substantial, but is more partial or even anecdotal for various aspects of behaviour, life history and physiology. Full validation of the island syndrome in birds will require the less-studied components to be treated in a comparative framework, and for covarying components to be examined in an integrated way. An improved description of the scope of the syndrome will pave the way to understanding its drivers.

Keywords: birds, colouration, ecological naivety, flightlessness, generalism, insularity, island biogeography, island syndrome, life history, morphology

Significance statement

The island syndrome is an example of convergent evolution of organismal traits on a wide taxonomic and geographic scale. We review the literature on components of this syndrome in island-dwelling birds, in order to lay the foundation for the development of a framework with which to investigate the interconnected drivers of island evolution in bird traits.

Introduction

The distinctiveness of island communities and species has captivated generations of biologists (MacArthur & Wilson, 1967). In the 20th century, recurring patterns of change in behaviour, ecology and morphology were noted (Foster, 1964), with the term 'island syndrome' introduced to describe consistent size, behaviour and life history shifts in island rodents (Adler & Levins, 1994). Components of this biological phenomenon have been characterised for a variety of organisms, including birds (Clegg & Owens, 2002; Covas, 2012), mammals (Lomolino, 2005; Lomolino et al., 2013), lizards (Novosolov, Raia, & Meiri, 2013), insects (Leihy & Chown, 2020) and plants (Biddick, Hendriks, & Burns, 2019; Burns, 2019; Nürk, Atchison, & Hughes, 2019). They include changes such as species becoming larger or smaller; producing fewer offspring that take longer to mature; and losing defence and escape adaptations such as flight. The taxonomic generality of some island syndrome patterns has been questioned (Itescu, Karraker, Raia, Pritchard, & Meiri, 2014; Meiri, Cooper, & Purvis, 2008), as not all aspects of the island syndrome are exhibited among taxa to an equal extent (Meiri, Dayan, & Simberloff, 2004; Orrock, 2010). Nevertheless, the evidence for the generality of the island syndrome is substantial, and the occurrence of such a widespread pattern is remarkable given differences in latitude, area, topography, isolation, and other island attributes (Ali, 2017; Weigelt, Jetz, & Kreft, 2013).

Such extensive convergent evolution has been attributed to the consistent ways in which island communities differ from mainland ones (Adler and Levins, 1994; Burns, 2019; Whittaker, Fernández-Palacios & Matthews, 2023). In general, island communities are

depauperate compared to mainland ones, with a lower number of species overall (Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017). Some functional groups, such as predators, are particularly under- or unrepresented on islands, creating a disharmonic community structure (Whittaker et al., 2023). This can lead to island populations undergoing density-compensation, with higher population densities than are observed on a similar-sized area of mainland (MacArthur, Diamond & Kerr, 1972; Wright, 1980). These differences extend from the theory of island biogeography (MacArthur & Wilson, 1967) and the dual limitations imposed by land area and geology (Valente et al., 2020; Whittaker et al. 2017), as well as island isolation (Valente et al., 2020), that interact with organismal traits such as dispersal ability and life history characteristics. The resulting biological communities often have lower predation, lower interspecific competition, lower resource availability and increased intraspecific competition (Lomolino, Sax, Palombo, & van der Geer, 2012). While a change in magnitude and predominant type of biotic interactions experienced by an island organism is often given as an intuitive explanation of a pattern observed (Lomolino et al., 2012), the relative contributions of drivers are rarely evaluated in a quantitative way. Smaller and more isolated islands should have communities most distinct from continental and hence are thought to favour evolution of the island syndrome (Lomolino, 2005; Lomolino et al., 2012). Indeed, comparative studies of body size in mammals (Lomolino et al., 2012; Benítez-López et al., 2021), and in birds, reptiles, and amphibians (Benítez-López et al., 2021) have shown stronger size shifts in smaller and more isolated islands. Furthermore, ecological release, immigrant selection, and resistance to climate have also been shown as

potential drivers (Lomolino et al., 2012), implying that both evolved differences, as well as filtering for certain traits that favour island colonisation, may contribute to such patterns.

While the original formulation of many of the components of the island syndrome was made using data from mammals (Adler and Levins 1994; Foster 1964), birds offer a very suitable case study for assessing widespread patterns and their underlying drivers because they are a well-studied group with a robust understanding of functional traits (Pigot et al., 2020), phylogeny (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), ecology and distribution (del Hoyo & Allen, 2020; Wilman et al., 2014). Approximately 19% (>1900 species) of birds are endemic to islands, and many individual components of the island syndrome have been examined; including size shifts (Benítez-López et al., 2021; Clegg & Owens, 2002), aspects of life history (Beauchamp, 2021; Covas, 2012; Sandvig, Coulson, & Clegg, 2019), dispersal limitations and flightlessness (Wright, Steadman, & Witt, 2016). Here we provide a review of avian functional traits on islands from the perspective of the island syndrome. In addition to including literature known to us, we identified studies on established and potential components of the island syndrome by performing simple searches on Web of Knowledge ('island bird [phenomenon of interest]), and by examining the reference lists of these sources. The resulting comparative and descriptive studies, both neo- and palaeontological, varied in the weight of evidence supporting the patterns, from well to partially supported, down to more anecdotal accounts. While not exhaustive, our review effectively captures four main aspects of bird biology relevant to the island syndrome: morphology (focusing on body size, bill morphology, brain size and flight apparatus), behaviour (predator naivety, ecological

niche, mating systems, and tool use and cognition), signalling (vocal and visual signalling), and life history and physiology (parental investment, growth and survival, and physiology). Many components of the island syndrome are inextricably linked, for example body size and pace of life history display covariance within and between species (Sibly & Brown, 2007; Sibly et al., 2012), therefore treating each in isolation inhibits a thorough understanding of the wider phenomenon. Hence, we highlight cases where trait covariation is well-established or intuited to encourage an integrated approach to understanding this phenomenon in birds, and we recommend further steps to better understand the avian island syndrome, and to expand this understanding to other taxa.

The functional span of the island syndrome in birds

We discuss the evidence for the island syndrome in species traits considered separately, because most studies focus on single traits. However, many of these traits evolve in tandem, responding to the same pressures or driving change in each other (**Figure 1 and Table S1**). The nature of covariation among traits will influence the order and magnitude of shifts and as such, the island syndrome should not be considered an 'all-or-nothing' phenomenon within or across species. Below, we summarise the existing evidence for morphological, behavioural, signalling, life history and physiological traits; with the caveat that covariation among these traits should always be considered.

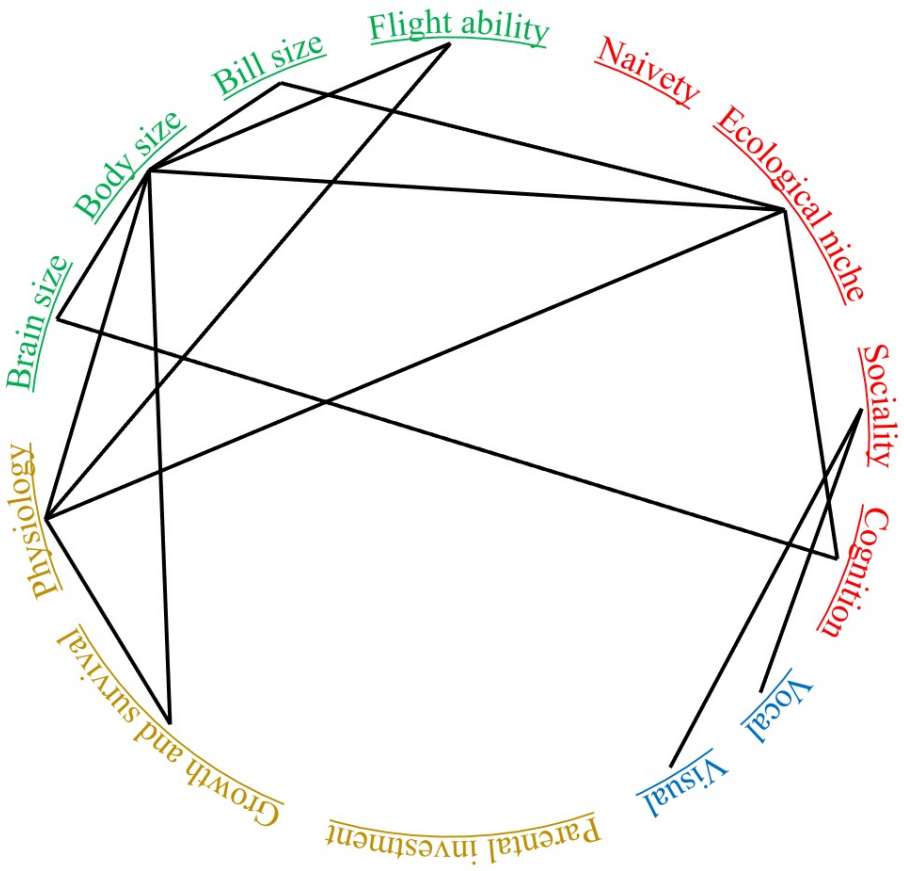

Figure 1. Examples of trait covariation that have been either explicitly investigated in the context of the island syndrome, or have been implied as highly-likely in publications about the island syndrome. Trait covariation is depicted by black lines. Links are based on example studies cited in **Table S1**.

Morphology

Changes in morphology in island taxa are wide-ranging. They include changes in body size, proportional bill size, brain size, and limbs, along with resultant changes in flight ability. While evolution of body size is expected to also result in allometric change in multiple aspects of morphology, allometric relationships often break down in island forms with traits

being exaggerated or diminished relative to body size. Body size evolution and reduction/loss of flight are perhaps the best supported general trends of the avian island syndrome, though neither is ubiquitous. Islands are also known for the evolution of some highly specialised morphologies, rarely found in continental birds (Mayr, 2017), such as wing clubs in the extinct Rodrigues Solitaire *Pezophaps solitara* (Hume & Steel, 2013) and Jamaican Ibis *Xenicibis xympethicus* (Longrich & Olson, 2011), hypothesised to have been used for fighting (Hume & Walters, 2017). The frequency and form of specialised morphological traits have not been comparatively assessed.

Body size

The pattern referred to as the 'island rule', originally described in mammals (Foster, 1964) describes a tendency to evolve towards medium body size on islands; species with large continental ancestors become smaller, and vice versa (Lomolino et al., 2013). The island rule is thought to occur due to nearly the full scope of proposed explanations for the island syndrome: resource limitations, release from predation and competition, and filtering during dispersal (immigrant selection), all acting in tandem to determine the extent of change in size (Lomolino et al., 2012). While controversial as a ubiquitous pattern (Lomolino et al., 2013; Meiri et al., 2008), it is currently well-verified in land vertebrates (Benítez-López et al., 2021) and plants (Biddick et al., 2019). Body size evolution in island birds has been studied using large comparative datasets as well as species and population comparisons of continent-island pairs, and a diversity of size indices, including mass (e.g. Clegg and Owens 2002), and indices derived from body measurements such as principal components (e.g.

Bell 2018). Multiple comparative studies have shown that birds on islands follow the island rule, a pattern most pronounced on remote, small islands (Bell, 2018; Benítez-López et al., 2021; Boyer & Jetz, 2014; Clegg & Owens, 2002). Furthermore, a recent study of 120 island-continental bird species pairs has demonstrated that the island rule shows a stronger pattern in the absence of predators, supporting the traditional idea of the role of this biotic interaction (Ponti, Doutrelant, & Covas, 2023). The island rule is also apparent in comparisons of the same species occurring on both islands and continents: among subspecies (e.g. Varied Tit *Poecile varius* (Fujita, Nishiumi, Yamaguchi, Fujita, & Higuchi, 2014), Emu *Dromaius novaehollandiae* (Heupink, Huynen, & Lambert, 2011), Silvereye *Zosterops lateralis* (Estandía, Sendell-Price, Robertson, & Clegg, 2023)); and among populations (e.g. Coal Tit *Periparus ater* (Norberg & Lindhe Norberg, 2015), Grey Jay *Perisoreus canadensis* (Strickland & Norris, 2015)), even those recently introduced to islands (e.g. Great Kiskadee *Pitangus sulphuratus* (Mathys & Lockwood, 2009)). Some exceptions occur, e.g. White-fronted Chat *Epthianura albifrons* populations not changing in size as expected (Major, 2012). However, the generality of the island rule in birds is robustly supported among hundreds of species (see Benítez-López et al., 2021).

In addition to a general tendency to evolve medium body size on islands, there is also the more frequent occurrence of ‘giants’ or ‘dwarfs’ (defined as large scale deviations from size of most congeners) on islands than on continents (Meiri, Raia, & Phillimore, 2011). Neither phylogeny or ecology appears to account for the evolution of insular giants and dwarfs; both are scattered throughout the avian phylogeny, and they represent a wide variety of forms with

respect to the original ecological niche. Island giants have experienced high extinction rates, likely due to their extreme specialisation (Fromm & Meiri, 2021), including flightlessness (Sayol, Steinbauer, Blackburn, Antonelli, & Faurby, 2020), and are well known from fossils and subfossils. Island dwarfs may once have been more common, and experienced similar extinctions, but as small fossils are less likely to survive, there may be a taphonomic bias in the record of size distributions of extinct island birds. Additionally, there may be a publication bias towards charismatic island giants. Alternatively, because birds are overall quite small in size relative to other vertebrates (Pigot et al., 2020) there may be more scope for giantism given a particular starting point. Many of the largest known members of bird families, or higher taxonomic levels, are island endemics (e.g. Dodo *Raphus cucullatus* among Columbidae, South Island Takahē *Porphyrio hochstetteri* among Rallidae, Hercules Parrot *Heracles inexpectatus* among parrots (Worthy, Hand, Archer, Scofield, & De Pietri, 2019)). The hummingbirds (Trochilidae), which account for much of the lower end of mass distribution of birds (Tobias et al., 2022), only have 19 out of 353 species as island endemics (including the smallest known bird, the Bee Hummingbird *Mellisuga helenae*). Outside of hummingbirds, the four smallest bird species (the Pygmy Bushtit *Aegithalos exilis*, Handsome Sunbird *Aethopyga bella*, Lovely Sunbird *Aethopyga shelleyi*, and the Flamecrest *Regulus goodfellowi*) are all island endemics. However, island dwarfism has received limited attention in birds (but see Meiri et al., 2011), and evolution of avian size extremes would merit a more comparative approach, as has been recently done in plants (Burns, 2022).

Bill size and shape

Changes in overall body size might be accompanied by concomitant changes in other traits due to allometric scaling, but there may also be changes in relative proportions as allometric relationships are decoupled. Bills have received significant attention due to their role in adaptation to feeding niches, signalling and thermoregulation (Friedman et al., 2019; Pigot et al., 2020), with early studies describing non-allometrically longer, wider, and deeper bills in insular birds versus their continental counterparts (Grant, 1965). However, the inclusion of species with a greater range of starting sizes revealed that bills follow island rule-like patterns with changes in feeding being a potential driver (Clegg and Owens 2002) (see 'Behaviour: Ecological release' and 'Tool use and cognition' sections below). Multiple studies have noted that passerines on islands have longer or larger (deeper and wider) billed forms such as reed warblers *Acrocephalus* (Bell, 2018; Leisler & Winkler, 2015); white-eyes *Zosterops* (Clegg et al., 2002; Dutson, 2008); Hawaiian honeycreepers (Fringillidae) (Lovette, Bermingham, & Ricklefs, 2002); New Holland Honeyeaters *Phylidonyris novaehollandiae* (Myers, Brown, & Kleindorfer, 2010); Great Kiskadees *Pitangus sulphuratus* (Mathys & Lockwood, 2009); Song Sparrows *Melospiza melodia* (Greenberg & Danner, 2013); Yellow Warblers *Setophaga petechia* (Luther & Greenberg, 2014); Dark-eyed Juncos *Junco hyemalis* (Aleixandre, Hernández Montoya, & Milá, 2013); Eurasian Jays *Garrulus glandarius* (Aoki, Iwami, & Takagi, 2021); towhees *Pipilo* (Olson & Wingate, 2012) and Gulf of Guinea thrushes *Turdus* (Melo et al., 2010). Smaller bills in island passerines, despite increased body size, have also been noted e.g. in Superb Fairywren *Malurus cyaneus* (Dudaniec, Schlotfeldt, Bertozzi, Donnellan, & Kleindorfer, 2011). Among other bird families, a tendency for longer

bills has been found in pigeons (Andrade et al., 2021; Heathcote, De Ruyck, Des Brisay, Grieef, & Koper, 2021), oystercatchers (Collar, Donald, & Kirwan, 2021) and herons (Kushlan, 2009), but not in some moorhen subspecies (DesRochers, Silbernagle, Nadig, & Reed, 2010). In addition to size changes, cases of highly modified bills evolving in insular contexts include the Dodo *Raphus cucullatus* and the Rodrigues Solitaire *Pezophaps solitara* (Mayr, 2017), adzebills (Mayr, 2017; Worthy, Tennyson, & Scofield, 2011), Hawaiian honeycreepers (Navalón, Marugán-Lobón, Bright, Cooney, & Rayfield, 2020) and vangas (Jønsson et al., 2012). While examples focusing on individual populations/subspecies, and sometimes bird families, are common, island bird bill size and shape trends could be revisited with a comparative approach, especially in the light of novel availability of trait data for all bird species (Tobias et al., 2022).

Brain size

Island birds have relatively larger brains than continental relatives, providing another example of a deviation in allometric relationships (Sayol, Downing, Iwaniuk, Maspons, & Sol, 2018). The pattern found from examining 1931 species of birds from across the avian phylogeny represented *in situ* evolution on islands, as island-colonisers were not more likely to originate from large-brained groups. In this study, brain size was correlated with increased behavioural flexibility and slower pace of life, highlighting covariation between island syndrome traits (Sayol et al., 2018). In other studies, brain size has been linked to many phenotypes common in island endemics, including flightlessness (Nakao, Yamasaki, Ogihara, & Shimada, 2022), being resident (Sol et al., 2010), and higher territoriality (Hardie

& Cooney, 2023). Local modifications of brain structure are also described for island birds, though their taxonomic extent may be more limited. These include modifications of the olfactory bulbs and optic lobes in the elephant birds of Madagascar (Aepyornithiformes) (Torres & Clarke, 2018), the kiwis (Apterygidae) (Witmer, Ridgely, James, Olson, & Iwaniuk, 2017), and Rodrigues Owls *Otus murivorus* (Duhamel, Hume, Guenser, Salaviale, & Louchart, 2020) and expansions of somato-sensory systems as in the Mole Duck *Talpanas lippa* (Iwaniuk, Olson, & James, 2009; Witmer et al., 2017). These result in olfaction and tactile sense-driven sensorics, as opposed to vision as is more common in birds (Martin et al., 2007). Therefore, evolution of the proportionally larger brain size as part of the island syndrome appears well supported, however focusing on finer details of evolution of brain anatomy could reveal further patterns associated with sensory systems.

Flightlessness and reduced flight ability

Flightlessness, defined as complete or near-complete loss of flight, evolved up to 150 independent times across the bird phylogeny (Sayol et al., 2020) and is predominantly an island phenomenon, with 468 of 581 known flightless species occurring on islands. Loss of flying ability is closely linked to variation in body size, as flightlessness tends to evolve in tandem with increased body size, and breaking of allometric scaling with evolution of shorter wings relative to body size (Livezey, 2003). Some bird clades have a particular proclivity to evolve flightless species, and these tend to be island endemics (Sayol et al., 2020). These include gruiforms (cranes and rails, especially Rallidae rails) (Boast et al., 2019; Garcia-R, Gibb, & Trewick, 2014; Livezey, 2003; Oswald et al., 2021) and anseriforms (Iwaniuk et al.,

2009; Williams, 2015; Witmer et al., 2017). Even passerine birds (Passeriformes) have flightless representation, especially New Zealand wrens Acanthisittidae, but also buntings Emberizidae (Millener, 1988; Rando, Alcover, & Illera, 2010; Rando, López, & Seguó, 1999). Biological traits that might predispose a taxon to evolve flightlessness on islands remain uncertain, though ideas include having shorter wings than expected for body size (McCall, Nee, & Harvey, 1998) and exhibiting simultaneous moult (Terrill, 2020).

Island-dwelling birds may not experience drastic loss of flying ability, but rather a general shift in the proportions of wings, legs, and pectoral muscles, resulting in greater hindlimb over forelimb investment, reduced flight ability and hence reduced dispersal capacity (Wright et al. 2016). Examples include Eurasian Blackcaps (*Sylvia atricapilla*) and Common Snipe (*Gallinago gallinago*) in the Azores (Andrade et al., 2015; Rodrigues, Andrade, Rodrigues, & Gonçalves, 2018); Grey Jays (*Perisoreus canadensis*) on Anticosti Island (Strickland & Norris, 2015) Guadalupe Junco (*Junco hyemalis insularis*) (Aleixandre et al., 2013) and São Tomé Short-Tail (*Motacilla bocagii*) (Alström et al., 2015). These changes occur even in clades with no flightless members, such as kingfishers or tanagers (Wright et al., 2016). Therefore, loss of flight ability seems to be strongly supported across multiple comparative studies, but may be underestimated due to frequent lack of incorporation of palaeobiological data. The gradient of changes in flight ability may evolve in the face of the same drivers – as predation becomes less likely, the maintenance of expensive flight apparatus may be too costly. As there is evidence of a tendency to have slower metabolism in island birds (see the ‘Life history and physiology: Physiology’ section), both complete and

partial weakening of flying ability may be an energy-saving strategy, with the outcome dependent on other aspects of species' biology, such as body size change, moult, and diet.

A large comparative study revealed that the wing aspect ratio, as measured by hand-wing index (HWI), is higher in island species (Sheard et al., 2020). HWI is interpreted to represent flight capacity, therefore this result is contrary to what is known from behavioural and other morphological studies. A degree of flightlessness can even occur without morphological change, due to the phenomenon of behavioural flightlessness (Diamond, 1981), where a bird is reluctant to fly, either completely or over longer geographic distances. This results in loss of dispersal and migratory propensity and has been suggested as a precursor to morphological flightlessness (Diamond, 1981). Loss of distant dispersal and migration ability may be extreme on islands, as exemplified by the non-migratory Polynesian Sandpipers *Prosobonia* (De Pietri et al., 2020), which belong to the highly migratory family Scolopacidae. However, losses of migratory behaviour or other examples of behavioural flightlessness have not been quantified beyond these anecdotes in island species, and would merit further natural history study to generate comparative data.

Behaviour

In comparison to morphology, behaviour has received less attention in terms of the island syndrome. While island species have frequently been included in bird behaviour studies, a more comparative approach has rarely been used other than for sociality and reproductive behaviours. Colonising and establishing on an island can be a significant challenge for birds, likely requiring behavioural flexibility and novel ways to exploit resources (Gavriilidi, De Meester, Van Damme, & Baeckens, 2022). A range of behavioural traits may be exploited to meet these challenges, and altered landscapes of biotic interactions may cause rapid behavioural responses (Gavriilidi et al., 2022; Tebbich, Sterelny, & Teschke, 2010). In birds, behavioural traits covary with each other (e.g. dispersal and aggressive behaviour, other aspects of biology, including body size, brain size, bill size, and pace of life (see **Table S1** and references therein).

Predator naivety

Tameness and predator naivety are often associated with island species, and attributed to the absence or reduction in the predator threat (Hume & Walters, 2017) because maintaining anti-predator responses is energetically expensive (Beauchamp 2015, Cooper & Blumstein, 2015). However, empirical studies are few, with the common perception of 'naïve' island endemics mostly stemming from older travel accounts (Hume & Walters, 2017). Some evidence that island birds change their behaviour come from studies of flight initiation distance (FID), the distance at which a bird can be approached before it flies away, frequently used as a proxy of fear (Blumstein, 2003). However, the evidence is mixed. In the

Small Ground Finch (*Geospiza fuliginosa*) of the Galapagos Islands, FID is much lower in pristine habitats as opposed to those with invasive predators (Gotanda, 2020). In the Bull-headed Shrike (*Lanius bucephalus*) that established breeding populations on the Ryukyu islands in 2012, higher FID occurs on islands (Shoji Hamao, Torikai, Yoshikawa, Yamamoto, & Ijichi, 2020). However, quantitative comparative studies of flight initiation distance or other measures of naivety are lacking in island birds (but see Cooper, Pyron, & Garland, 2014 for one such study in lizards). In the absence of such studies at this point, extinctions on islands may serve as a proxy of whether predator naivety was common or not (Berger, Swenson, & Persson, 2001). Bird extinctions are positively correlated with numbers of introduced predators to islands (Blackburn, Cassey, Duncan, Evans, & Gaston, 2004). At least 22 avian extinctions on islands can be directly attributed to novel predators (Medina et al., 2011), and other negative impacts are particularly common with threats unique on islands such as generalist ground mammals (e.g. rats) (Harper & Bunbury, 2015). Therefore, it can be assumed that predator naivety may be a common aspect of the island syndrome in birds, but confirmation requires comparative data, keeping in mind that species displaying extreme naivety are more likely to have suffered anthropogenically driven extinctions.

Ecological release

The term ecological release encompasses both niche widening and niche shifts that occur when biotic constraints such as interspecific competition are removed (Herrmann, Stroud, & Losos, 2021). Island birds undergo ecological release in that they tend to have wider ecological niches than mainland counterparts (Diamond, 1970; Scott, Clegg, Blomberg,

Kikkawa, & Owens, 2003). Wider niche availability is afforded by having fewer interspecific competitors and lower risk of predation. A wider population-level niche can be achieved by all individuals having a broad niche, or each individual having a narrower but different niche (Bolnick et al., 2003). Few studies have examined how niche expansion is achieved at the individual level, but generalist populations consisting of individual specialists have been reported for several island bird populations (Price, 1987; Scott et al., 2003; Werner & Sherry, 1987). The distinction is important in the context of the island syndrome because feeding ecology may influence multiple morphological components including body and bill size (Clegg & Owens, 2002), as well as brain size (Hardie & Cooney, 2023). Niche shift patterns are also known from numerous observational studies (Alström et al., 2015; Diamond, 1970). Niche width and niche shift patterns on islands have not been investigated in a large comparative or phylogenetic framework. Because of the relative ease and long history of collecting bird feeding observations and habitat associations, it is likely that a treasure-trove of quantitative data could be extracted from dispersed sources (e.g. from classic texts Lack & Gillmor, 1971; Mayr, Diamond, & Pratt, 2001 and older papers e.g. Diamond & Marshall, 1977). However, the manner in which individual variation influences the nuances of niche expansion on islands requires further data collection from a range of species to determine generalities.

Mating systems and sociality

Changes in mating systems and the breeding biology of island birds manifest in a number of ways, and comparative studies have demonstrated clear differences between island and

continental species. Lower levels of extra-pair paternity in island passerines were previously reported (Griffith, 2000) and some of the lowest levels of extra-pair paternity in birds are found in the island-rich Madagascar and Oceania zoogeographical realms (Valcu, Valcu, & Kempenaers, 2021). However the accumulation of studies showing that some island species have similar or higher rates of extra-pair paternity than nearest mainland relatives suggests that the comparative pattern should be revisited (see for example: African Blue Tits (*Cyanistes teneriffae*) (Garcia-Del-Rey, Kleven, & Lifjeld, 2012), Eurasian Blue Tits (*Cyanistes caeruleus*) (Charmantier & Blondel, 2003), Hihi (*Notiomystis cincta*) (Brekke, Bennett, Santure, & Ewen, 2011), Seychelles Warblers (*Acrocephalus sechellensis*) and Chatham Islands Black Robins (*Petroica traversi*) (Forsdick, Cubrinovska, Massaro, & Hale, 2021)).

Co-operative breeding occurs more frequently on islands (Covas, 2012). In a sample of 237 species pairs, 17.3% of island species bred cooperatively compared to 9% on continents, and additionally they were more frequently found to be living in family groups (19% on islands compared to 14.8% on mainlands) (Covas, Bliard, Ribeiro, Paquet, & Griesser, 2022). Exceptions occur, for example in insular White-Winged Fairy-Wrens (*Malurus leucopterus*), where populations are socially monogamous rather than co-operative breeders as seen on the mainland (Rathburn & Montgomerie, 2003). Social monogamy is generally common among birds (Lack, 1968), and examples of well-characterised socially monogamous breeding systems on islands also show genetic monogamy like in the Capricorn Silvereye (*Zosterops lateralis chlorocephalus*) (Robertson, Degnan, Kikkawa, & Moritz, 2001), New Zealand Saddlebacks (*Philesturnus carunculatus*) and New Zealand Robins (*Petroica*

australis) (Taylor, Boessenkool, & Jamieson, 2008). The occurrence of bi-parental care between island and continental species is similar (Covas, 2012). While these conclusions are largely based on comparative analyses, they rely on just two papers, and therefore investigation into differences between island and continental bird species sociality and mating systems should be continued and expanded. Suggested selective drivers for an increase in the occurrence of co-operative breeding on islands include a combination of restricted resources, high density populations; and higher survival of island birds (Covas, 2016) (and see 'Life History and Physiology' section below), however these ideas require investigation.

Tool use and cognition

Due to increased brain size, birds on islands may display more innovative and flexible behaviours (Sayol et al., 2018). Tool use in the wild appears more common in island bird species (Gavriilidi et al., 2022) except for nest construction and prey-dropping (Switzer & Cristol, 1999). There are multiple examples of foraging-based tool use in island birds. The Woodpecker Finch (*Camarhynchus pallidus*) uses cactus needles to pry insects out of wood (Tebbich, Taborsky, Fessl, & Dvorak, 2002). The Hawaiian Crow (*Corvus hawaiiensis*) and the New Caledonian Crow (*Corvus moneduloides*) fashion elaborate tools for the same purpose (Hunt & Gray, 2004; Rutz et al., 2016). In parrots, Goffin Cockatoos (*Cacatua goffini*) of the Tanimbar Archipelago (Auersperg, Szabo, von Bayern, & Kacelnik, 2012), and the New Zealand Kea (*Nestor notabilis*) (Goodman, Hayward, & Hunt, 2018) show a range of innovative tool uses. Additionally, the New Zealand Kākā (*Nestor meridionalis*) has been

recently observed to engage in potential anti-predatory tool use by throwing wood on a falcon (Burns, 2021). Overall, the topic of cognition in island birds remains relatively unexplored and requires further natural history observation (Gavriilidi et al., 2022), but new reports on tool use are appearing frequently e.g. Fayet, Hansen, & Biro, 2020 which may allow comparative analyses in the future.

Signalling

We consider two aspects of signalling, songs (and calls) and colouration, in relation to the island syndrome. We have separated signalling from behaviour despite partial overlap. Signalling will be very closely linked to other behavioural traits that may impact how signals are generated, along with morphology and physiology that determine the size, shape, form and quality of signals (Hamilton & Zuk, 1982). Both song and colouration of island forms have been investigated with comparative approaches. Studies have ranged from tens or hundreds of comparisons, and examination of different facets of these complex traits, and consistent patterns have not always emerged.

Vocal communication

Bird song is a highly conspicuous, well-studied and important signal used by birds in interacting with other individuals, including in terms of sexual and territory advertisement (Catchpole, Slater, & Mann, 2008). Song can diverge following island colonisation as a result of population bottlenecks during founding, cultural drift, acoustic adaptation to new environments and/or changed sexual selection regimes (Potvin & Clegg, 2015). Furthermore,

changes in body size alter the qualities of songs as larger species tend to produce lower frequency songs (Mikula et al., 2021), while changes in mating systems and loss of migratory behaviour may also cause song divergence (Read & Weary, 1992). Morinay, Cardoso, Doutrelant, & Covas, (2013) found in a study of 49 species pairs that song on islands are less likely to include potentially aggressive elements, such as rattles and buzzes, but did not significantly differ in complexity metrics, such as syllable diversity. A comparison of 11 species pairs from mainland Africa with species on Sao Tome and Madeira found no significant differences in syllable diversity, delivery rate or song duration (Robert, Lengagne, Melo, Gomez, & Doutrelant, 2022). Reudink et al., (2021) examined species pairs for 731 species of Meliphagidae (honeyeaters), Fringillidae (finches) and Monarchidae (monarch flycatchers), and reported no significant differences in aspects of song complexity or performance, though birds inhabiting smaller islands tended to have fewer syllables in their songs. In the Eurasian Chaffinch (*Fringilla coelebs*) there is progressive loss of song structure from continental Africa to more remote islands in Macaronesia (Lachlan et al., 2013). Song complexity in island populations or subspecies changes in variable ways. For example, it decreases in Red-Capped Robins (*Petroica goodenovii*) and Singing Honeyeater (*Gavicalis virescens*) on Rottnest Island, Australia (Baker, Baker, & Tilghman, 2006), in the Japanese Bush Warbler (*Horornis diphone*) on Ogasawara Islands (Hamao & Ueda, 2000) and in the Zebra Finch (*Taeniopygia guttata*) on Timor (Lansverk et al., 2019), but increases in complexity in the Western Gerygone (*Gerygone fusca*) on Rottnest Island (Baker et al., 2006) and in the Guadalupe Junco (*Junco hyemalis insularis*) (Aleixandre et al., 2013). Time since colonisation has been shown to affect patterns of song diversity as the influence of different

drivers change (Potvin & Clegg, 2015). Initial changes to song may be largely due to population bottlenecks associated with island colonisation, but syllable innovation and acoustic adaptation to island environments may proceed with time. This may partially explain why the results of both large-scale comparative studies and single case studies have reported variable results. While there is a considerable body of comparative work on song, clearly further investigation is needed to ascertain the direction of changes. As bird song and calls are now readily available for nearly all bird species on databases such as xeno-canto, studies encompassing the full suite of bird diversity could search for the most consistent pattern of vocal evolution in island birds. Studies below the species level likely require the collection of more recordings to quantify population variability.

Colouration

Colouration is a complex trait, that can be used actively and passively in signalling, and be moderated by both morphology and behaviour. In the island syndrome literature, there has been a long-held notion that birds on islands are less colourful – and this is supported by recent large scale comparative studies. Doutrelant et al., (2016) found that birds on islands tend to be less bright and colourful, and males also have a significantly decreased number of colour patches, related to lower number of same-family sympatric species. Particular examples include reduced brightness in island male wildfowl (Figuerola & Green, 2000), increased dullness of island species in Western Palearctic birds (Fitzpatrick, 1998), increased uniformity of male colour of *Terpsiphone* flycatchers on islands (Fabre et al., 2012), and decreased male colouration (but increased female colouration) in Pacific Robins

(*Petroica* sp.) (Kearns, Joseph, Austin, Driskell, & Omland, 2020). While the pattern generally holds, there are some cases where particularly colourful groups occur in insular settings, such as birds of paradise (Paradisaeidae), predominantly occurring in New Guinea, with some species also found in Australia. Recent studies have shown that fewer predators occurring on islands are correlated with evolution of more colourful plumage in a sample of 110 species pairs (Bliard et al., 2020). In birds of paradise specifically, aspects of mating systems, and the unique displays of these birds, affect the degree of sexual dichromatism and colouration as well (Miles & Fuxjager, 2018). However, the ways in which the evolutionary trend to increase in colour with fewer predators interacts with the general tendency towards duller plumage, potentially promoted by relaxed species recognition requirements in lower diversity communities (Doutrelant et al. 2016), is currently unclear. Because evolution of colouration will be affected by an interplay of sexual selection, the need for separation from other species, and interaction with predators, it would particularly benefit from investigation of further drivers, some of which may currently be unknown.

Melanism (darker colouration) patterns are known to systematically vary in some groups. A tendency for repeated evolution of melanism on islands has been observed, for example in *Monarcha* flycatchers (Uy & Vargas-Castro, 2015). Some well-known melanistic forms occur exclusively on islands, including melanistic Tahiti Reed-Warblers (*Acrocephalus caffer*) (Cibois, Thibault, & Pasquet, 2012), Canarian Oystercatcher (*Haematopus meadewaldoi*) (Collar et al., 2021) (but note that within *Haematopus* there are multiple continental and island species in the Southern Hemisphere, so biogeographic origin may matter), or the

'Veiled' Eurasian Blackcap (*Sylvia atricapilla*) morph of Macaronesia (Berthold, Mohr, & Querner, 1997). In contrast, within the Barn Owl complex (39 taxa of *Tyto alba* ssp. or *Tyto* sp.) island owls tend to be lighter with less eumelanistic (dark) colouration, and more pheomelanistic colours (brown and rufous) than continental forms (however as islands become smaller birds become darker than on larger islands) (Romano, Séchaud, & Roulin, 2021; Roulin & Salamin, 2010). The possibility of increased melanism as an island syndrome component warrants a wider comparative approach, as current examples are too few and phylogenetically disparate.

Life history and physiology

Changed selective pressures on islands will significantly affect life history, and concurrently physiology. Firstly, as the environment is expected to favour competitive individuals, slower pace of life focusing on quality, not quantity, is likely to evolve. Secondly, changes across morphology and behaviour are also likely to be intertwined with a shift towards slower life histories. Slower pace of life generally translates into smaller clutches of larger-sized offspring, longer developmental periods, increased survival, and higher longevity (Stearns, 1992). Despite the popularity of birds as models with which to study life history, relatively little of it has been studied in an island context. Only some aspects of avian life histories and physiology have been examined comparatively, often with relatively small species sample sizes.

Investment in offspring

Comparative studies reveal that island birds generally have smaller clutch sizes after accounting for latitudinal effects (Covas, 2012; Jetz et al., 2012). Specific examples include community-wide decreases in clutch size in Sri Lankan passerines relative to other regions of the Indian subcontinent (Padmanabhan & Yom-Tov, 2000), and island populations of Japanese Bush Warblers (*Horornis diphone*) (Hamao & Hayama, 2015), rails (Rallidae) (McNab & Ellis, 2006), Southern House Wren (*Troglodytes aedon chilensis*) (Ippi, Vásquez, Moreno, Merino, & Villavicencio, 2012), Eurasian Blue Tits (*Cyanistes caeruleus*) (Blondel, Pradel, & Lebreton, 1992), African Blue Tits (*Cyanistes teneriffae*) and Ma'oma'o (*Gymnomyza samoensis*) (Stirnemann, Potter, Butler, & Minot, 2016). Exceptions occur such as the Eastern Bluebirds (*Sialis sialis*) of Bermuda, which show comparable clutch size to mainland populations (Matson, Mauck, Lynn, & Tieleman, 2014). Smaller clutch sizes are associated with increased egg size in birds (Blackburn, 1991), resulting in more parental investment per offspring. Specific studies of egg size in island forms show variable support for the expectation of larger eggs in island birds. In the extinct Emu subspecies (*Dromaius novaehollandiae* ssp.) egg sizes of the smaller-sized island subspecies were within the range of the continental Emu (Hume & Robertson, 2021), hence egg size is increased relative to body mass. However, a study of birds introduced to New Zealand found that, for those species where egg size changed, smaller eggs were produced (Congdon & Briskie, 2010). While island clutch size patterns are generally well established, a broader taxonomic perspective would help to identify exceptions and mechanisms. The subsequent

expectation of larger egg sizes associated with smaller clutches remains to be tested in a comparative framework.

Growth, development, and survival

Other stages of life history show consistent patterns of slow-down in island birds. Slower developmental periods in island birds are evidenced by longer incubation times (36 species pairs (Covas, 2012)), and a tendency for slower growth rates (264 altricial bird species, including 33 island growth rates (Sandvig et al., 2019)). Longer brood-rearing time is known from single-species cases e.g. 59-63 days in Hawaiian Hawks (*Buteo solitarius*) compared to average of 43 days for temperate congenerics (Griffin, Paton, & Baskett, 1998). Annual survival for both juvenile and adult life stages is higher in island birds (adult survival rates from 697 species including 154 island species (Beauchamp, 2021); juvenile survival rates from 342 species including 51 island species (Beauchamp, 2022)). Wasser and Sherman found that longevity of island species is almost twice that of continental counterparts (longevity data on 470 species including 76 island species (Wasser & Sherman, 2010)). In many of these studies, the proportion of island species was relatively low, reflecting the lack of life history studies in island populations. Thus, increased survival as part of the island syndrome is considerably well supported across a diversity of species. However, the pace of growth needs more examination, as while the patterns are tentatively promising, they are based on too few species to be certain of generality.

Physiology – metabolism and immune function

Multiple examples of slower metabolic rates are known for both flightless and volant island birds, likely related to an increase in size and the slowing down of life histories. A shift to flightlessness allows energy conservation achieved via lower flight muscle mass and basal metabolic rate, and therefore strongly links with slower overall metabolism, as seen in kiwis (*Apterus* sp.) (McNab, 1994), Kakapos (*Strigops habroptilus)* (McNab & Salisbury, 1995), flightless rails Rallidae (McNab & Ellis, 2006) and flightless ducks Anatidae (McNab, 2003). Examples of volant island birds with very low metabolic rates compared to continental relatives include flighted Anatidae of New Zealand (McNab, 2003) and pigeons Columbidae of the South Pacific (McNab, 2000). Exceptions have been noted, such as the honeyeater Tūī (*Prosthemadera novaeseelandiae*) endemic to New Zealand, that has a similar basal metabolic rate relative to honeyeaters Meliphagidae of the Australian mainland (McNab, 2016). Another dimension of lower rates of metabolism on islands may stem from nutritional stress, as has been shown for Red-billed Choughs (*Pyrrhocorax pyrrhocorax*), where Canary Islands populations show clear signs of nutritional stress attributed to low insect abundance, and a subsequent shift to fruit-eating (Blanco, Laiolo, & Fargallo, 2014). As interpretations about metabolic rate changes on islands stem from mostly species-specific papers, with a comparative perspective only for New Zealand taxa, further empirical work is needed.

Isolated islands and archipelagos can provide an evolutionary refuge from parasites and disease. The maintenance of immune function is costly (Hanssen, Hasselquist, Folstad, &

Erikstad, 2005; Martin, Scheuerlein, & Wikelski, 2003), and a loss of immune function and high susceptibility to disease have been observed in some of the most isolated island avian communities, such as in the Galapagos (Wikelski, Foufopoulos, Vargas, & Snell, 2004), or among Hawaiian Honeycreepers (Mohoidae) (LaPointe, Atkinson, & Samuel, 2012) where historical introductions of diseases have had devastating consequences. In less isolated situations, reduced parasite loads are sometimes (Loiseau et al., 2017), but not always (Ishtiaq et al., 2010) observed. Following from this, patterns of immune function shifts are varied. Barthe et al., (2022) showed that among immunity-related genes in 34 species of birds including 20 island cases, only major histocompatibility complex II showed evidence of relaxed selection, while major histocompatibility complex I, Toll-like receptors and beta-defensins showed no such signals. Similarly, immune indices measured from 25 species, encompassing continental and island populations in the Nearctic, showed no obvious attenuation in island populations, and even increases in some (Matson, 2006). Finally, across 21 species comparisons of populations on the islands of São Tomé and Príncipe versus continental West Africa, the island populations had lower immunoglobulin levels, but no significant change in haptoglobins (Lobato, Doutrelant, Melo, Reis, & Covas, 2017). Immune function is a complex trait and can change along various axes (Matson 2006). Information from many more island species would help to reveal if there are general or specific changes in immune capabilities of island birds.

Conclusion

The aim of this review was to draw together disparate empirical and anecdotal evidence regarding the evolution of avian traits on islands. We have collated a large number of examples that highlight patterns consistent with the current understanding of the island syndrome, exceptions to these patterns, and components that with more data, might form part of the island syndrome. With this framework, shortfalls in the scope of traits studied are apparent. Only body size has received a somewhat comprehensive treatment, where significant proportions of avian diversity have been compared for differences between island and continental taxa. Comparative treatments have been applied to other aspects of morphology, mating systems and sociality, song, reproduction, growth strategies and immunological differences, but all of these considered a limited number of taxa. Few studies examine more than 100 species on islands, which corresponds to less than 5% of island avian diversity, and not all treat the data in a phylogenetic or paired comparison framework (but see Benítez-López et al., 2021; Clegg & Owens, 2002; Covas, 2012; Sayol et al., 2018; Wright et al., 2016). A much larger proportion of bird diversity will need to be examined to ascertain the generality of the patterns observed in smaller comparative studies. In some traits, such as occurrence of unique morphological structures, predator naivety, widened use of ecological resources, tool use, colouration, egg size or physiology, the evidence for an island syndrome mostly relies at single-family or lower taxonomic level studies, and broader generality requires further empirical data and comparative treatment. Additionally, the island syndrome literature generally neglects marine birds such as shearwaters and petrels, because their lifestyle connects them to the open seas. However, they are very frequently

island breeders, and the pressures on these parts of their life history likely have some parallels with terrestrial island birds e.g. behavioural naivety to nest predators, and components of life history variation. Therefore, they warrant inclusion in studies of the island syndrome.

A more comprehensive characterisation of patterns in individual traits should also consider covariation among traits, which will ultimately shed light on the drivers of the island syndrome. Relatively few studies of the island syndrome have focused on how traits evolve in concert, as traits are frequently studied separately. We have highlighted likely links among traits and suggested drivers for the components of the island syndrome that could be investigated further. While we have a general appreciation for the suite of drivers underlying the island syndrome (Lomolino et al., 2012), the relative importance of changed biotic interactions requires quantification from multiple systems. Furthermore, the role of immigrant selection at colonisation needs further attention. The direction of shifts in some traits appears broadly supported, but traditional ideas for particular traits have been challenged or are only weakly or inconclusively supported by the available data. Hence, the way that drivers interact could be more idiosyncratic than previously appreciated.

The amount of information available on birds continues to grow and be collated (e.g. avian functional variation has been characterised (Pigot et al., 2020; Tobias et al., 2022)), while other aspects of biology such as behaviour, diet, and life histories have been painstakingly collected by professionals and citizen scientists alike, e.g. in *Birds of the World* (Billerman,

Keeney, Rodewald, & Schulenberg, 2020). Distributions of birds are mapped in unparalleled detail (del Hoyo & Allen, 2020; BirdLife International and Handbook of the Birds of the World, 2020), and phylogenetic and genomic data is increasingly available (Feng et al., 2020; Jetz et al., 2012). With these tools, more detailed phylogenetically controlled studies can be performed that will fill in the gaps in avian island syndrome research. However, it is paramount that palaeobiological data is included, where trait types allow it. Many of the examples we have collated refer to extinct taxa. With regards to IUCN-classified species, about 8% of all endemic species of island birds are now extinct (Matthews et al., 2022). However, island extinctions have been occurring well before timescales considered by the IUCN (1500 CE) (Hume & Walters, 2017; Steadman, 2006), and 22% of all species known to have lived in the past 125,000 years are extinct (Matthews et al., 2022). In addition, it is likely that there are many unknown anthropogenic bird extinctions. For example, estimates suggest that in the Pacific islands alone, 731 to 1,332 species of non-passerine birds have gone extinct during the time of human habitation (Duncan, Boyer, & Blackburn, 2013). The Pacific Ocean is particularly island-rich, but if these numbers reflect potential scales of extinction elsewhere, then possibly nearly half of the endemic island birds that co-occurred with humans may have gone extinct. These extinctions are problematic for the further study into the island syndrome, as they cause loss of data that will result in statistical biases. Already, it has been shown that not including extinct species would underestimate the rate of evolution of flightless birds, the majority of which are island endemics, four-fold (Sayol et al., 2020). This issue will be significant for other traits, including size, as the largest bird species on islands are the most likely to be extinct (Fromm & Meiri, 2021). In mammals, both

larger size, and having undergone the largest island rule-related shifts, predispose species to extinction (Rozzi et al., 2023). Furthermore, traits that do not fossilise – such as behaviour or many elements of life history, may be forever beyond the reach of scientific study. Therefore, the investigation into the island syndrome is urgent, and island birds provide a rich seam of information to more fully characterise this widespread phenomenon, and ultimately to understand its drivers in birds and other species.

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Supplementary Material

Table 1. Example studies that invoke or show a degree of trait covariation occurring in the context of the island syndrome. We have qualified studies that either mention likeliness of trait covariation due to studies in non-island context, or studies that have explicitly investigated trait covariation, or accounted for it in their analysis.

.	Body size	Brain size	Bill size	Flight ability	Naivety	Ecological niche	Sociality	Cognition	Vocal signalling	Visual signalling	Parental investment	Growth and survival	Physiology
Body size	X	(Sayol, Downing, Iwaniuk, Maspons, & Sol, 2018)	(Clegg & Owens, 2002)	(Wright, Steadman, & Witt, 2016)		(Clegg & Owens, 2002)						(Sandvig, Coulson, & Clegg, 2019)	(McNab, 2000)
Brain size	X	X						(Sayol et al., 2018)					
Bill size	X	X	X			(Clegg & Owens, 2002)							
Flight ability	X	X	X	X									(McNab, 1994)
Naivety	X	X	X	X	X								
Ecological niche	X	X	X	X	X	X		(Gavriilidi, De Meester, Van Damme, & Baeckens, 2022)					(Blanco, Laiolo, & Fargallo, 2014)
Sociality	X	X	X	X	X	X	X		(Potvin & Clegg, 2015)	(Doutrelant et al., 2016)			
Cognition	X	X	X	X	X	X	X	X					
Vocal signalling	X	X	X	X	X	X	X	X	X				
Visual signalling	X	X	X	X	X	X	X	X	X	X			
Parental investment	X	X	X	X	X	X	X	X	X	X	X		
Growth and survival	X	X	X	X	X	X	X	X	X	X	X	X	(Blanco et al., 2014)
Physiology	X	X	X	X	X	X	X	X	X	X	X	X	X

Chapter 2 – Birds that breed exclusively on islands have smaller clutches.

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Berthelot's Pipit (*Anthus berthelotti*), an endemic to Macaronesia, which has a smaller clutch size than the sister species Tawny Pipit (*Anthus campestris*). © Michał T. Jezierski

Abstract

The ‘island syndrome’ refers to similarity in the biology of island organisms, but its generality is questionable, as the scope of species and traits examined are often limited. Here, I show that birds breeding exclusively on islands (breeding island endemics) evolved smaller clutches, using a dataset of 4,530 bird species. Using an inclusive definition of a breeding island endemic, which also encompasses migratory species and seabirds, I examine the evolution of clutch sizes in island breeding species using phylogenetic generalized linear models. Across disparate phylogenetic hypotheses, and after accounting for biological and geographical co-variables, I show that breeding island endemic landbirds (470 species) evolved smaller clutch sizes than continental breeding species (3,818 species). I show that the evolution of clutch size follows the expectations of the island syndrome, as among breeding island endemic landbirds there is a positive relationship between clutch size and breeding range area. Finally, I reinforce the view that the island syndrome is a general pattern in birds, spanning diverse phylogenetic and ecological groups, by showing that in a seabird-only dataset (242 species), breeding island endemic seabirds show evolution of smaller clutch sizes. In a model of the full dataset of both landbirds and seabirds (4,530 species) there was no evidence of an interaction of being a seabird with breeding island endemicity, showing that seabirds and landbirds respond in the same way. This study, using more than 40% of all bird species, provides the first evidence of a general evolutionary response in a life history trait, clearly showing the island syndrome as a general evolutionary tendency associated with island environments.

Keywords: birds, clutch size, islands, island syndrome, phylogenetic, latitude, life history, seabirds

Lay summary:

- The island syndrome is a phenomenon of similarity in morphology, behavior and life history between island organisms.
- Even among birds, its extent is not fully studied – it's not clear which traits (particularly behavioral and life history traits) are involved, and how generally it applies across the whole diversity of birds (more than 10,000 species).
- Using a dataset of 4,530 species with established molecular phylogenies, I examined whether birds that nest exclusively on islands consistently differ from continental-breeding species in terms of a key life history trait – clutch size.
- I found that breeding island endemic landbirds have smaller clutches. Among island breeding endemic landbirds, breeding range area was positively correlated with clutch size, as expected in the island syndrome. Seabirds show the same evolutionary response in clutch size as landbirds.
- This study shows that a life history trait is part of the island syndrome across a representative sample of the avian phylogeny, and shows that seabirds also exhibit the island syndrome.

Introduction

Geography determines the distribution of species diversity and trait occurrence on Earth (Violle et al. 2014), generating patterns of biological variation following basic features like latitude or insularity (Willig et al. 2003; Whittaker et al. 2023). On islands, area limitation and isolation result in decreased species diversity, and communities with vacant niches (MacArthur and Wilson 1967; Whittaker et al. 2023). These island communities are thought to have relaxed predation and inter-specific competition, and higher population densities compared to mainland counterparts (MacArthur and Wilson 1967; Whittaker et al. 2023). As these conditions are repeated across the world's islands, they are hypothesized to result in similarities in morphology, behavior, and life history between island-living organisms – 'the island syndrome' (Adler and Levins 1994; Lomolino et al. 2013; Jezierski et al. 2023). The island syndrome has been shown to occur in one form or another in all major groups of vertebrates (Benítez-López et al. 2021) and in plants (Burns 2019). Among those, birds are prime island colonizers, with nearly 2,000 out of >10,000 species being island endemics (Tershy et al. 2015). They exhibit some of the best examples of the island syndrome, including a tendency towards 'medium' body size (Clegg and Owens 2002; Benítez-López et al. 2021), a shift towards less flight-reliant locomotion (Wright et al. 2016), or a complete loss of flight (Sayol et al. 2020). However, even in birds, the generality of the island syndrome, in terms of the traits involved and its taxonomic scope (i.e. number of species; clades involved), remains unclear (Meiri et al. 2008). Many behavioral and life history traits have only been partially examined, and phylogenetic comparative methods have seen limited use (Jezierski et al. 2023). These significant omissions preclude a proper understanding of the pattern of the island syndrome, and thus hinder the study of its

evolution (Whittaker et al. 2023) and its contribution to the threats experienced by island species today (Matthews et al. 2022).

Life histories are a key area of study in the island syndrome literature, due to their partial treatment to date (Jezierski et al. 2023), and their importance to individual fitness (Stearns 1992). Previous studies have shown that birds on islands have smaller clutch sizes (Covas 2012), slower growth (Sandvig et al. 2019, Cooney et al. 2020), and higher survival (Beauchamp 2021, 2022). However, due to data limitations, many of these studies have examined less than 5% of total bird diversity, which cannot be used to ascertain the island syndrome as a global pattern. Only some of them have used phylogenetic trees in their statistical models (Sandvig et al. 2019; Cooney et al. 2020), a problem repeated in other studies of the island syndrome (Jezierski et al. 2023; Whittaker et al. 2023). Furthermore, many studies on the island syndrome have excluded seabirds (e.g. shearwaters, auks or penguins). The reasoning for this exclusion is the unique marine ecology of these birds, which decouples most of their adult life from selection on islands (Clegg and Owens 2002), and makes it difficult to define an island endemic, despite hundreds of seabird species breeding exclusively on islands. The contemporary accessibility and scope of phylogenetic hypotheses (Jetz et al. 2012), as well as extensive data on bird biology (Billerman et al. 2020), makes it possible to examine the evolution of life history traits on islands across hundreds of independent island colonizations, whilst explicitly including phylogenetic hypotheses. If the island syndrome manifests due to evolutionary change when a species becomes an island endemic, then we should observe a significant association between life history traits and island endemicity. The island syndrome is thought to be exacerbated

when species inhabit smaller and/or more isolated islands, as they are the most limited in terms of species diversity (Lomolino et al. 2012). Therefore, if the observed evolution in life history traits is indeed due to conditions on islands, we should observe evolutionary associations of traits with breeding area in island species, as island area has been shown to affect e.g. body size (Benítez-López et al. 2021). And finally, we can expect that aspects of life histories that take place exclusively on islands will be affected by island conditions. Therefore, by focusing on reproductive life histories of birds on islands, we can create a more inclusive definition of a breeding island endemic – a bird that breeds exclusively on islands, which can include seabirds and migratory species in island syndrome studies.

One such reproductive trait is clutch size, which is a well understood aspect of life history, and is a very direct measure of fecundity (Lack 1947, 1948; Bennett and Owens 2002). Bird clutch sizes have been studied extensively through professional and citizen science efforts (Crick et al. 2003), and are one of the best characterized bird life history traits (Jetz et al. 2008). The availability of data on clutch size allows for studies of geographical variation globally, whilst knowledge of clutch size evolution allows us to make inferences about drivers, and follow up with experimental studies. Islands are thought to generate conditions for 'slow' life histories (Covas 2012; Beauchamp 2021), due to lower predation (MacArthur and Wilson 1967) and higher population densities (MacArthur et al. 1972). This results in high life-time survival, and a need to maintain competitive ability, favoring maximizing individual quality rather than fast reproduction (Stearns 1992). In birds, 'slow' life histories are characterized by smaller clutch sizes, higher overall survival, and longer life (Robinson et al. 2010). Clutch size and related

life history traits vary markedly with multiple aspects of avian biology and distribution, beyond being a breeding island endemic. Larger species of birds tend towards slower life histories, with smaller clutch sizes (Sæther 1987). Mode of development (altricial or precocial) is also a significant driver of clutch size, with precocial species having larger clutch sizes, presumably due to their less-intensive parental care allowing for more offspring (Jetz et al. 2008). Finally, migratory species tend to have larger clutches (Jetz et al. 2008), which might be explained by Ashmole's hypothesis that species breeding in seasonal environments (most migrants) will have larger clutches (Lundblad and Conway 2021). This hypothesis has also been invoked to explain the best-known pattern of macro-ecological variation in clutch size, which is the increase in clutch size with latitude (Lack 1948; Jetz et al. 2008). Whilst other explanations could result in lowering clutch sizes towards the equator (Martin 2015), latitude may impact island adaptations, as has been shown in previous studies of clutch size in island birds (Covas 2012). Namely, species living on temperate islands have smaller clutches than expected for a given latitude, which was suggested to stem from lower seasonality on temperate islands (Covas 2012). All these co-variables can confound the patterns of clutch size evolution (Jetz et al. 2008; Covas 2012), and in themselves are important intrinsic factors that determine clutch sizes. If the island syndrome is a general pattern of slower life histories on islands, then clutch sizes should be lower among island breeding endemics, irrespective of these other factors.

Here, I use estimates of avian clutch size for 4,530 species (approx. 40% of all bird species) to, for the first time, explore the evolution of a reproductive life history trait on islands across a significant chunk of global bird diversity, using phylogenetic

generalized linear modelling. I explore if breeding exclusively on islands results in changes to avian clutch sizes, and how clutch size evolution on islands is mediated by the known biological and latitudinal factors (Jetz et al. 2008; Robinson et al. 2010; Covas 2012). In line with the expectations of the island syndrome, I hypothesize that birds breeding exclusively on islands have evolved smaller clutches than continental-breeding species. To further support the role of island conditions in the observed evolutionary patterns, I explore whether the total area of the breeding range of breeding island endemics impacts the evolution of their clutch sizes. Finally, I examine whether the clutch size evolution of seabirds follows the patterns expected in the island syndrome, and whether seabirds show the same direction of evolutionary change in clutch sizes as landbirds.

Methods

Data collection

Data was collected only on species included in the phylogenies of Jetz et al. 2012, to use explicit phylogenetic hypotheses in explaining clutch size evolution. The two available phylogenies are based on (1) genetic data alone (6,670 species) or on (2) additional inference including subjective decisions (9,993 species). I chose to use the phylogeny based on genetic data alone with the Hackett backbone (Hackett et al. 2008), as it provides a purely molecular and more repeatable phylogenetic hypotheses, used in macro-evolutionary studies of bird traits (e.g. Pigot et al. 2020). The data I collected excludes brood parasites such as cuckoos, as their clutch sizes are not driven by the same trade-offs described above for nesting birds (Payne 1974). I defined breeding island endemic species as a binary variable (yes/no), as birds that exclusively breed on islands, but which may occur outside of islands in different parts of the year (e.g. seabirds). This definition is not commonly used in other studies of the island syndrome, but allows the inclusion of seabirds and migratory species, capturing all species whose breeding attempts are affected by island conditions. Data was collected from Birds of the World (Billerman et al. 2020) between October 2020 and April 2021. For all species in the dataset, I collected the following metadata: species name under the Clements naming convention (Clements 2019); whether a species is a breeding island endemic; minimum and maximum clutch size; and minimum and maximum body mass. If a single value was provided for either clutch size or body mass, it was used as both the minimum and maximum value (inc. averages). To match the clutch size dataset to both distributional and phylogenetic data used in the analysis, I translated the names of the Clements taxonomy used by Birds of the World to the

taxonomy of Jetz et al. 2012 and BirdLife taxonomy (del Hoyo 2020), using Avibase (Lepage et al. 2014). Additional life history data was collected at family level using Birds of the World, namely development mode (precocial vs altricial), following previous studies on clutch sizes (Jetz et al. 2008). To classify birds as land or seabirds, I classified every bird species that consistently uses marine habitats (coastal, offshore, or pelagic) throughout at least part of its life cycle as a seabird, using Birds of the World and *Seabirds: an identification guide* (Harrison 1985).

All data handling was performed in R v4.2.3 (R Core Team 2023) using the package *tidyverse* v2.0.0 (Wickham et al. 2019). Geographical data was handled using package *sf* v1.0-14 (Pebesma 2018). Plotting was performed using *ggplot2* v3.4.4 (Wickham and Sievert 2016), *gghalves* v0.1.4 (Tiedemann 2022) and *ggdist* v3.3.1 (Kay 2023). I used BirdLife distribution maps to obtain data on species' geographic distribution (latitude and area) (BirdLife International and Handbook of the Birds of the World 2020). Because the focus is on a breeding trait, I used BirdLife maps for: i) breeding ranges; and (ii) year-round ranges, only. The breeding ranges were additionally filtered to include only extant and native distributions. The filtered BirdLife ranges were used to also classify bird species as migratory or not. If a bird species was presented in the BirdLife dataset as having only a 'year-round' distribution, it was classified as resident. If it had a separate 'breeding-only' distribution, it was migratory, even if the bird was considered resident throughout parts of its range. BirdLife maps may include marine distributions for birds. I excluded these from area and latitude calculations, by intersecting BirdLife maps with land shapefiles from Natural Earth (https://www.naturalearthdata.com/downloads/50m-physical-vectors/50m-land/) at

1:50,000,000 resolution. To determine latitude associated with a given species, I calculated the centroid of each species' distribution using *st_centroid*() and extracted its latitude. Area was calculated using function *st_area*().

Modelling framework

To investigate the impact of geography on clutch size, I used phylogenetic generalized least squares models (Symonds and Blomberg 2014) applied using the R packages *nlme* v3.1-162 (Pinheiro et al. 2017), *ape* v5.7-1 (Paradis et al. 2004) and *phylolm* v2.6.2 (Ho and Ané 2014). Using minimum and maximum clutch sizes would focus on extremes, with maximum clutch sizes being heavily determined by sampling effort (same applies to body mass). Therefore, I calculated the geometric means of both clutch size and body mass to use in modelling. Outliers in clutch size had to be removed, as otherwise the models would break the expectations of normality as examined using the *qqnorm()* and *qqline()* functions in the base *stats* package in R. Manual removing of outliers would increase heterogeneity in the dataset, and potentially introduce additional bias. Therefore, outliers were filtered out of the dataset by removing all species with clutch sizes larger than Q75 + 1.5IQR and smaller than Q25 – 1.5IQR. As no species had clutches below the lower outlier limit, all removed outliers were at the upper end of the distribution. Full data for the analysis was available for 4,773 species out of the 6,670 included in the genetic-based phylogenetic data. After removing outliers (243 species, with all outliers having clutches larger than Q75 + 1.5IQR) the dataset consisted of 4,530 species (land-and-sea dataset). Of those, 242 were seabirds (seabird-only dataset), and 4,288 were landbirds (landbird-only dataset). The landbird-only dataset is used for the main analysis, and the analysis

of the impact of breeding range area in breeding island endemics (subsampled to 470 species). The seabird-only dataset is used to study whether seabirds show different evolution of clutch sizes on islands. The complete dataset is used to model if there is an interaction between being a seabird and a breeding island endemic. If such an interaction was significant, it would imply that seabirds respond to island environments differently than landbirds in terms of clutch size evolution.

All models were tested for collinearity of explanatory variables using the function *vif* of package *car* v3.1-2 (Fox et al. 2012), with 2.5 as the cut-off factor (Zuur et al. 2010). All variables in every model had variance inflation factors < 2. Every linear model was additionally tested for best fit of evolutionary models, comparing Brownian motion; Ornstein-Uhlenbeck models with fixed and random roots (Ho and Ané 2014); Pagel's lambda, kappa and delta (Pagel 1999); and Brownian motion with trend (Ho and Ané 2014) as implemented in *phylolm*. The performance of evolutionary models was evaluated using the function *model.sel* from package *MuMIn* v1.47.5 (Bartoń 2015) using AICc. Best model is reported in the results, with associated ΔAICc (AICc of the second best model – AICc of the best model) value to the nearest model. To examine model diagnostics, each model was first run in *nlme* with a correlation matrix defined by *corrPagel()* in *ape*. This approach was used for ease of access to model diagnostics, but it required reorganizing data to match the phylogenetic tree. This was performed using the function *comparative.data* as implemented in package *caper* v1.0.3 (Orme et al. 2018). All models were deemed suitable, and from this point *phylolm* was used for speed of calculation (both methods arrive at identical results). The trees provided by Jetz et al. 2012 are a posterior sample of thousands of equally likely trees. To

account for variation in the posterior sample of phylogenies, I ran each phylogenetic generalized linear model 100 times using different phylogenetic trees from Jetz et al. 2012 using a custom approach based on the package *sensiPhy* (Paterno et al. 2018), collecting all model estimates, errors, p-values and R^2 values. These methods were applied to all the models described below.

Hypothesis testing

Every hypothesis was tested using phylogenetic generalized least squares, as described above. To examine whether breeding island endemic species evolved clutch sizes distinct from their continental relatives, the following model was fitted to the dataset of all landbirds (4,288 species): *clutch size ~ breeding island endemicity*absolute latitude + developmental mode + migratory status + body mass*. Developmental mode, migratory status and body mass were used, as they are known to impact clutch sizes and need to be controlled for (Jetz et al. 2008; Covas 2012). To examine whether breeding island species follow the expectation of more exacerbated adaptations in species inhabiting smaller areas, I used the breeding island endemic-only landbird dataset (470 species) and fitted the following model: *clutch size ~ log_{10} of the area of breeding range + absolute latitude + developmental mode + migratory status + body mass*. In order to test if seabirds follow the expectations of the island syndrome I tested two models: a) model on seabird-only dataset (242 species): *clutch size ~ breeding island endemicity*absolute latitude + developmental mode + migratory status + body mass* to test if island and continental breeding seabirds differ; b) model on seabird + landbird dataset (4,530 species) to test if land- and seabirds differ in their response to being a breeding island endemic: *clutch size ~ breeding island*

*endemicity*seabird/landbird + latitude + developmental mode + migratory status + body mass*. All model results are reported in a form of: *median [5th quantile, 95th quantile]*.

Results

The best supported evolutionary model for all landbirds (n = 4,288 species) was Pagel's lambda model with high support (ΔAICc = 640.54). Across all landbirds, breeding island endemics had a geometric mean clutch size of 2.32 compared to 2.84 for continental breeding species (**Figure 1A**). This difference is significant, and across all 100 phylogenetic hypotheses, being a breeding island endemic has a negative impact on clutch size (β = -0.194 [-0.215, -0.169], p-values = 0.001 [<0.001, 0.005]). Other significant terms in the model were developmental mode, migratory status, and latitude. I found no evidence of a significant impact of body mass across any of the 100 phylogenies (**Table S1, Figure 1C**). Being precocial resulted in higher clutch sizes than altricial species (β = 0.623 [0.548, 0.715], p-values = 0.015 [0.004, 0.036]). Resident species had lower clutch sizes than migratory species (β = -0.305 [-0.313, -0.297], p-values = <0.001) (**Figure 1B**). This model explained 0.188 [0.184, 0.193] of the observable variation, and I detected high phylogenetic signal in the dataset, with Pagel's λ values being 0.850 [0.831, 0.870].

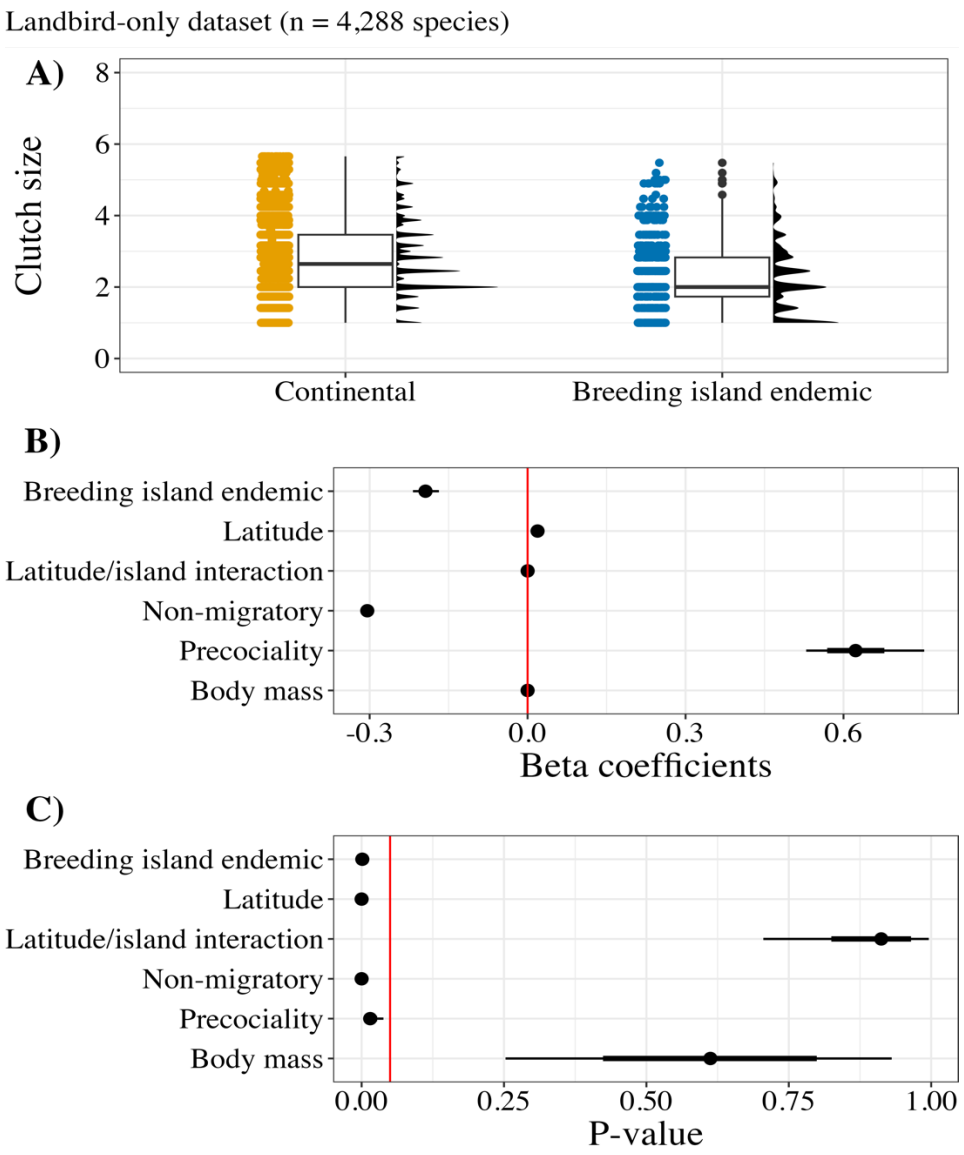

Figure 1. Landbirds breeding exclusively on islands have smaller clutches, an effect significant regardless of phylogenetic hypotheses or other factors. **A)** Distributions of geometric means of clutch size between continental breeding species and breeding island endemics. NB: Horizontal point jitter was added for clarity using function geom_jitter() of *ggplot2*. Each point corresponds to a single species. **B)** and **C)** show the results of phylogenetic generalized linear models run across 100 phylogenies obtained from Jetz et. al. 2012, with the distribution of **B)** model β coefficients with the

vertical line at 0; and **C)** p-values with the vertical red line at 0.05 to denote the significance threshold. Distributions show 5th to 95th quantiles.

Across all phylogenetic hypotheses, absolute latitudinal midpoint had a weak positive effect (β = 0.019 [0.019, 0.019], p-values = <0.001) (**Figure 1B, C**). However, there was no evidence of an interaction of latitude with breeding island endemicity (**Figure 1C, Figure 2**). Both island and continental species show an increase in clutch size with latitude, but there is no significant difference between slopes (β = 0.000 [-0.001, 0.001], p-values = 0.912 [0.750, 0.990] (**Figure 2**).

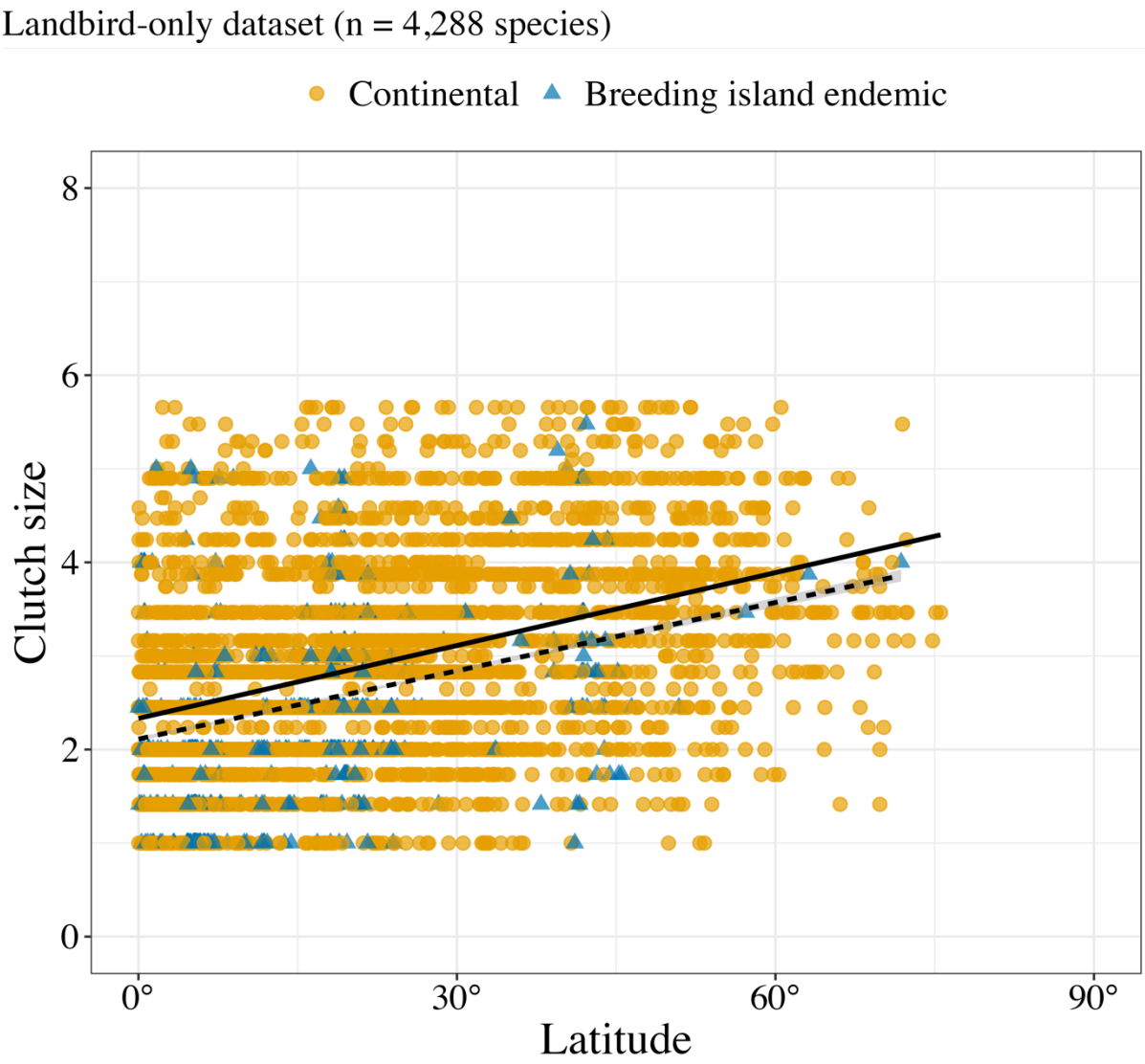

Figure 2. Clutch sizes increase with latitude, but with no interaction of being a breeding island endemic or a continental breeder (solid line – continental species; dashed line – breeding island endemic species). The lines were parametrized using an example phylogenetic tree, the 95% confidence interval is shown by gray shading (tiny and thus not visible for the continental line). NB: Horizontal point jitter added for clarity.

To investigate the impact of breeding range area on clutch size within the breeding island endemics, Pagel's lambda was again the best evolutionary model (ΔAICc = 16.24). Among breeding island endemic landbirds (n = 470 species), I found breeding range area to have a significant positive association with clutch size (β = 0.093 [0.089, 0.095], p-values = <0.001) (**Figure 3**). In the dataset of breeding island endemics, latitude was still a significant positive predictor of clutch size (β = 0.024 [0.023, 0.025], p-values = <0.001], but developmental mode, migratory status and mass were not significant (**Table S2**). The model explained less variation in breeding island endemic species only (R^2 = 0.154 [0.146, 0.161]), and phylogenetic signal was even higher than in the landbird dataset (λ = 0.901 [0.883, 0.920]).

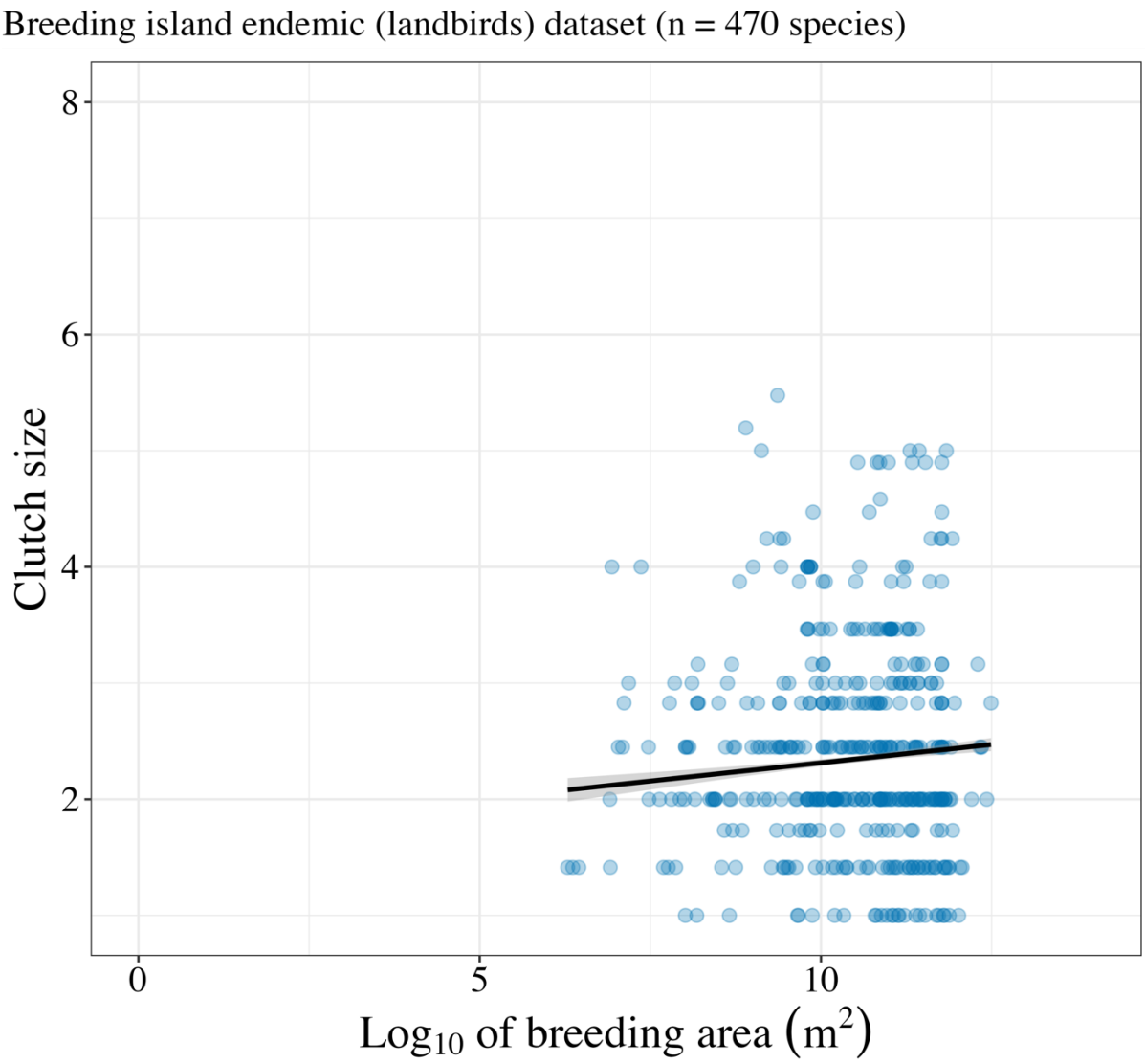

Figure 3. Breeding island endemics with smaller breeding areas have smaller clutches. Each point corresponds to a different species. Thick black line represents the line of best fit, with grey shading representing the 95% confidence interval. The line was parametrized using an example phylogenetic tree. NB: Horizontal point jitter added for clarity.

For the seabird-only dataset (n = 242 species), Pagel's lambda was the best evolutionary model (ΔAICc = 15.68). I found that seabirds breeding exclusively on islands evolved lower clutch sizes than their relatives breeding on continents. Breeding island endemicity consistently had a negative impact on clutch size (β = -0.411 [-0.437, -0.374], p-values = 0.002 [<0.001, 0.003]) (**Figure 4**). In seabirds only, latitude was no longer a significant predictor of clutch size (**Table S3**), and migratory status or breeding island endemicity*latitude interaction were also both non-significant. Being precocial had a significant positive impact on clutch sizes of seabirds (β = 0.749 [0.690, 0.823], p-values = 0.015 [0.007, 0.029]). In the seabird-only model, phylogenetic signal estimated by Pagel's lambda was lower (λ = 0.820 [0.783, 0.845]), and the model explained (R^2 = 0.060 [0.052, 0.068]) of the observed variation.

In a dataset of both land- and seabirds (n = 4,530 species), Pagel's lambda remained the best evolutionary model (ΔAICc = 627.98). The interaction term between breeding island endemicity and being a seabird was non-significant (β = 0.113 [0.093, 0.131], p-values = 0.315 [0.248, 0.415]). Meanwhile, being a seabird results in a lower clutch size across all phylogenies (β = -0.493 [-0.532, -0.454], p-values = <0.001). The addition of seabirds to the dataset resulted in development mode no longer being significant, while all other variables remained qualitatively the same after including seabirds in the model (**Table S4**).

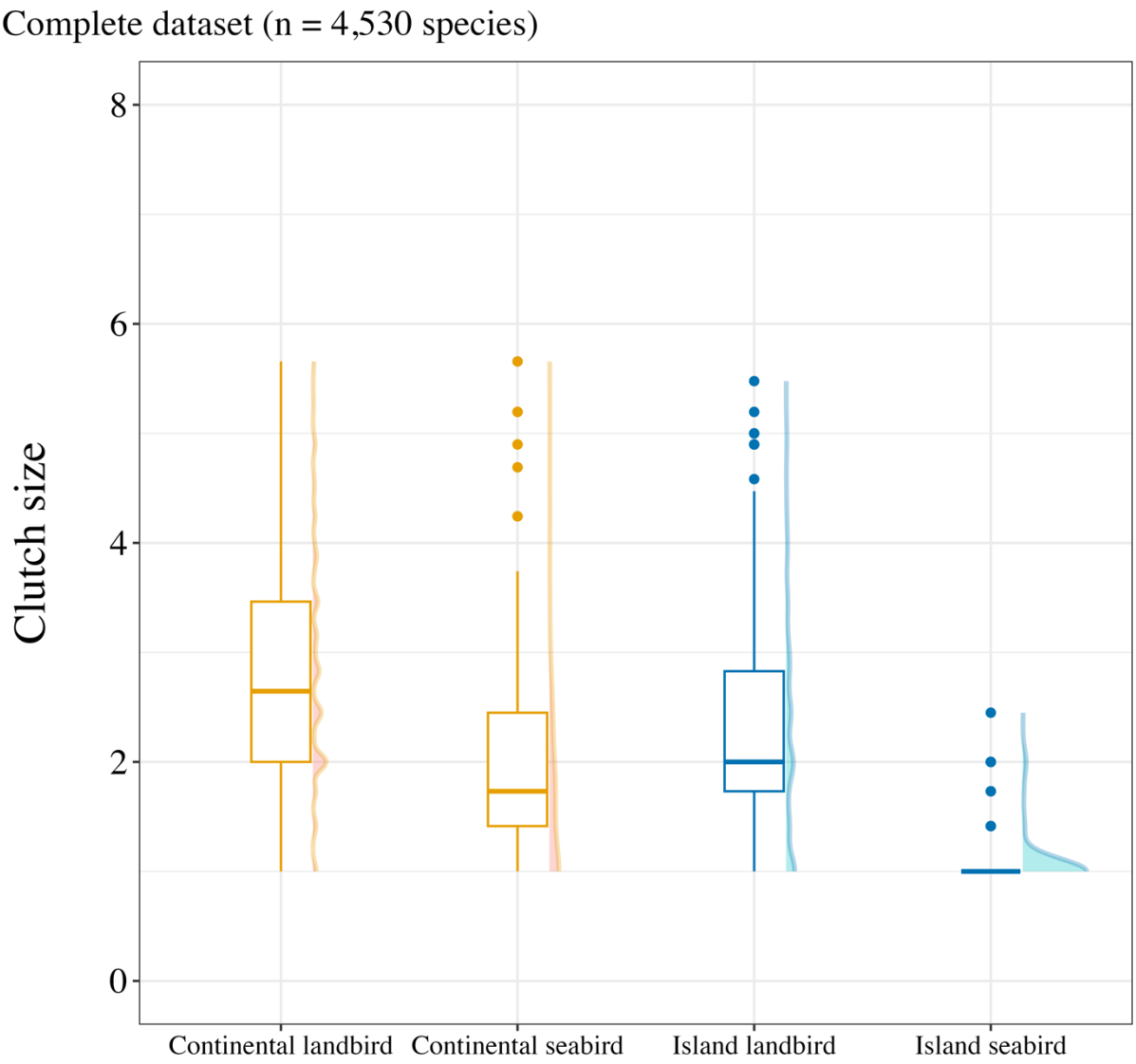

Figure 4. Seabirds breeding exclusively on islands have lower clutch sizes than continental-breeding relatives. Slabs to the right of boxplots show the distribution of clutch sizes per species in each category and are scaled to the total number of species in a given category.

Discussion

The results of this study confirm that birds breeding exclusively on islands have smaller clutches, in accordance with the expectations of reproductive life history forming a part of the island syndrome. Using one of the largest samples of species to study the island syndrome to date, the results reinforce the previous findings on bird reproduction (Covas 2012), and the pattern of slower avian life history on islands (Covas 2012; Sandvig et al. 2019; Cooney et al. 2020; Beauchamp 2021, 2022). I found that lower clutch sizes evolved in breeding island endemics, even if latitude and other aspects of life history are considered. Using an explicitly phylogenetic modelling framework implies that the observed differences co-occur with becoming a breeding island endemic along bird evolutionary history. This means that selection caused by island environments is likely acting on breeding island endemics, and the observed patterns of the island syndrome at least partially stem from evolutionary change, and not only, for example, filter effects of successful island colonization (Lomolino et al. 2012). Evolutionary change towards an element of 'slower' life histories reinforces the notion that it might be an adaptation to low-predation, high-conspecific competition environments (MacArthur and Wilson 1967; Lomolino et al. 2012; Whittaker et al. 2023), which are thought to characterize islands, provided such conditions occur (which could be examined in field studies).

Evolution of smaller clutch sizes on islands was recovered in every model, even if other biological and geographical co-variables were considered. This yielded the somewhat surprising result of body mass not being a significant predictor of clutch size, contrasting with some previous work (Sæther 1987; Jetz et al. 2008), but in agreement

with others (Martin et al. 2006). However, some of these previous works have considered limited geographical and taxonomic samples of birds (Sæther 1987; Martin et al. 2006), and none of them considered phylogenetic relationships in their models, which may explain the discrepancy in results. Other aspects of life history such as developmental mode and migratory status correlated with clutch size as expected, in line with the results of previous studies (Jetz et al. 2008).

My results corroborate the pattern of increased clutch size with absolute latitude (Lack 1948; Jetz et al. 2008). However, I did not recover the previously reported interaction of latitude with island endemicity, where temperate species lay smaller clutches on islands for a given latitude (Covas 2012). There are significant differences in design between that study and the one reported here, and likely reasons for the different results include significantly larger sample size and explicit phylogenetic modelling in this study. Covas 2012 invoked stability of climate on islands as a potential driver of the island syndrome, and argued that the interaction may be driven by lower seasonality on temperate islands. The discrepancy between our two studies suggests that this could be explored using the dataset presented here in conjunction with environmental data. A further idea to explore is that latitude often acts as a catch-all variable that strongly covaries with productivity and strength of biotic interactions. For birds, biotic interactions are thought to increase with lower latitude, for example through higher predation risk (McKinnon et al. 2010; Freeman et al. 2020). Islands should lower the slope of that gradient due to a significant drop in the risk of predation,

and thus also result in an interaction between latitude and island endemicity, although of the opposite direction to the one found by Covas 2012.

To further reinforce the fact that the unique selective pressures on islands lead to the evolution of traits encompassed by the pattern of the island syndrome, I showed that breeding island endemics inhabiting smaller breeding areas evolved even smaller clutches. Island area is a significant determinant of community structure, with smaller islands tending to be more disharmonic and losing functional diversity (MacArthur and Wilson 1967, Whittaker et al. 2023). As empty niches and low predation are the proposed drivers of the island syndrome (Lomolino et al. 2012; Ponti et al. 2023), it should be strongest on the smallest islands. It is indeed the case across some measurements, e.g. in body sizes of island vertebrates (Benítez-López et al. 2021), but island area has not always been recovered as an important predictor (Schwarz et al. 2020). The result of this study shows that area impacts clutch size evolution. However, due to differences in study design, there are some limitations to the interpretation. Whilst other studies have performed meta-analyses of studies from particular islands, where a measurement of a trait can be linked to an exact island (Benítez-López et al. 2021), my study examines a species-wide mean. Whilst many island endemic species or breeding island endemics inhabit individual islands, there are species that inhabit entire archipelagos and move between islands (e.g. the Nicobar Pigeon (*Caloenas nicobarica*) (Billerman et al. 2020)), yet still undoubtedly are limited to islands. Therefore, the studied value of clutch size cannot be easily linked to an individual island, and the analysis is thus not identical to previous studies. However, this still

strongly suggests that insularity drives trait evolution, and can be further investigated in a meta-analytic framework in which island populations are studied.

This study has, for the first time, explicitly examined if seabirds also show patterns of trait evolution consistent with the island syndrome. It was possible due to the use of a more inclusive definition of being a breeding island endemic – which many seabird species are, even though their adult life is largely spent at sea. The results of this study show that breeding island endemic seabirds evolved smaller clutches than their continental breeding seabird relatives, just like landbirds do. The impact of breeding island endemicity was nearly double that of the effect in the landbird dataset, due to the frequent clutch size of a single egg in island breeding seabirds. Furthermore, by analyzing land and seabirds together, I show that the direction of evolutionary change in clutch size in breeding island endemics is the same between seabirds and landbirds. Even though all seabirds have significantly lower clutch sizes than landbirds, there is no interaction between being a seabird and breeding island endemicity in the model. Therefore, seabirds may be needlessly excluded from studies of the island syndrome (as they were in e.g. Clegg and Owens 2002), or at least should not be excluded when the studied traits can directly, or indirectly, be affected by selective conditions on islands. Further inclusion of seabirds in island syndrome studies could be particularly fruitful, as many traits of seabirds ('slow' life history, evolution of unique ecologies) are in general considered parts of the island syndrome (Jezierski et al. 2023, Whittaker et al. 2023).

To conclude, this study is the largest characterization of a reproductive life history trait in the context of the island syndrome, and one of the largest investigations into the island syndrome at all (Benítez-López et al. 2021) in terms of the number of species considered. Its results conclusively show that breeding island endemicity is associated with the evolution of smaller clutch sizes. By comparing different datasets and aspects of evolution on islands (i.e. breeding endemicity, area), I show that the recovered evolutionary patterns in clutch size evolution are consistent with the island syndrome. Furthermore, thanks to the taxonomic scope and inclusion of seabirds, I have been able to demonstrate that the evolutionary change on islands applies across all birds, and across very disparate avian lifestyles, that nevertheless converge on islands during reproduction.

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Supplementary Materials

Table S1. Results of the model *clutch size ~ log of the area of breeding range + absolute latitude + developmental mode + migratory status + body mass* applied across 100 different phylogenetic hypotheses for 470 species of island endemic birds. Results are given as median [min, max] values, and to three significant figures. Where p-values reported as <0.001 all of the variation was lower than 0.001 and thus not reported.

Predictor	**Estimate**	**Standard Error**	**P-values**
Area	0.093 [0.087, 0.098]	0.024 [0.023, 0.025]	<0.001
Latitude	0.024 [0.023, 0.026]	0.003 [0.003, 0.003]	<0.001
Developmental mode - precocial	-0.090 [-0.211, 0.035]	0.460 [0.425, 0.497]	0.842 [0.651, 0.995]
Migratory status - resident	-0.187 [-0.244, -0.099]	0.191 [0.184, 0.196]	0.328 [0.198, 0.602]
Body mass	<0.001	<0.001	0.305 [0.081, 0.658]

Table S2. Results of the model *clutch size ~ island endemicity*absolute latitude + developmental mode + migratory status + body mass* applied across 100 different phylogenetic hypotheses for 242 species of seabirds. Results are given as median [min, max] values, and to three significant figures. Where p-values reported as <0.001 all of the variation was lower than 0.001 and thus not reported.

Predictor	**Estimate**	**Standard Error**	**P-values**
Island endemic	-0.411 [-0.460, -361]	0.129 [0.124, 0.133]	0.002 [<0.001, 0.005]
Latitude	-0.003 [-0.004, -0.003]	0.002 [0.002, 0.002]	0.134 [0.077, 0.212]
Developmental mode – precocial	0.749 [0.639, 0.883]	0.306 [0.280, 0.334]	0.015 [0.006, 0.038]
Migratory status - resident	-0.030 [-0.065, 0.008]	0.086 [0.083, 0.089]	0.729 [0.442, 0.992]
Body mass	<0.001	<0.001	0.240 [0.149, 0.361]
Latitude*island endemicity interaction	0.005 [0.004, 0.005]	0.003 [0.003, 0.003]	0.122 [0.077, 0.198]

Table S3. Results of the model *island endemicity*seabird/landbird* + *latitude* + *developmental mode* + *migratory status* + *body mass* applied across 100 different phylogenetic hypotheses for all 4,530 species for which data was available. Results are given as median [min, max] values, and to three significant figures. Where p-values reported as <0.001 all of the variation was lower than 0.001 and thus not reported.

Predictor	**Estimate**	**Standard Error**	**P-values**
Island endemic	-0.203 [-0.216, -0.187]	0.0371 [0.037, 0.037]	<0.001
Latitude	0.017 [0.016, 0.017]	<0.001	<0.001
Developmental mode – precocial	0.438 [0.318, 0.545]	0.225 [0.214, 0.239]	0.053 [0.014, 0.152]
Migratory status - resident	-0.302 [-0.311, -0.287]	0.032 [0.032, 0.033]	<0.001
Body mass	<0.001	<0.001	0.822 [0.339, 0.999]
Seabird	-0.493 [-0.548, -0.449]	0.119 [0.111, 0.128]	<0.001
Seabird*island endemic interaction	0.113 [0.082, 0.140]	0.113 [0.111, 0.116]	0.315 [0.216, 0.476]

Chapter 3 - Global environmental drivers of variation in bird nest architecture.

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Author contributions

MTJ acquired funding, conceptualized the study, including methodology, collected and analysed the data, visualized the data, wrote the first draft and reviewed it throughout. SMC, EES, RBJB and WJS helped conceptualize the study, including methodology and advised on investigation. SMC helped acquire the funding. RBJB helped with visualization.

Data availability

All data and associated code will be deposited in full in the Supplementary Material and a GitHub repository upon acceptance.

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Shearwaters, which include Manx Shearwaters (*Puffinus puffinus*) pictured above, frequently nest on islands, and show construction of simple nests in burrows. © Michał T. Jezierski.

Abstract

Nests mediate the interaction of offspring with the environment in both invertebrate and vertebrate animals[1,2]. This extended phenotype, an external manifestation of an animal's phenotype[3], is especially important to birds[4], where virtually all species use nests. Despite the importance of nests to animal life history[2], and increasing knowledge of how nests are built[5,6] there is currently limited understanding of the influence of abiotic and biotic factors on the evolution of nest architecture. Here we use a global nest trait dataset to characterize bird nest architecture as a multivariate trait, and explore its relationship with climate variation and predator diversity. We show that predation diversity and adult body size are the strongest predictors of nest architecture, despite majority of previous studies focusing on climatic correlates. However, climate predictors, primarily warm/wet-cold/dry axis are also significant correlates of variation in nest architecture. Finally, we show that island endemicity also impacts nest architecture, leading to the evolution of 'simpler' nests. Our results place the evolution of an extended phenotype in a macro-ecological and macro-evolutionary context, to further investigate the role of nest architecture in the adaptive history of the most diverse land vertebrates.

Main

Nests are receptacles for the development of offspring[1] across a wide diversity of animals[2], and are one of the most widely recognized examples of an extended phenotype – an external manifestation of an organism's observable traits, which directly affects its fitness[3]. Among birds, virtually all species have been observed to use nests as sites of egg development, with the majority of species also using nests to raise chicks[1]. Bird nests therefore act as focal sites for most or all of early avian life history, with life-long fitness consequences for individuals[7].

Bird nests come in a variety of forms. They range from the elaborate domes of the Sociable Weaver (*Philetairus socius)* to mere placement of an egg on a substrate by White Terns (*Gygis alba*) [1,8]. Extremes of nest form may even occur within a single family, such as the ovenbirds (Furnariidae, Passeriformes), where nests range from domes to cups to simple platforms[9]. The large diversity of nest forms, and their crucial role in reproduction, suggest that nest architecture may be structured by adaptation to both biotic and abiotic factors[10-12]. However, the potential drivers of variation in nest form at a global scale currently remain unclear, with debate over the relative importance of the main environmental pressures[4,13].

Numerous studies have explored the structural roles[11], thermal benefits[13,14], and protection from predators[15] provided by bird nests. Regional, multi-species comparisons have shown that certain aspects of nest architecture may correlate with climate[16,17], with predator occurrence[13], or with both climate and predation when examining aspects of nest height[18,19], orientation[20], and site selection[15]. Very recently,

aspects of nest architecture in birds were characterized across most species[5,6]. However, studies of the drivers of nest architecture mostly considered nest traits individually rather than as a multi-trait architecture (but see[17]), and have found conflicting trends in nest traits in association with abiotic conditions (e.g. [11, 14]). This, along with limited consideration of biotic interactions, leaves major gaps in our knowledge regarding the impact of variation in climate, ecology, and geography[21-23] on the distribution of bird nest forms. Therefore, a global study that considers nest architecture as a complex trait, affected by a diversity of biotic and abiotic covariables, is necessary to understand the evolution of nest architecture in birds.

Here we present a dataset of bird nest architecture spanning all extant bird species (10,538 species according to Clements taxonomy[24]), containing descriptions of five important nest traits. For the 2,996 species with complete data for nest architecture and environmental correlates, we document geographic variation of nest form, then use phylogenetic comparative methods to evaluate whether nest architecture evolution correlates with climate, potential predation, and geography. In doing so, we provide an investigation of an extended phenotype on a global scale[25,26], revealing the likely drivers of adaptation of a core reproductive feature in the most speciose group of land vertebrates in the world.

The diversity of nest architecture in birds

We recorded aspects of nest form for five traits: nest type, structure, site, attachment, and height, which together provide basic information on variation in nest architecture (**Fig. S1**). Among the 10,538 species of birds for which we collected data on nest traits (**Supplementary Information**), 3,217 possessed information on every trait. We used this data-complete subset to generate a 'morphospace' of nest architecture, which allows for study of nest trait co-occurrence in a multivariate framework. We recoded height as a categorical variable (matching the categorical status of the other variables and thus avoiding data non-comparability) and removed and/or modified some very rare nest traits from the morphospace analyses (see **Methods**) The reduced dataset is phylogenetically representative, including 3,217 species, 39 of 41 bird orders and 213 of 246 bird families (**Table S2**).

Our principal coordinates analysis (PCoA) returned 12 axes with non-zero eigenvalues (**Table S3**), of which the first four explain 75.9% of observed variation in nest architecture. Principal coordinate axis 1 (PCo1) explains 35.2% of the observed variation, primarily reflecting variation in nest site and height above ground **(Fig. 1C and 1E),** with ground nests associated with negative values, and elevated nests, either on cliffs or in vegetation, having positive values. Variation in PCo1 is largely contained within two clusters aligned along PCo2, which splits nests between cavity or non-cavity nest types (**Fig. 1A**). Nest attachment is also organized along this axis, with hanging nests having the highest values within each cluster (**Fig. 1D**). Variation in nest structure, and additional variation in nest height, is primarily organized by PCo3 and PCo4 (**Fig. S2**). Among passerines, terrestrial non-passerines, and seabirds, we see

significant overlap in nest architecture, with seabirds primarily restricted to the low nesting part of the morphospace (**Fig. 1F**). Passerine nest morphospace is expanded towards high values of PCo1 and PCo2 due to the high frequency of hanging nests in the clade (**Fig. 1D)**.

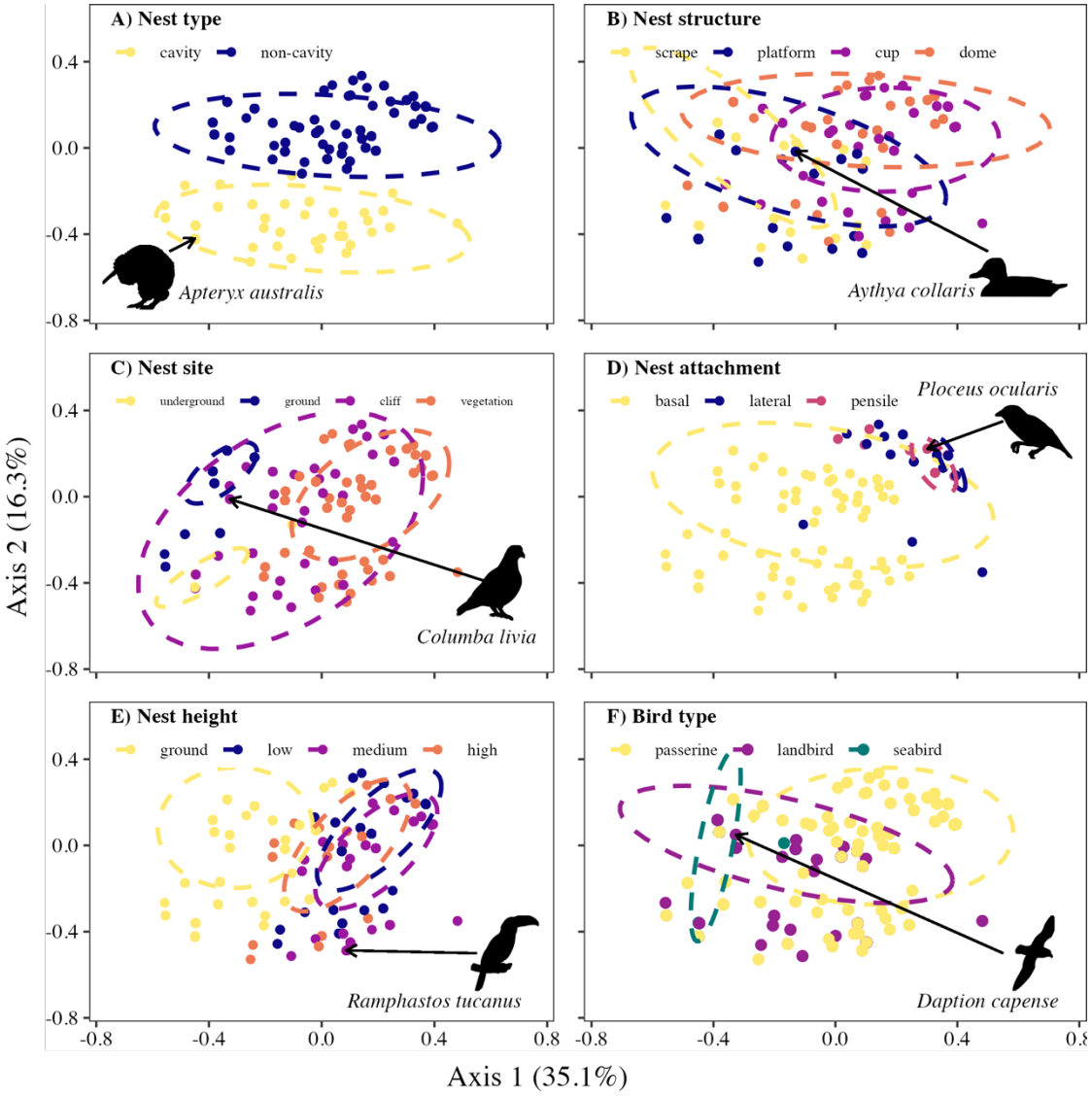

Fig. 1. The diversity of nest architecture in birds. Nest architecture morphospace shown for the 3,217 species of birds for which we have complete information across five nest traits. Due to sharing of categorical nest traits, points can completely overlap between species. Figures **A)** to **E)** show the distribution of each of the five nest traits (see **Methods**) and three broad exclusive taxonomic groupings of birds (passerines, non-passerine landbirds and seabird) in **F)**. Example bird species are featured in each plot using silhouettes (available from Phylopic; committed to public domain by Steven Traver, Andy Wilson, Federico Degrange, and Alexandre Vong).

Evolutionary correlates of bird nest architecture

Our dataset allows for study of variation in nest traits globally (**Fig. S3**). We found that nest traits vary with both latitude (**Fig. S4, Fig. S5,** see **Supplementary Information**) and island endemicity (**Fig. S6**). Evolution on islands may lead to convergent evolution of unique adaptations[27,28], with the expectation that species will show similar evolutionary tendencies as they become island endemics. These adaptations may be less affected by predation pressure, which tends to be lower on islands. However, we found that island endemics do not occupy unique portions of the nest morphospace, meaning that island birds generally do not evolve unique combinations of nest traits (**Fig. 2A**).

To further test the relationship between nest architecture, island endemicity[17], aspects of climate[16,17], predator diversity[29], and species body mass[11], we used multivariate phylogenetic regression models (see **Methods**). We modelled the response of all 12 axes of nest morphospace based on five predictors, including island endemicity, $\log_{10}$ of maximum bird body mass, principal component climate axes 1 and 2, and total predator diversity (see **Methods**). Models were run across 100 different posterior-sample phylogenies from[30] (**Table S4**) to account for uncertainty in branch lengths and topology of the avian tree of life. The models included 2,996 species of the 3,217 for which nest morphospace data were available, due to missing data in the dependent (body mass, climatic and biotic) variables of the models. Climate was characterized as the first two principal component axes based on non-scaled or centred average temperature, precipitation, wind speed, water vapor pressure, and solar radiation for

each species across its geographic range (**Fig. S7**)**,** which explained 81.3% of the variation in the climate among species.

All five predictors were included in the best-supported model and showed statistically significant correlations with nest traits (**Fig. 2; Table S4**). The phylogeny used in the analyses had a high impact on model results, showing considerable variation across each model run (for effect sizes, R^2, and p-values). Climate PC1 showed the greatest variation in parameter estimates, particularly with respect to R^2, but was statistically significant in most models. Despite this variation, predator diversity and maximum body mass consistently had the largest effect sizes (in terms of the median) across all five predictors of nest architecture (**Fig. 2B**, **Table S4).** The largest amount of variation in nest architecture was explained by predator diversity (median 6.4% of variance explained) and climate PC1 (median 1.8%), although the explanatory power of each predictor varied depending on the tree topology used in a given model (**Fig. 2C**, **Table S6**). Predator diversity and maximum body mass were statistically significant predictors of nest architecture in 95% of 100 model runs (**Table S4**). Island endemicity exhibited a weaker relationship with nest traits but remained significant in 90% of models. The variability in estimates of each model co-occurred with overall low phylogenetic signal, as expressed by Blomberg's K, with mean across 100 phylogenetic trees of K = 0.068 (95% confidence interval [0.056, 0.082], but minimum-maximum values of [<0.001, 0.20].

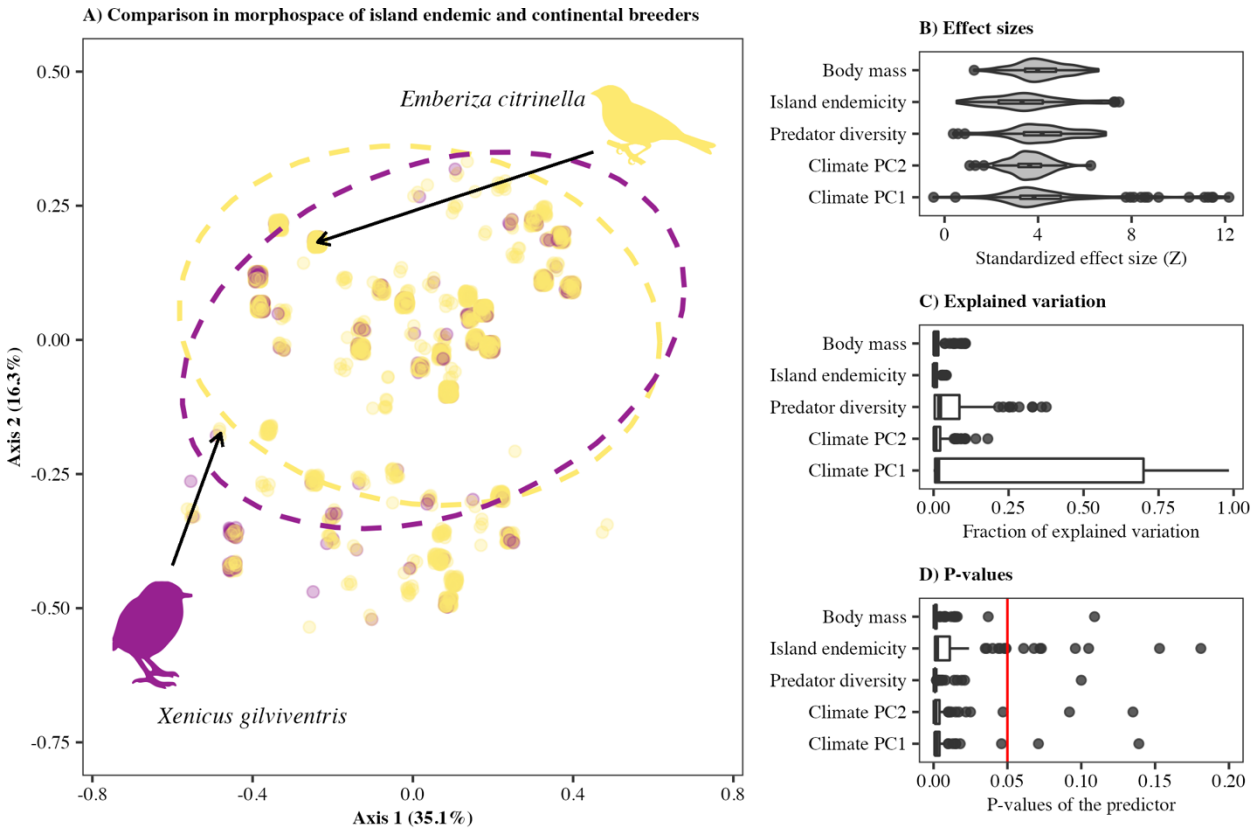

Figure 2. Evolution of nest architecture in birds is associated with predator diversity, body mass, climate, and island endemicity. **A)** The nest morphospace based on the first two PCoA axes, between island endemic (purple/dark) and continental (yellow/light) species. Points were jittered for clarity of presentation. The subplots show the summarised results of 100 multivariate phylogenetic models, testing the correlation between nest architecture and climate, predator diversity, maximum body mass, and island endemicity. NB: the results in the subplots do not present the relationship between estimates within the same run (i.e. which exact values for each predictor were estimated in the same model). The estimates would be different in another run). **B)** Distributions of the calculated effect size, *Z*, for each predictor. Dots symbolise outliers beyond the 95% confidence interval. The boxplots

show the inter-quartile range, with whiskers spanning the 95% confidence interval. **C)** Distributions of the coefficient of determination (R^2) attributed to each predictor (see **Methods**). The boxplots span the 95% confidence interval, with dots symbolising outlier estimates. **D)** The distribution of p-values for each predictor across the models. The boxplots show the inter-quartile range, with whiskers spanning the 95% confidence interval. The red line in **D)** represents a significance threshold of $\alpha = 0.05$. Example bird species for each group are featured using silhouettes (available from Phylopic; committed to public domain by Ferran Sayol).

The effects of each of our explanatory variables on nest architecture traits were visualised using their multivariate regression coefficients (see **Methods**, **Fig. S8-12**). We found that larger-bodied bird species tend to evolve simpler nests, including platform and scrape nests (no or little obvious nest structure) and cavity nests (**Fig. S8**, **Table S1**). Smaller species tend to evolve vegetation nests, situated further away from the ground and more often attached by hanging (laterally or from the top, **Table S1**). These patterns are congruent with the idea that nest architecture is determined by engineering principles, with structural support being a key element[11]. Heavier species therefore tend to evolve structurally sound nests (avoiding hanging nests, placing nests on ground, and cavity nests) and prefer nests that require less material, which would otherwise incur significant resources if the entire bird were to fit in the nest.

Species experiencing higher predator diversity, and therefore potentially higher predation intensity, show multiple signs of adaptation to potential predation (**Fig. S9**), despite the role of this factor being questioned in regional studies[13]. These species tend to evolve nest structures that are either cups, domes, or scrapes, while nest site tends to evolve towards placement either on the ground or in cliffs. Species in regions with high predator diversity also show a preference towards the three lower categories of nest height, below 10 m, and towards hanging nests (either lateral or pensile, **Table S1**).

We observe diverse responses to predator diversity, some of which (ground nesting, scrape nests, lower nest heights) may not appear to improve nest protection from predators. For example, increasing nest height might seem a more intuitive response to predator diversity, and has been observed previously as a response to the introduction of mammalian predators in the O'ahu 'Elepaio (*Chasiempis ibidis*) [19]. However, adaptive responses to predation may be complex and depend on predation modes (e.g. ground predation vs aerial predation). Moreover, camouflage and concealment of nesting adults[1,15], the nests themselves[31], or modifications of parental care patterns seen in many songbirds[21,32], may be a more common response to predation threat than changes in nest height. The traits found to be associated with high predator diversity can favor concealment: e.g., ground and scrape nests can well match the surface on which nests are placed[33], or hanging nests could be better covered by site features such as foliage. Information on the interaction of nest traits, concealment, and other types of predator avoidance behaviors, along with mode of predation, would be required to resolve the associations observed. Notably, as defined in this study, predator diversity is not colinear with latitude in our study but could be correlated with local species richness. Therefore, the variable does not purely reflect latitudinal patterns, but the observed variation could also be related to diversity of other species (e.g. parasites, competitors).

In addition to predator diversity, we found the principal components summarizing climate variation to be strong predictors of nest architecture (**Fig. S10-S11**), confirming associations that have previously been found at continental scales[16,17]. The clearest association of climate with nest architecture is the tendency to evolve cup and scrape nests in warmer and wetter environments (**Fig. S10**), where solid cover from the environment may not be needed. However, in sunnier, windier, and drier conditions, there is a tendency for domed nests, or nests that are located underground (**Fig S11**). Covered nests would provide extra protection, as sunny and dry conditions can drastically alter the conditions experienced in the nest[34,35]. In Australian songbirds, the occurrence of domed nests has been related to dry conditions (measured by humidity) [16], but not solar radiation[17]. Both associations emerge in our study, emphasizing how the scale of comparison, and the abiotic variation it encompasses, can influence interpretations.

We recovered a weaker, though frequently significant, signal of island endemicity as a predictor of nest architecture, with a tendency for island species to build simpler nests – scrapes or platforms, placed basally, and a tendency to evolve either ground-level nests or nests located 10 or more meters above ground (**Fig. S12**). This pattern of nest simplification in island birds may be part of a wider pattern of evolutionary simplification of traits in island species[27,28], which include loss of flight[29] or drabber coloration[36] in birds. Distinct evolutionary trajectories on islands are thought to be a product of relaxed selection in the form of a more stable climate, lower interspecific competition, and lower predation risk[37]. It remains unclear which of these factors are the primary driver, although recent work has suggested predation (or lack thereof) to

have a particularly significant role[38]. Island endemicity was a significant predictor of nest architecture despite the inclusion of predator diversity and climate variables, suggesting the 'island syndrome' in nest architecture may exist for reasons other than low predation intensity.

Beyond functional correlations, our study highlights significant biases and gaps in available data. For some nest traits, more than 50% of all bird species were classified as unknown (e.g. attachment, see **Fig. S1**). Additionally, the distribution of missing data is highly biased across taxonomic levels. We found that cavity nesting species often have their structure and attachment undescribed, and that there are clear latitudinal patterns in unknown traits (**Fig. S4** and **S5**), reflecting common biases in trait data distribution[39,40]. Inevitably, these biases must be considered when interpreting the results of our study, with almost 70% of bird species missing from the analysis of the drivers of nest architecture. Despite our attempt to capture nest architecture as a holistic metric, the total of median R^2 values of each model explain only about 11% of the variation in nest architecture, across a taxonomically representative sample containing 39/41 of all bird orders and 213/246 of all bird families. This reveals that nest architecture is overall weakly correlated with the environmental co-variables in our broad approach. Furthermore, we show overall weak, but variable, phylogenetic signal in the multivariate metric of nest architecture. This variation confirms a significant degree of phylogenetic uncertainty in modelling nest evolution in birds. Whilst individual nest traits, particularly nest type, generally have high phylogenetic signal, e.g. in pan-avian analyses[41] and in tyrant flycatchers and allies Tyrannida[42], this pattern does not hold for all nest characteristics. Even in pan-

avian analyses, traits such as nest site can show little evidence of significant phylogenetic signal[41], whilst individual bird families may differ greatly in conservatism of their nest traits (e.g. high conservatism in Tyrannida[42], as opposed to high variation of all nest traits in ovenbirds Furnaridae[9]).

We provide the first global investigation of evolution of multivariate nest architecture, mirroring recent advances in understanding the broad scale patterns of avian morphological evolution[43]. We find that predator diversity, body mass, climate, and island endemicity clearly impact the evolution of nest architecture. As data incompleteness is resolved through continued study of avian natural history, and as other aspects of bird nest architecture are characterized, including nest orientation[44], microhabitat[45], or concealment[15], we expect our database to provide a strong foundation to examine micro- and macroecological patterns in the evolution of avian nests. In this comprehensive, global analysis of extant bird species, we clearly show the influence of abiotic and biotic factors on evolution of nest architecture, presenting a global analysis of the drivers of an animal extended phenotype.

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Methods

Data collection

We collated data on nest architecture for 10,538 species of extant birds using *Birds of the World*[1]. We documented variation at the species-level following previous functional trait studies of birds[2]. We chose five traits based on these previous studies[3,4], including nest type (whether nests are in a cavity or not); nest structure (whether the nest is a scrape, a platform, a cup or a dome); nest site (whether the nest is placed in vegetation, on cliffs, on the ground, on water bodies, underground, or in ant nests); nest attachment (whether the nest connects to its site basally, laterally, or from the top); and the minimum recorded nest height (in meters). Character states for each of these traits are described in **Table S1**. All traits were coded by one author (MTJ) for consistency. A trait was considered missing if any aspect of the description was unclear or absent. When the distinction was made, we only coded nests used for breeding, and not for display or roosting. For each species, we recorded taxonomic information (order, family, genus, and species), whether the breeding range was exclusively insular, and the maximum body size (in grams) using measurements of adult sexed birds, where available. The database was collated between October 2020 and April 2021. As *Birds of the World* is constantly updated, nest traits were based on versions of species accounts available between those dates.

The nest dataset was initially organized following the Clements/eBird[5] taxonomy of *Birds of the World*. To maintain compatibility, mismatches with IUCN/BirdLife taxonomy[6] and birdtree.org were identified and corrected using Avibase[7] (https://avibase.bsc-eoc.org/avibase.jsp) and original names provided alongside the

data. Classification as passerine/non-passerine and landbird/seabird were derived from *Birds of the World* and used to present nest architecture across three distinct evolutionary groups in birds. Passerine birds were all members of Passeriformes. A bird was classified as a seabird if it consistently utilized marine habitats (coasts, offshore waters, pelagic waters) during a part of its annual cycle. All birds that did not meet these conditions were classified as land birds. Note there are no known marine passerines, therefore each category is exclusive.

Describing nest architecture

We captured variability in species' overall nest architecture using metric scaling in the form of principal coordinate analysis (PCoA), with five nest traits. The continuous nature of the nest height trait would obscure patterns of organization imposed by the other categorical traits. We therefore constructed nest height categories, which additionally served to improve the behavior of metric scaling while still recognizing significant functional distinctions and similarities among nest height levels. To this end, we categorized nest height as follows: ground (0m), low (<1m), medium (1-10m) and high (>10m). These categories were considered to best represent the different heights within which birds build their nests.

Metric scaling requires complete data across all variables. Data imputation is sometimes used in analysis of datasets with missing data, but we decided not to impute missing data due to uncertainties associated with the imputation of categorical data [8] and because describing data gaps is also an aim of our study. Hence, we restricted the dataset to 3,217 species for which complete information were available.

Principal coordinates were calculated from a Gower distance matrix using the R v4.1.2 [9] package *cluster v. 2.1.3*[10] via the 'daisy' function on default settings.

Multivariate phylogenetic regression

Predictor variables

We tested how nest architecture correlates with five predictors, including principal component axes of climate, whether a species is an island endemic, $\log_{10}$ of maximum body mass, and the mean number of potential predators.

Climatic predictors

We characterized the climatic conditions associated with each species geographic range using five variables, including mean annual: temperature, precipitation, wind speed, vapor pressure, and solar radiation. These conditions were then subject to a principal component analysis to reduce the dimensionality of climate variables, and summarized the diverse climates experienced by bird species. Climate data were obtained from WorldClim[11] at 1:50 000 000 resolution. We averaged the conditions across months, since data is lacking on seasonal breeding activities for many species, and many species breed year-round (even in climates with seasonal breeders). These annual climate layers were used to extract mean values for each of the five climate variables across the entire breeding range of each species in the BirdLife distribution maps, using the *raster* v. 3.5-21[12] and *sf* v. 1.0.7[13] R packages. Full data across the five climatic variables was available for 10,206 species. The PCA was performed using the function *prcomp()* from the base *stats* package.

Body mass & island endemicity.

Maximum body mass and island endemicity were collected from *Birds of the World*[1]. Maximum body mass was used, as it gives an upper requirement to nest architecture, and average estimates are not available for many species. Island endemicity was assessed by examining range maps and descriptive text in *Birds of the World*.

Predation pressure.

Data on predation pressure for birds does not exist at the scale required to examine global macro-evolutionary patterns. Thus, we used the diversity, here of potential predators, as proxy of intensity/threat, following previous work on bird biogeography[14,15]. Although this approach could lead to underestimates of predation (e.g., in cases where predator density is more important) or overestimates (e.g., in cases where predators differ markedly in rates of nest attack), previous work has suggested this proxy captures patterns at broad spatial scales[15]. We calculated average number of potential mammalian, avian, and reptilian predators encountered on a per-species basis. We collected the names of potential mammalian and avian predators using EltonTraits[16] to include all species known to consume endothermic vertebrates or unknown vertebrates in their diets. For reptiles, we included all snake families and monitor lizards, given the lack of comprehensive diet information for this group. To resolve mismatches in species names between EltonTraits and IUCN distribution maps, we used Avibase for birds and the IUCN Red List for mammals and reptiles[17]. We intersected ranges of potential predators at 10' resolution (the same as the climate data) to calculate the number of potential predator species in each grid cell across birds, mammals, and reptiles, returning a total count per grid cell. For each

bird species, we calculated the average number of potential predator species across their breeding range at 10' resolution.

Phylogenetic trees

We accounted for phylogenetic relationships in our multivariate regression models using the phylogeny from Jetz et al. 2012[18]. We downloaded 10,000 random time-calibrated posterior sample phylogenies for all species with genetic information (n = 6,670) included on birdtree.org[18] using the Hackett backbone[19]. We used the function *comparative.data()* from the package *caper* v.1.0.1[20], which resulted in 2,996 species ordered along the phylogeny with complete nest morphospace and environmental data. We calculated the phylogenetic signal using Blomberg's K[21], as applied in the package *geomorph* v. 4.0.4[22], across the same phylogenies as used for modelling.

Model framework

To investigate the impact of our chosen abiotic, biotic, and geographic variables on nest architecture, we used multivariate phylogenetic regression models, specifically the geometric morphometric application of phylogenetic least squares[22]. This method allowed us to account for the full multivariate spectrum of nest morphospace, rather than examining individual axes in isolation. We used all non-zero axes (Axis 1 – Axis 12, **Table S3**) as dependent variables in our models, applied in the package *geomorph*.

The five predictor variables were tested for collinearity using variance inflation factors implemented in the R package *car* v.3.1.1[23]. We set a cut-off VIF as <2.5, recommended when the signal may be weak, to avoid false positives[24].

We ran our models over 100 different random trees obtained from Jetz et al. 2012[18]. We saved the result of each run and used data from across all 100 runs to represent the results using packages *ggplot2* v. 3.3.6[25], *ggdist* v. 3.2.0[26], and *cowplot* v. 1.1.1[27]. To visualize the results of the model, we extracted model coefficients from procD.pgls objects in R. The model assigns coefficient values to each species, and they correspond to the actual values of predictors fed to the model. We extracted the coefficients for each species across all 100 trees, resulting in 100 coefficients per species. We performed model comparison, of testing changes to R^2 and significance of variables, following[28], and the model including all variables of interest was the best fit.

Biogeographical analyses

To obtain estimates of latitudinal extent for each bird species, we used distributional maps from BirdLife[29]. All handling of geographical data was performed in R, using the package *sf*[13] and *tidyverse* v. 1.3.2[30]. We filtered distributional maps to retain only: a) ranges that are native; b) ranges that are either year-round breeding or breeding ranges; and c) extant ranges. We intersected these distributional maps with land surface area obtained from NaturalEarth (https://www.naturalearthdata.com/), to ensure that only terrestrial ranges were included. We calculated the latitudinal midpoint of the breeding range from the terrestrial distributional ranges. To generate data on bird

presence in each 1° latitudinal bin, we intersected the bird distribution simple features with a grid of latitudinal bins and calculated the total number and identity of species in each of them.

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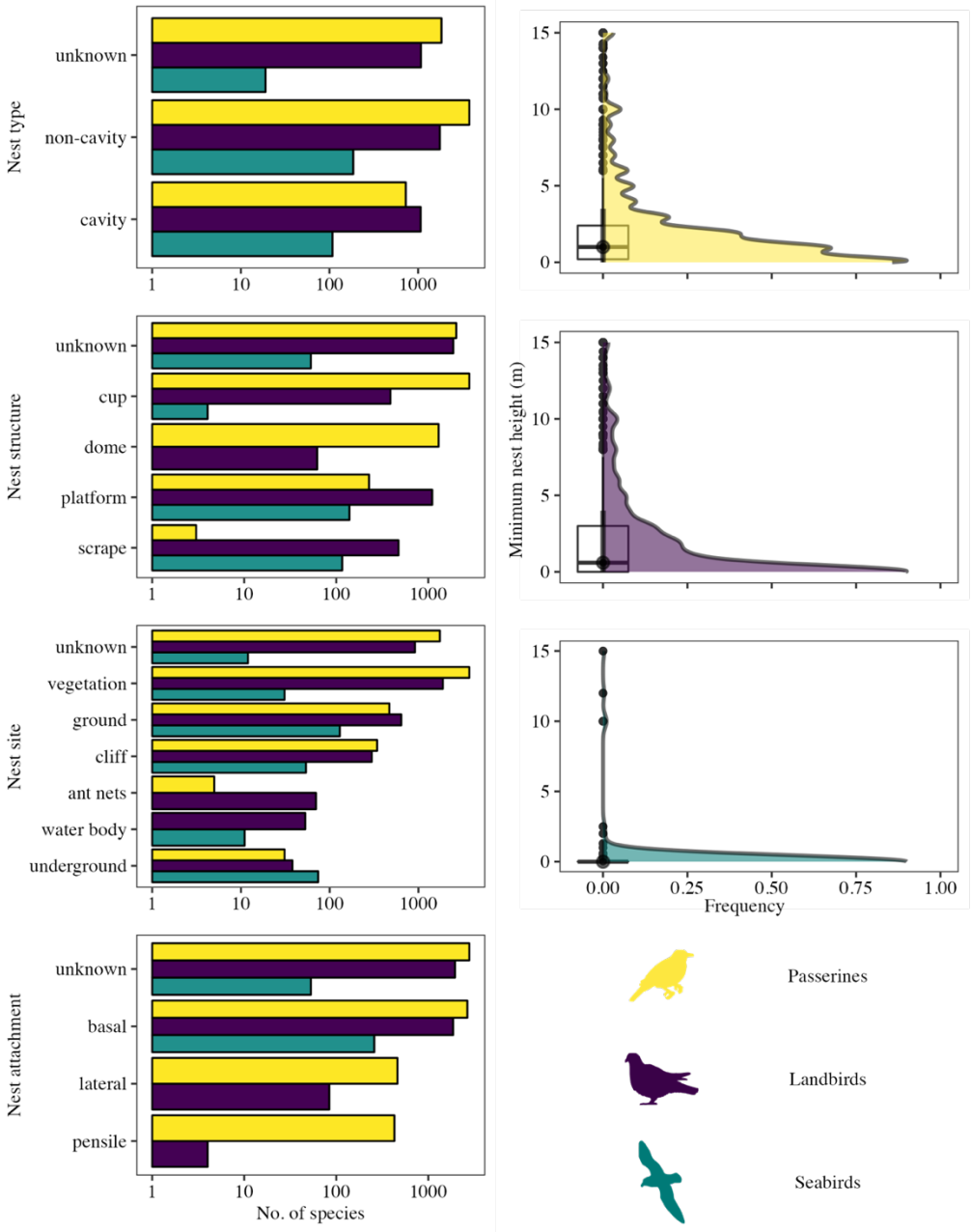

Fig. S1. Distribution of nest traits among bird species and across the three broad evolutionary groups: passerines, non-passerine land birds, and seabirds. The three groups have been specified as described in the Material and Methods. For the distribution of nest height, a cut-off 15 meters was used for clarity of presentation, removing 156 species from the distribution presented.

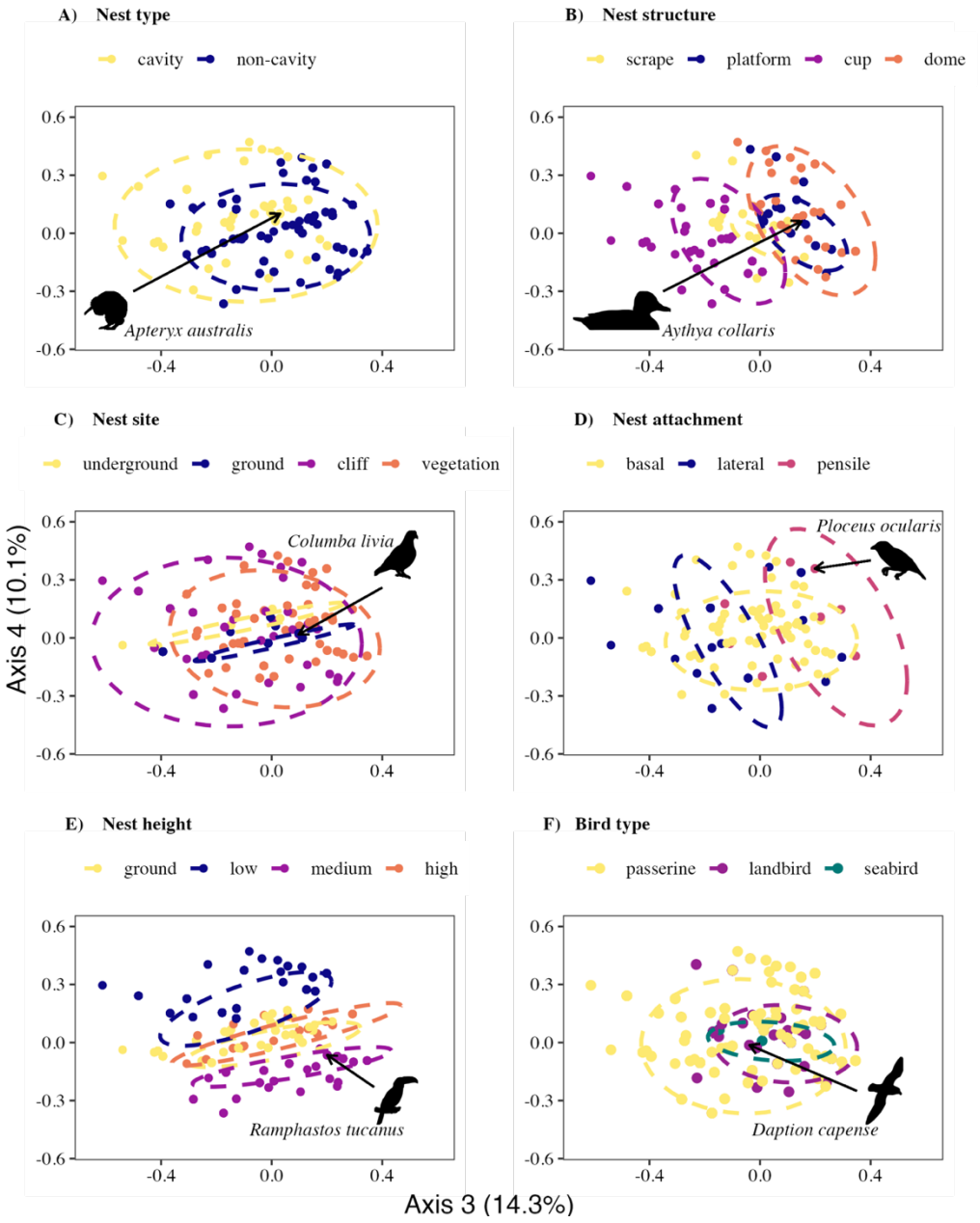

Fig. S2. The nest morphospace as represented by the third and fourth largest axes of variation. These axes no longer separate bird species by nest type (A) or nest site (C) but do separate birds in terms of nest structure (B) and nest height. Example bird species (same as in Fig. 1) are featured in each plot using silhouettes (available from Phylopic; committed to public domain by Steven Traver, Andy Wilson, Federico Degrange, Alexandre Vong).

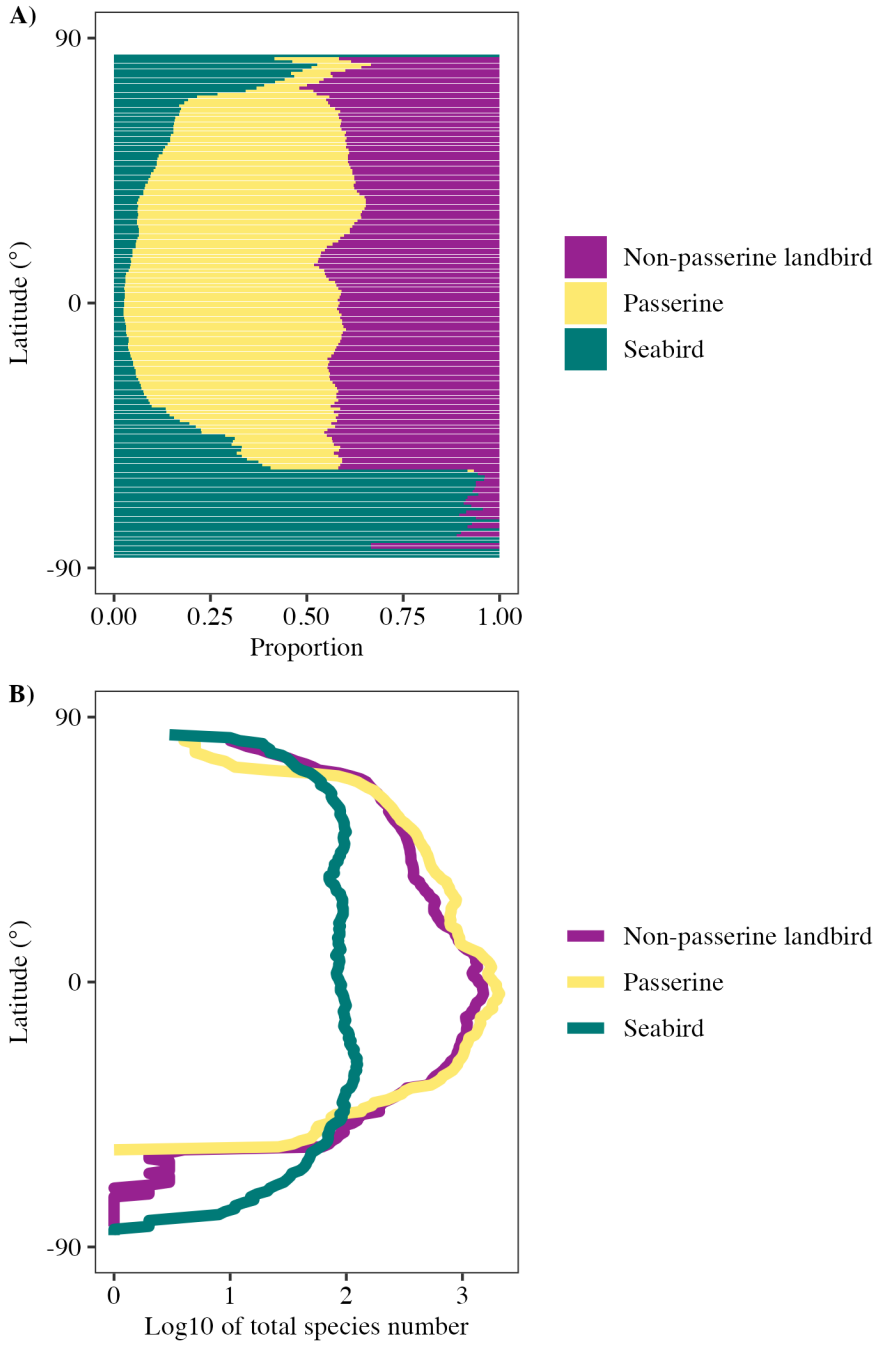

Fig. S3. The latitudinal distribution of passerines, non-passerine land birds, and seabirds. A) shows the proportion of each group per latitudinal bin; B) shows the $\log_{10}$ of the total number of species. Species total and proportions are calculated for 1° latitudinal bins.

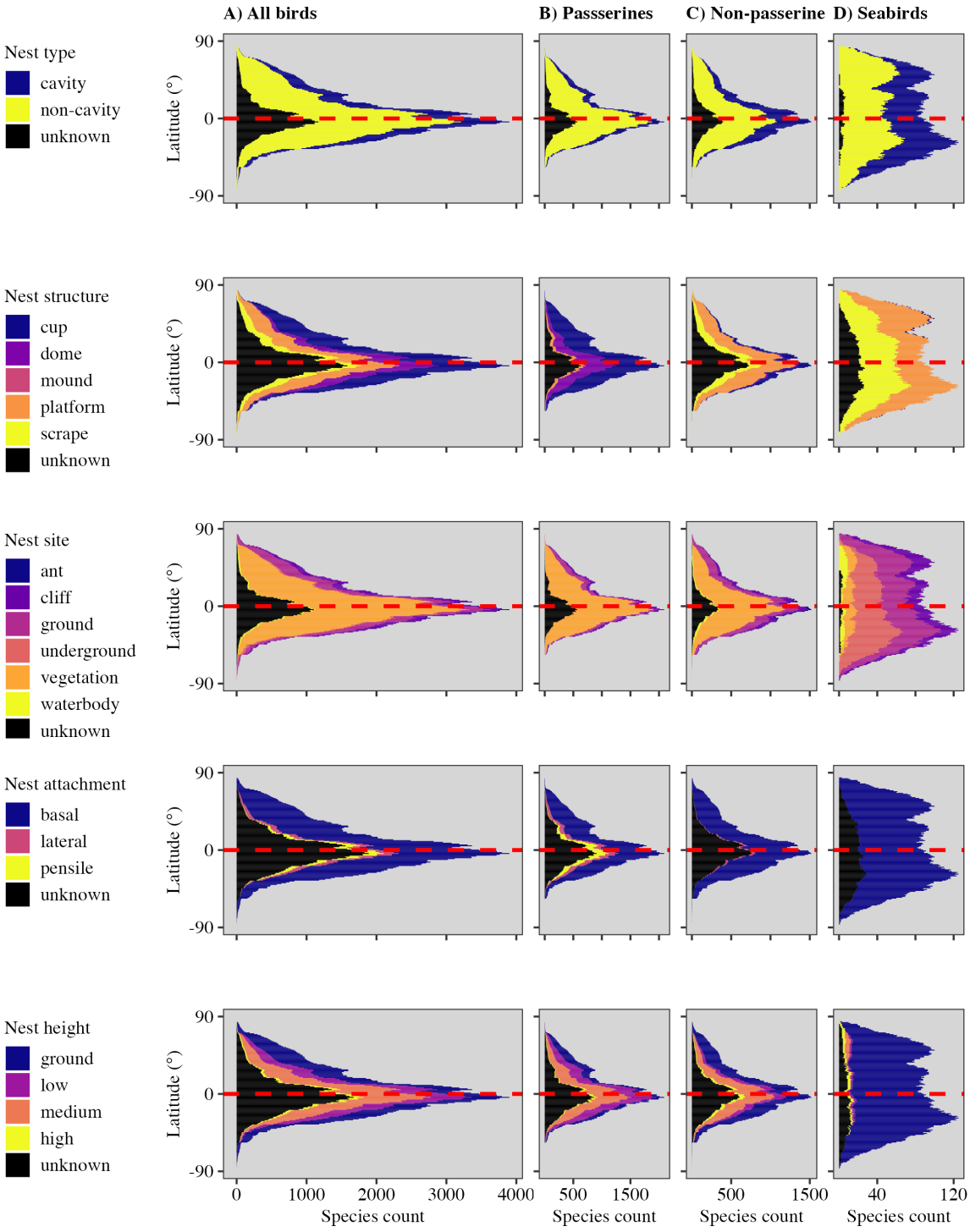

Fig. S4. Latitudinal patterns of nest traits and species richness. Species richness and associated nest trait data are shown for 1° latitudinal bins. The plots are replicated for A) all birds; B) passerines only; C) non-passerine land birds only; and D) seabirds (see Materials and Methods). A red line is placed at 0° latitude to show the symmetry around the equator.

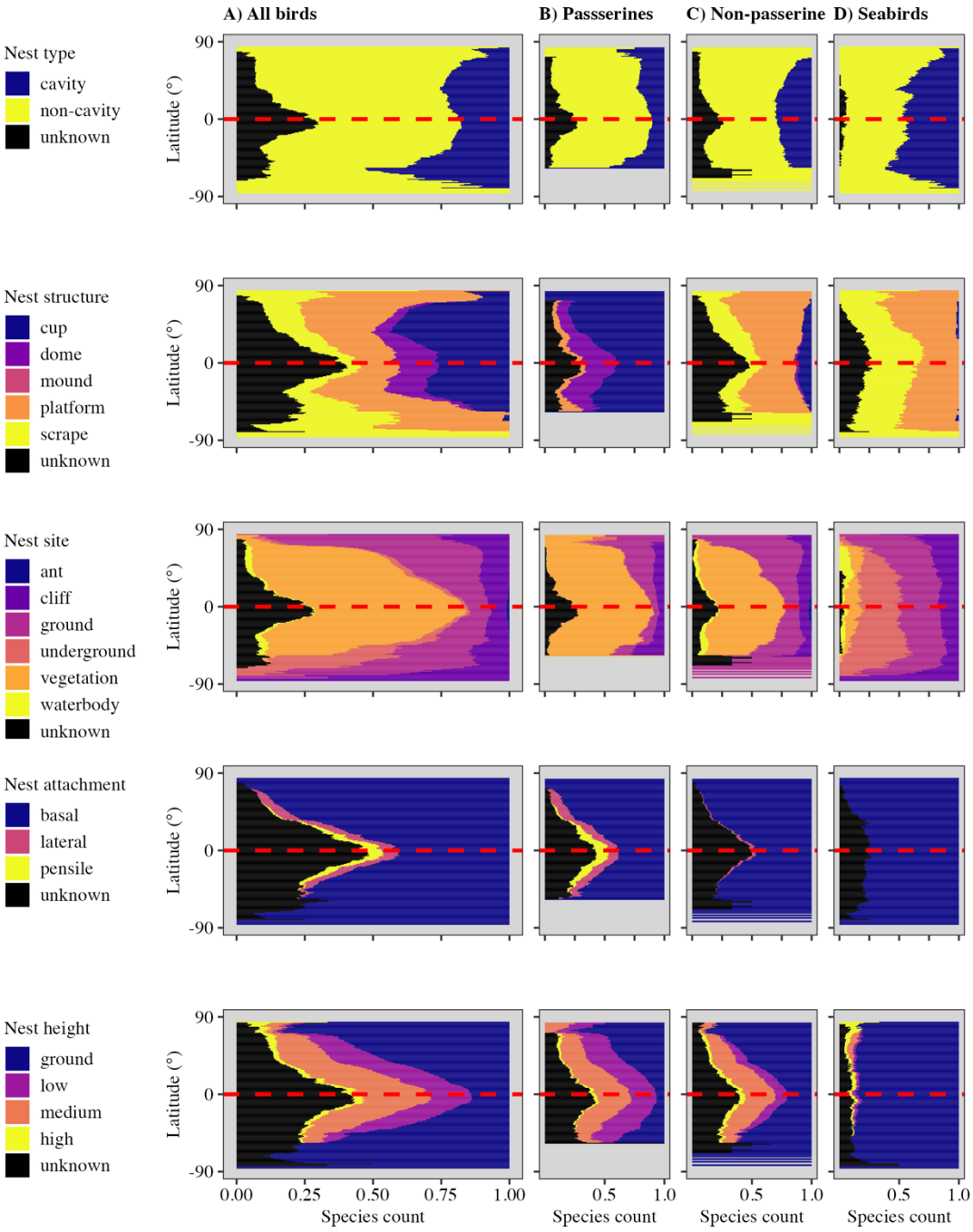

Fig. S5. Latitudinal patterns in nest trait proportions. Proportional nest trait data are shown for 1° latitudinal bins. The plots are replicated for A) all birds; B) passerines only; C) non-passerine land birds only; and D) seabirds (see Materials and Methods). A red line is placed at 0° latitude to show the symmetry around the equator.

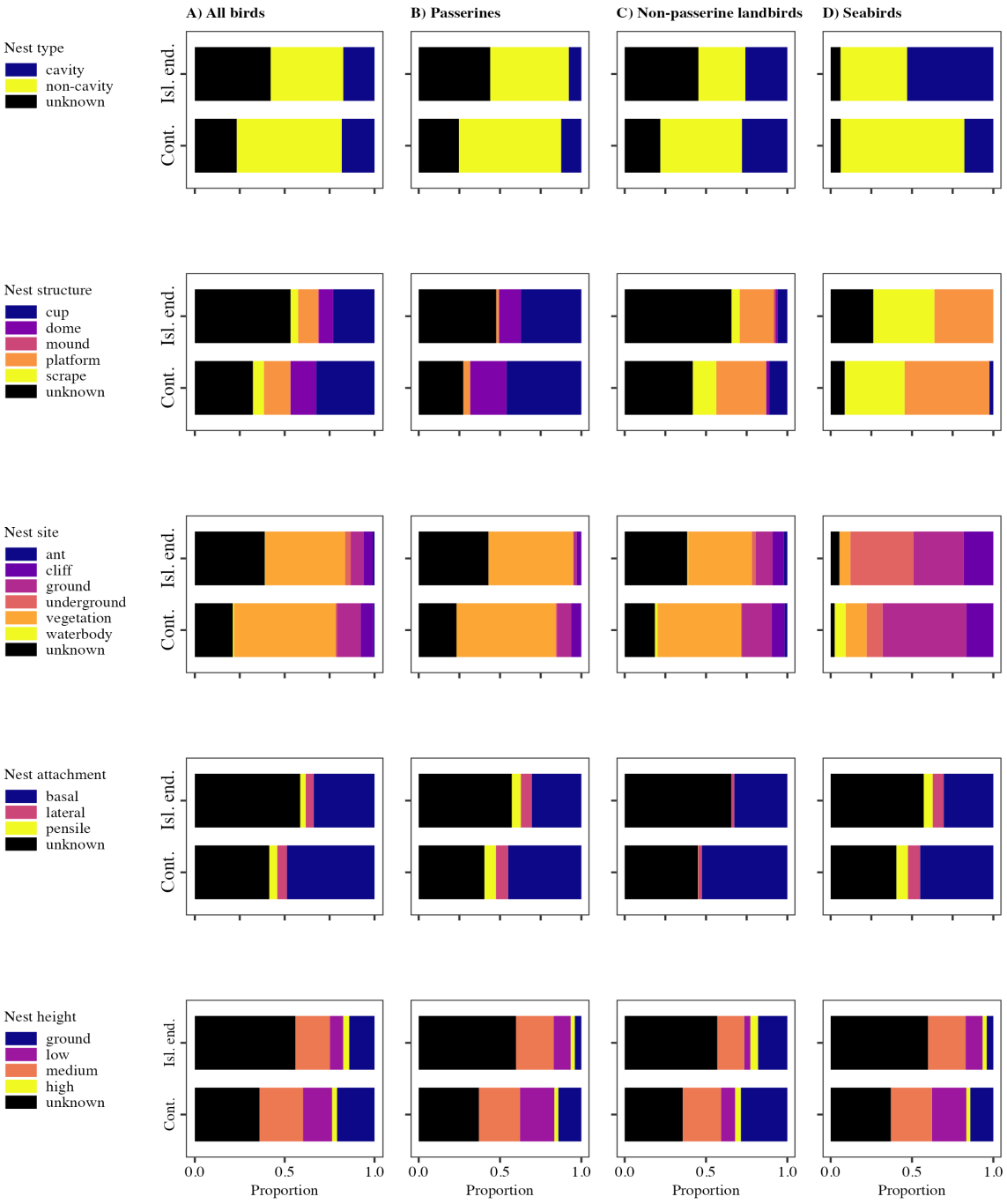

Fig. S6. Nest trait proportions between island endemic (Isl. end.) and continental (Cont.) species. The plots are replicated for A) all birds; B) passerines only; C) non-passerine land birds only; and D) seabirds (see Materials and Methods).

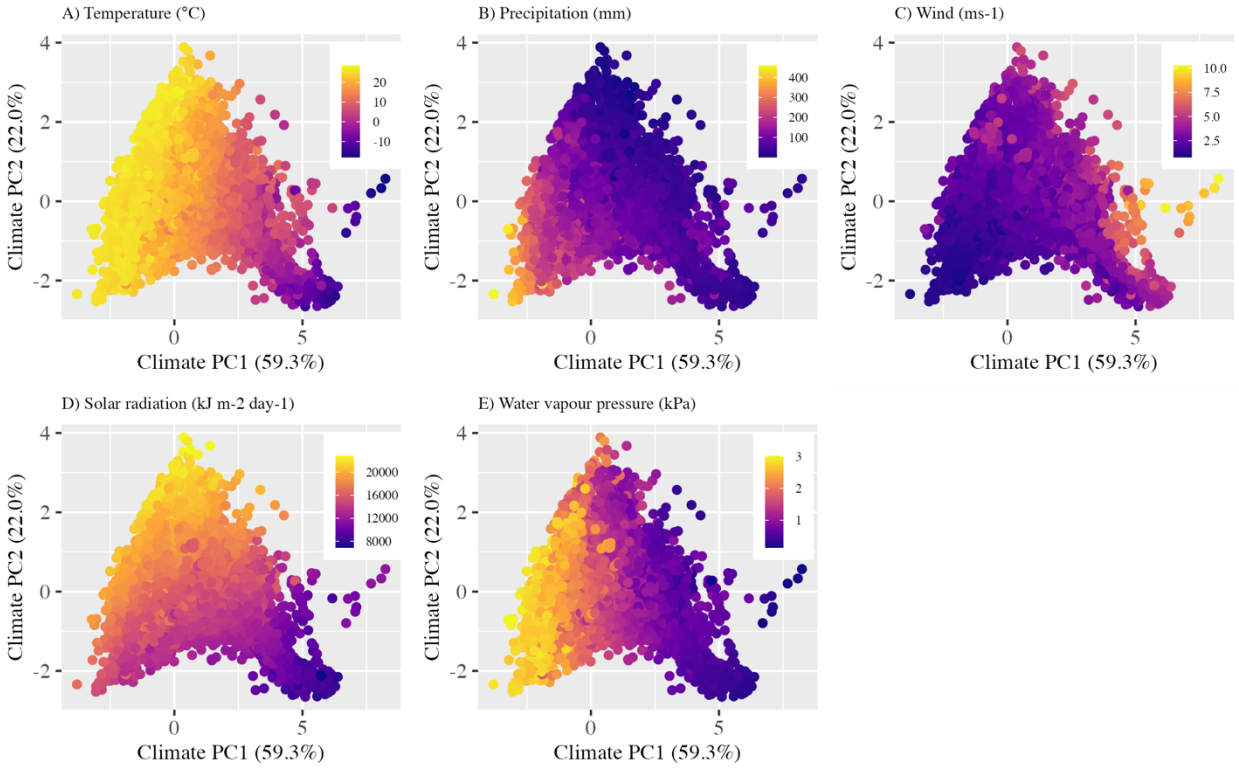

Fig. S7. The principal component of climate for the full dataset of 10,206 species for which distributional and climate data was available. The principal components were generated using annual means of the five climatic variables, averaged across the breeding ranges of each species. Each subplot show the distribution of values of the climatic variables along the two main axes of the PCA.

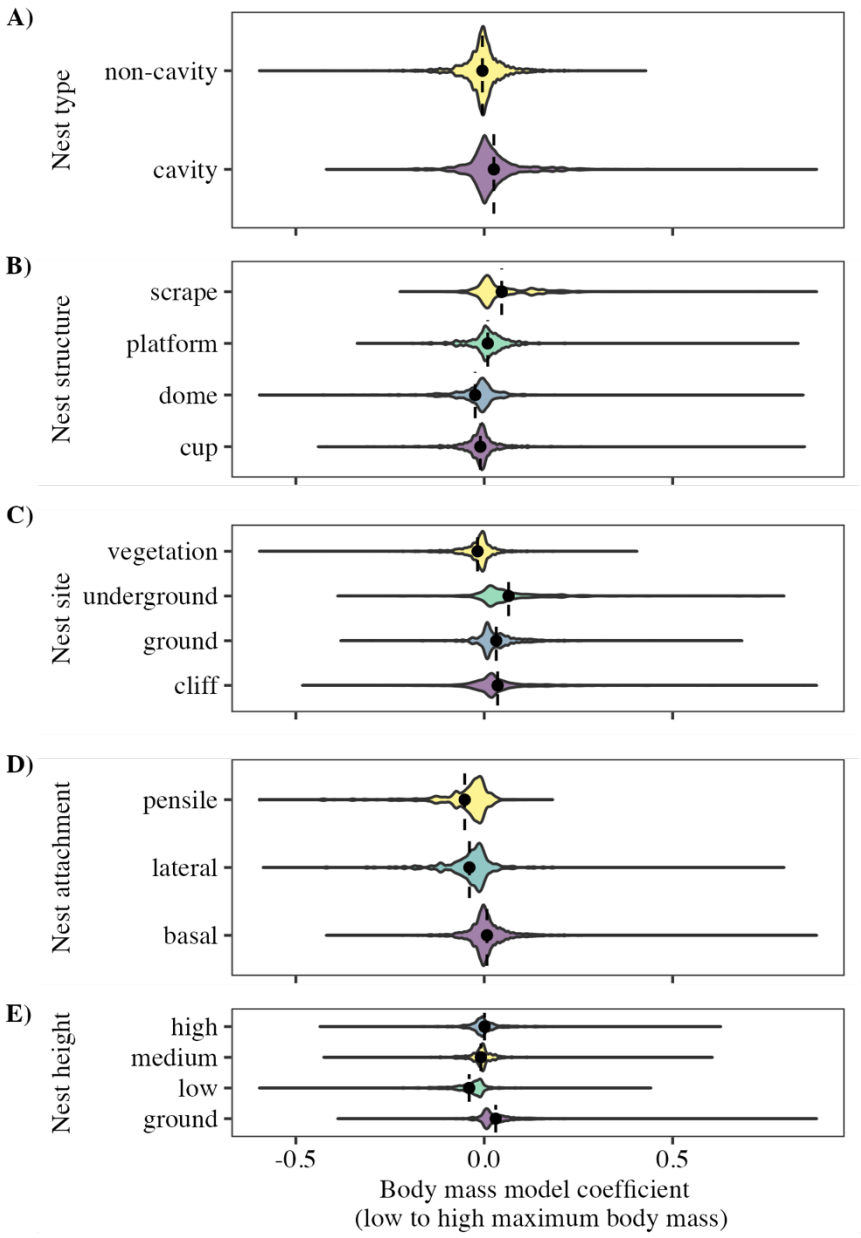

Fig. S8. Distribution of body mass model coefficient across the nest traits. For explanation of coefficients, see Materials and Methods. Here coefficients indicate increasing maximum body mass from negative to positive values. The dotted and dashed lines indicate the mean value of the coefficient for a given nest trait.

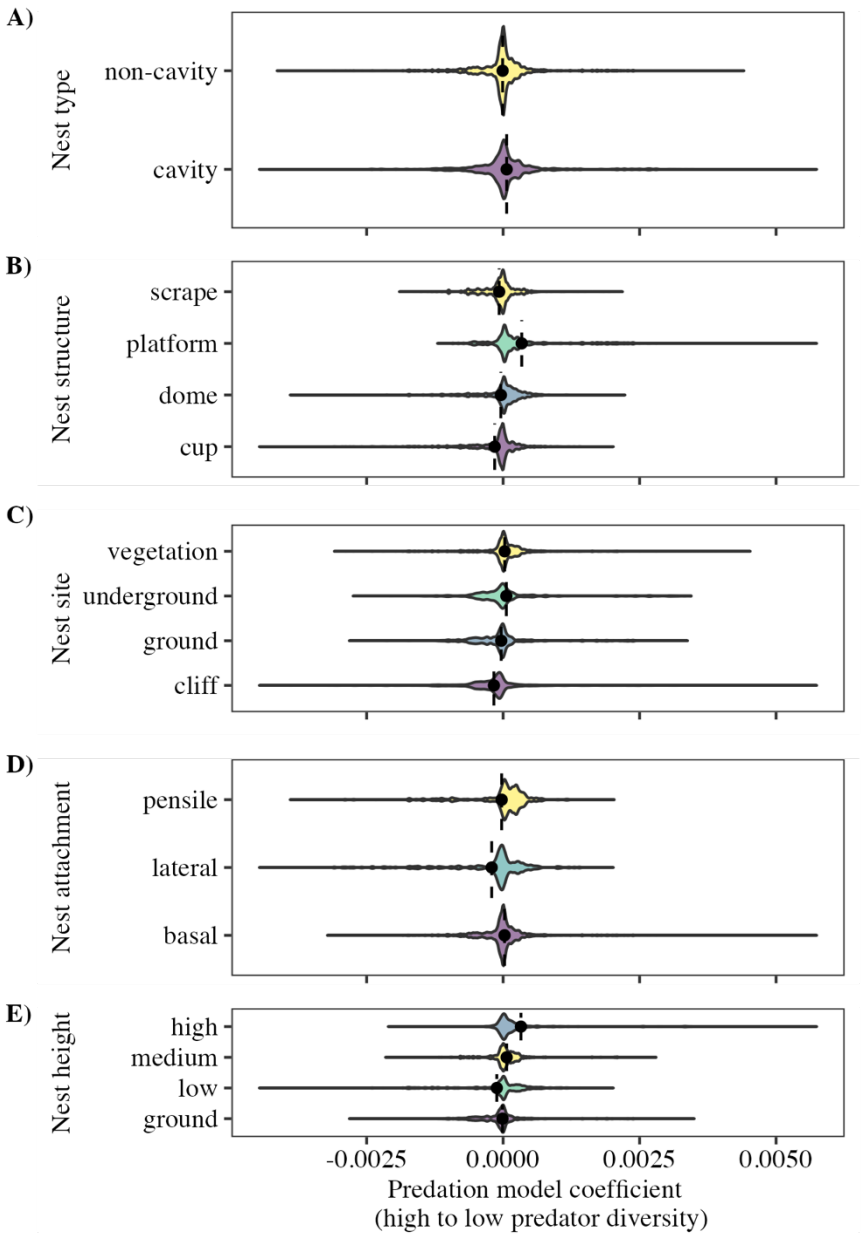

Fig. S9. Distribution of predator diversity model coefficient across nest traits. For explanation of coefficients, see Materials and Methods. Here coefficients indicate decreasing diversity of potential predators from negative to positive values. The dotted and dashed lines indicate the mean value of the coefficient for a given nest trait.

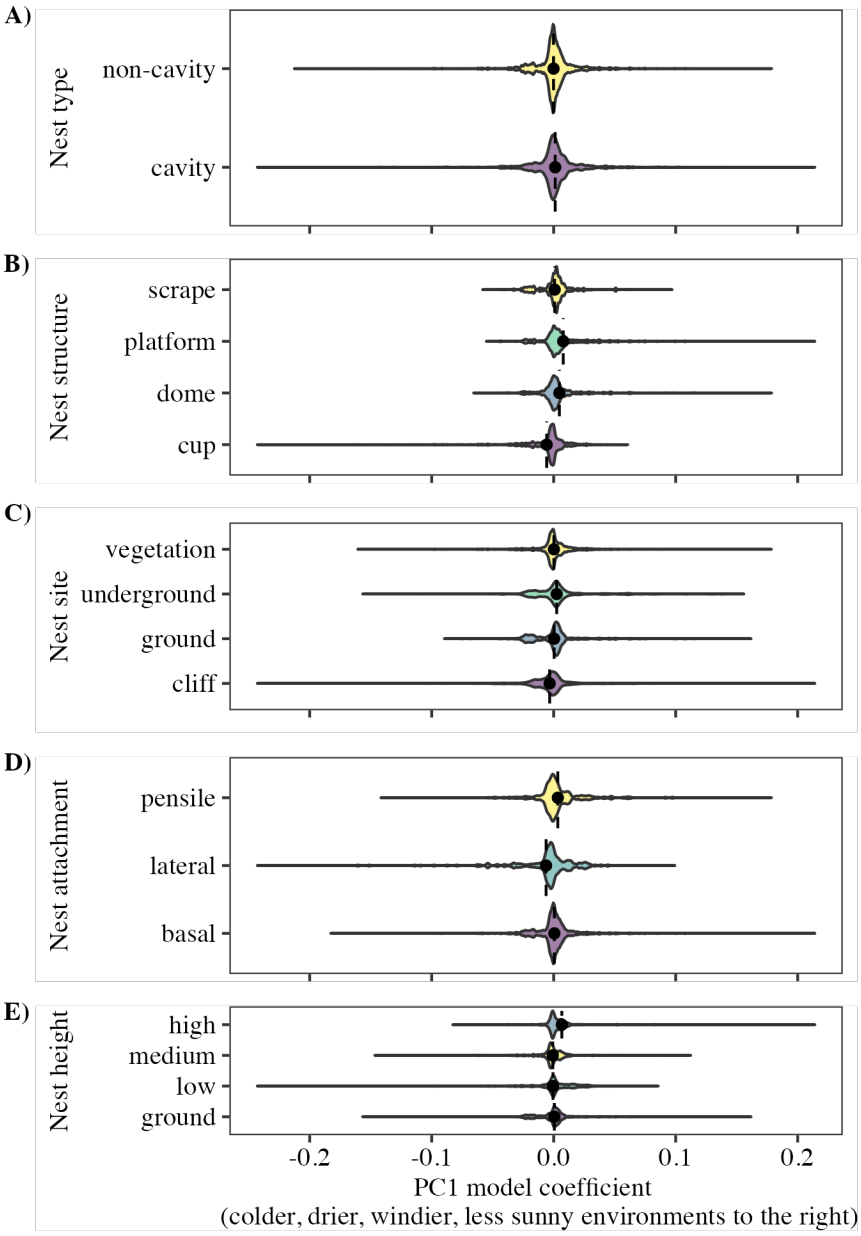

Fig. S10. Distribution of PC1 model coefficient across the nest traits. For explanation of coefficients, see Materials and Methods. Here coefficients indicate increasing PC1 values, from negative to positive. The dotted and dashed lines indicate the mean value of the coefficient for a given nest trait.

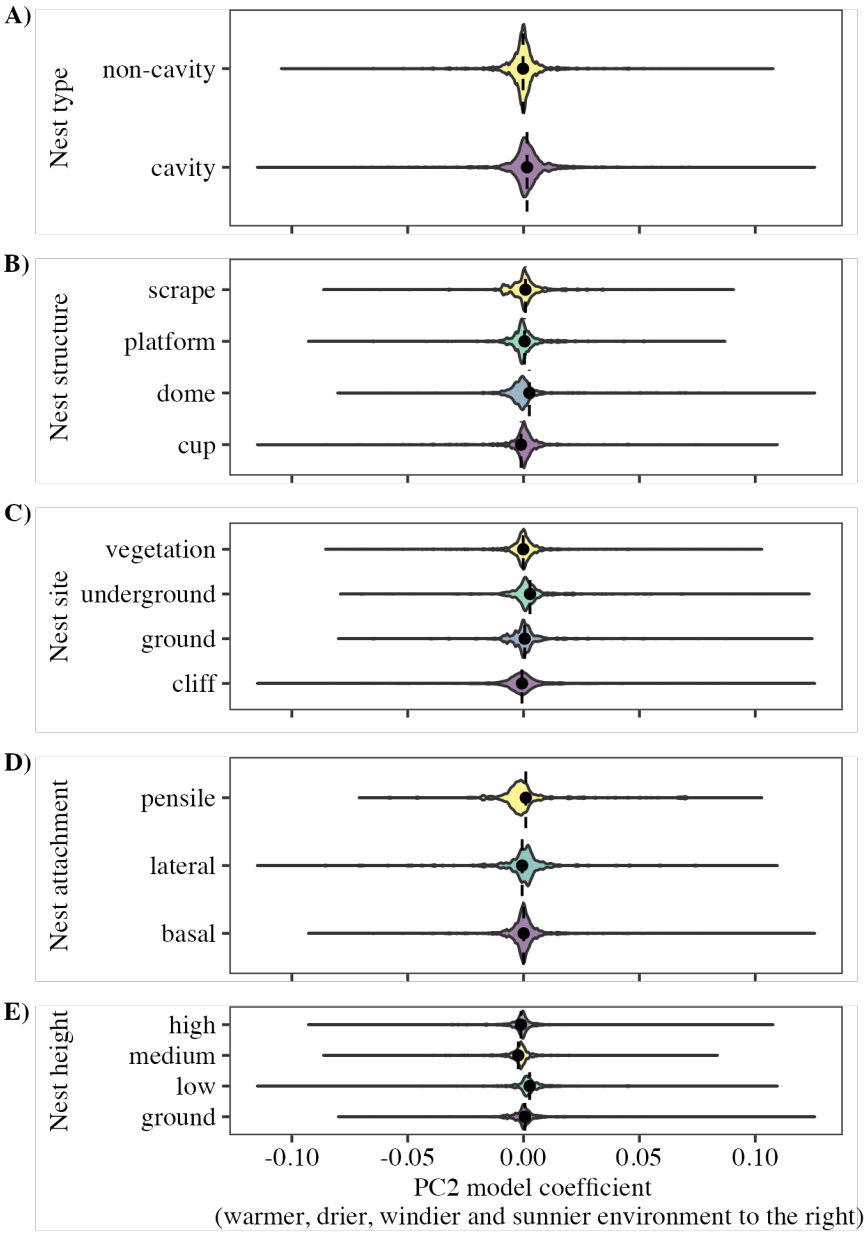

Fig. S11. Distribution of PC2 model coefficient across the nest traits. For explanation of coefficients, see Materials and Methods. Here coefficients indicate increasing PC2 values, from negative to positive. The dotted and dashed lines indicate the mean value of the coefficient for a given nest trait.

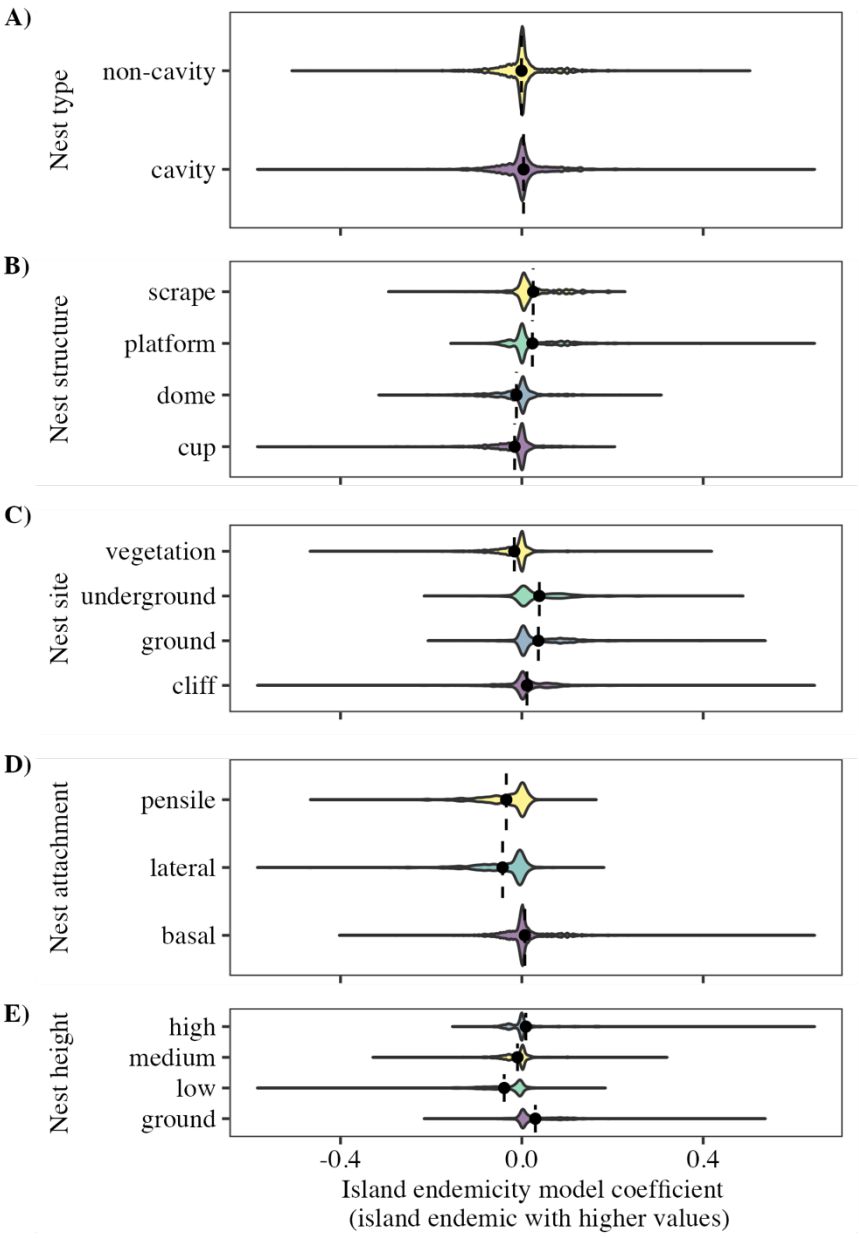

Fig. S12. Distribution of island endemicity model coefficient across the nest traits. For explanation of coefficients, see Materials and Methods. Here island endemics tend towards higher values of the coefficient. The dotted and dashed lines indicate the mean value of the coefficient for a given nest trait.

Table S1. Character states described for the five categorical nest traits (nest type, structure, site, attachment, and height). The nest traits were based on consensus across previous studies (*42, 43*).

Nest type	*Non-cavity*	Nest not placed in any rocky or wooden cavity.
	Cavity	Nests located in rocky or wooden cavities, whether excavated by the bird or not.
Nest structure	*Scrape*	The scrape type indicated that eggs were laid in a place with no obvious nest-construction or with only brief scratching or cleaning (3)
	Platform	A platform nest was a nest where feathers, leaves, sticks or vines were stacked or loosely intertwined to form a platform (3).
	Cup	A cup nest can be distinguished from a platform nest by an erected, surrounding rim made by interweaving nest materials or mud (3). Cup nests could vary in their depth, but parental birds could not hide their whole bodies inside the nests (i.e., expose whole or partial bodies outside).
	Dome	Domed nests referred to the nests where parental birds could sit inside without exposing any part of their bodies (3).
Nest site	*Ground*	A ground site was recorded when birds laid eggs on the ground (3).
	Vegetation	Vegetation sites included those on trees, bushes, bamboo, or thick tangled herbaceous vegetation (such as vines or reeds) that occupies forest understory, grassland, or wetland habitats (3).

	Cliff	When birds built nests in cliffs, river banks, or piles of soil or rocks, the sites of these nests were categorized as cliff/bank (3).
	Underground	For the nests built in burrows underground (3).
	Water bodies	If the nests were built on the surface of water or piled up from the bottom of lakes or ponds and thus surrounded by water, their sites were assigned as water bodies (3)
	Termite/ant nests	For the nests built in termite/ant nests (3)
Nest attachment	*Basal*	The basally attached nests referred to those supported mainly from their bottom, including those sitting among multiple interweaving tree or bush branches and those inside cavities (3).
	Lateral	The laterally attached nests were those attached to supporting objects such as branches or rocks solely by their lateral parts (3).
	Pensile	A pensile attachment referred to the approach that nests were hanged down from a supporting object with its upper, narrower attachment part (3).
Nest height	*Ground*	Nest placed exactly 0m above the ground (corresponds to every nest with nest site being ground).
	Low	Nests placed more than 0m but less or equal to 1m above ground.

	Medium	Nest placed more than 1m but less or equal to 10m above ground.
	High	Nest placed more than 10m above ground.

Table S2. Orders and families included in the nest architecture dataset based on Clements taxonomy (*22*), as used in Birds of the World (*5*), and the numbers of species in both the full (all bird species) and the morphospace (complete nest trait information) datasets.

Order	**Family**	**No. of species: full dataset**	**No. of species in the morphospace dataset**
Accipitriformes	Accipitridae	249	110
Accipitriformes	Pandionidae	1	1
Accipitriformes	Sagittariidae	1	1
Anseriformes	Anatidae	165	115
Anseriformes	Anhimidae	3	2
Anseriformes	Anseranatidae	1	1
Apterygiformes	Apterygidae	5	4
Bucerotiformes	Bucerotidae	59	4
Bucerotiformes	Bucorvidae	2	0
Bucerotiformes	Phoeniculidae	8	2
Bucerotiformes	Upupidae	2	1
Caprimulgiformes	Aegothelidae	10	1
Caprimulgiformes	Apodidae	96	4
Caprimulgiformes	Caprimulgidae	98	52
Caprimulgiformes	Hemiprocnidae	4	3
Caprimulgiformes	Nyctibiidae	7	3

Caprimulgiformes	Podargidae	15	5
Caprimulgiformes	Steatornithidae	1	1
Caprimulgiformes	Trochilidae	345	84
Cariamiformes	Cariamidae	2	1
Casuariiformes	Casuariidae	4	3
Cathartiformes	Cathartidae	7	4
Charadriiformes	Alcidae	24	17
Charadriiformes	Burhinidae	10	7
Charadriiformes	Charadriidae	72	32
Charadriiformes	Chionidae	2	1
Charadriiformes	Dromadidae	1	1
Charadriiformes	Glareolidae	17	8
Charadriiformes	Haematopodidae	11	7
Charadriiformes	Ibidorhynchidae	1	1
Charadriiformes	Jacanidae	8	5
Charadriiformes	Laridae	97	75
Charadriiformes	Pluvianellidae	1	1
Charadriiformes	Pluvianidae	1	1
Charadriiformes	Recurvirostridae	9	4
Charadriiformes	Rostratulidae	3	2
Charadriiformes	Scolopacidae	91	58
Charadriiformes	Stercorariidae	7	7
Charadriiformes	Turnicidae	17	6
Ciconiiformes	Ciconiidae	19	8
Coliiformes	Coliidae	6	0
Columbiformes	Columbidae	327	83
Coraciiformes	Alcedinidae	118	4
Coraciiformes	Brachypteraciidae	5	3
Coraciiformes	Coraciidae	13	5
Coraciiformes	Meropidae	28	1
Coraciiformes	Momotidae	14	0

Coraciiformes	Todidae	5	1
Cuculiformes	Cuculidae	143	18
Eurypygiformes	Eurypygidae	1	1
Eurypygiformes	Rhynochetidae	1	1
Falconiformes	Falconidae	64	25
Galbuliformes	Bucconidae	44	1
Galbuliformes	Galbulidae	11	0
Galliformes	Cracidae	54	9
Galliformes	Megapodiidae	21	0
Galliformes	Numididae	6	4
Galliformes	Odontophoridae	33	8
Galliformes	Phasianidae	179	81
Gaviiformes	Gaviidae	5	5
Gruiformes	Aramidae	1	0
Gruiformes	Gruidae	15	13
Gruiformes	Heliornithidae	3	2
Gruiformes	Psophiidae	3	2
Gruiformes	Rallidae	135	26
Gruiformes	Sarothruridae	11	1
Leptosomiformes	Leptosomidae	1	0
Mesitornithiformes	Mesitornithidae	3	3
Musophagiformes	Musophagidae	23	19
Opisthocomiformes	Opistocomidae	1	1
Otidiformes	Otididae	26	19
Passeriformes	Acanthisittidae	2	2
Passeriformes	Acanthizidae	64	25
Passeriformes	Acrocephalidae	55	32
Passeriformes	Aegithalidae	11	5
Passeriformes	Aegithinidae	4	1
Passeriformes	Alaudidae	97	33
Passeriformes	Artamidae	24	4

Passeriformes	Atrichornithidae	2	1
Passeriformes	Bernieridae	11	5
Passeriformes	Bombycillidae	3	2
Passeriformes	Buphagidae	2	1
Passeriformes	Calcariidae	6	5
Passeriformes	Callaeidae	4	0
Passeriformes	Calyptomenidae	6	5
Passeriformes	Calyptophilidae	2	0
Passeriformes	Campephagidae	89	28
Passeriformes	Cardinalidae	49	21
Passeriformes	Certhiidae	11	8
Passeriformes	Chaetopidae	2	1
Passeriformes	Chloropseidae	11	3
Passeriformes	Cinclidae	5	1
Passeriformes	Cinclosomatidae	12	1
Passeriformes	Cisticolidae	155	16
Passeriformes	Climacteridae	7	4
Passeriformes	Cnemophilidae	3	2
Passeriformes	Conopophagidae	11	4
Passeriformes	Corcoracidae	2	2
Passeriformes	Corvidae	129	37
Passeriformes	Cotingidae	65	15
Passeriformes	Dasyornithidae	3	0
Passeriformes	Dicaeidae	47	15
Passeriformes	Dicruridae	29	15
Passeriformes	Donacobidae	1	0
Passeriformes	Dulidae	1	0
Passeriformes	Elachuridae	1	0
Passeriformes	Emberizidae	44	19
Passeriformes	Estrildidae	140	21
Passeriformes	Eulecestomatidae	1	0

Passeriformes	Eupetidae	1	1
Passeriformes	Eurylaimidae	9	7
Passeriformes	Falcunculidae	1	1
Passeriformes	Formicariidae	11	4
Passeriformes	Fringillidae	209	73
Passeriformes	Furnariidae	302	82
Passeriformes	Grallariidae	55	10
Passeriformes	Hirundinidae	86	27
Passeriformes	Hyliotidae	4	1
Passeriformes	Hylocitreidae	1	0
Passeriformes	Hypocoliidae	1	0
Passeriformes	Icteridae	104	41
Passeriformes	Icteriidae	1	1
Passeriformes	Ifritidae	1	0
Passeriformes	Irenidae	2	1
Passeriformes	Laniidae	33	13
Passeriformes	Leiothrichidae	146	18
Passeriformes	Locustellidae	61	13
Passeriformes	Macherirhynchidae	2	1
Passeriformes	Macrosphenidae	21	6
Passeriformes	Malaconotidae	50	17
Passeriformes	Maluridae	33	2
Passeriformes	Melampittidae	2	1
Passeriformes	Melanocharitidae	10	2
Passeriformes	Melanopareiidae	4	0
Passeriformes	Meliphagidae	186	66
Passeriformes	Menuridae	2	1
Passeriformes	Mimidae	34	11
Passeriformes	Mitrospingidae	4	1
Passeriformes	Modulatricidae	3	2
Passeriformes	Mohouidae	3	3

Passeriformes	Monarchidae	96	30
Passeriformes	Motacillidae	66	25
Passeriformes	Muscicapidae	322	151
Passeriformes	Nectariniidae	143	29
Passeriformes	Neosittidae	3	1
Passeriformes	Nesospingidae	1	0
Passeriformes	Nicatoridae	3	1
Passeriformes	Notiomystidae	1	1
Passeriformes	Oreoicidae	3	1
Passeriformes	Oriolidae	36	7
Passeriformes	Orthonychidae	3	3
Passeriformes	Oxyruncidae	7	3
Passeriformes	Pachycephalidae	57	13
Passeriformes	Panuridae	1	1
Passeriformes	Paradisaeidae	42	16
Passeriformes	Paramythiidae	2	1
Passeriformes	Pardalotidae	4	2
Passeriformes	Paridae	63	22
Passeriformes	Parulidae	110	74
Passeriformes	Passerelidae	130	56
Passeriformes	Passeridae	43	4
Passeriformes	Pellorneidae	59	19
Passeriformes	Petroicidae	49	28
Passeriformes	Peucedramidae	1	1
Passeriformes	Phaenicophilidae	4	0
Passeriformes	Philepittidae	4	2
Passeriformes	Phylloscopidae	77	34
Passeriformes	Picathartidae	2	0
Passeriformes	Pipridae	53	20
Passeriformes	Pittidae	44	16
Passeriformes	Pityriasidae	1	0

Passeriformes	Platylophidae	1	1
Passeriformes	Platysteiridae	31	10
Passeriformes	Ploceidae	117	23
Passeriformes	Pnoepygidae	5	1
Passeriformes	Polioptylidae	20	7
Passeriformes	Pomatostomidae	5	4
Passeriformes	Promeropidae	2	1
Passeriformes	Prunellidae	13	4
Passeriformes	Psophodidae	5	1
Passeriformes	Ptiliogonatidae	4	3
Passeriformes	Ptilonorhynchidae	27	9
Passeriformes	Pycnonotidae	149	46
Passeriformes	Regulidae	6	4
Passeriformes	Remizidae	11	3
Passeriformes	Rhagologidae	1	1
Passeriformes	Rhinocryptidae	60	9
Passeriformes	Rhipiduridae	53	16
Passeriformes	Rhodinocichlidae	1	0
Passeriformes	Sapayoidae	1	1
Passeriformes	Scotocercidae	36	5
Passeriformes	Sittidae	26	12
Passeriformes	Spindalidae	4	0
Passeriformes	Stenostiridae	9	8
Passeriformes	Sturnidae	117	33
Passeriformes	Sylviidae	69	15
Passeriformes	Teretistridae	2	0
Passeriformes	Thamnophilidae	234	74
Passeriformes	Thraupidae	377	54
Passeriformes	Tichodromidae	1	1
Passeriformes	Timaliidae	52	18
Passeriformes	Tityridae	33	17

Passeriformes	Troglodytidae	85	22
Passeriformes	Turdidae	169	75
Passeriformes	Tyrannidae	422	137
Passeriformes	Urocynchramidae	1	0
Passeriformes	Vangidae	39	14
Passeriformes	Viduidae	19	0
Passeriformes	Vireonidae	63	20
Passeriformes	Zeledoniidae	1	0
Passeriformes	Zosteropidae	135	28
Pelecaniformes	Ardeidae	63	29
Pelecaniformes	Balenicipitidae	1	1
Pelecaniformes	Pelecanidae	8	5
Pelecaniformes	Scopidae	1	0
Pelecaniformes	Threskiornithidae	35	12
Phaethontiformes	Phaethontidae	3	2
Phoenicopteriformes	Phoenicopteridae	6	4
Piciformes	Capitonidae	14	0
Piciformes	Indicatoridae	17	0
Piciformes	Lybiidae	41	4
Piciformes	Megalaimidae	34	0
Piciformes	Picidae	233	17
Piciformes	Ramphastidae	36	2
Piciformes	Semnornithidae	2	0
Podicipediformes	Podicipedidae	19	12
Procellariiformes	Diomedeidae	15	15
Procellariiformes	Hydrobatidae	18	6
Procellariiformes	Oceanitidae	9	4
Procellariiformes	Procellariidae	94	34
Psittaciformes	Cacatuidae	21	1
Psittaciformes	Psittacidae	167	6
Psittaciformes	Psittaculidae	179	5

Psittaciformes	Strigopidae	3	1
Pterocliformes	Pteroclidae	16	5
Rheiformes	Rheidae	2	2
Sphenisciformes	Spheniscidae	18	17
Strigiformes	Strigidae	211	29
Strigiformes	Tytonidae	18	5
Struthioniformes	Struthionidae	2	1
Suliformes	Anhingidae	4	3
Suliformes	Fregatidae	5	5
Suliformes	Phalacrocoracidae	39	6
Suliformes	Sulidae	10	7
Tinamiformes	Tinamidae	46	13
Trogoniformes	Trogonidae	43	7

Table S3. All non-zero axes of nest morphospace calculated using principal coordinate analysis, based on 3,217 species of extant bird species. For each numbered axis, the eigenvalue is shown. Percentage of variation explained was calculated as eigenvalue/sum(of non-zero eigenvalues), and rounded to one significant figure.

Axis number	Eigenvalue	Variation explained (%)
1	222.835676	35.2%
2	103.582272	16.3%
3	90.670047	14.3%
4	63.808211	10.1%
5	50.643073	8.0%
6	27.556951	4.4%
7	24.471756	3.4%
8	18.680278	3.0%
9	13.437097	2.1%
10	8.387600	1.3%
11	7.313328	1.2%
12	2.407552	0.4%

Table S4. Results of geometric morphometric phylogenetic modelling summarized across 100 random phylogenetic hypotheses. Model results are presented for mean sum of squares (MS), R^2, standardized effect size (Z), and p-values. Results are shown as a median followed by the full min-max range of the variable across the 100 different model runs with different phylogenetic trees from Jetz et al. 2012 (*28*). These results are graphically presented in **Figure 2** of the main text.

Predictor	**MS**	**R^2**	**Z (effect size)**	**P-value**
Climate PC1	1.87 [0.01, 7953.00]	0.018 [<0.001, 0.733]	3.74 [0.046, 10.5]	0.002 [0.001, 0.497]
Climate PC2	3.29 [0.02, 3866.00]	0.014 [<0.001, 0.480]	3.85 [1.05, 9.85]	0.001 [0.001, 0.149]
Predator diversity	7.89 [0.06, 2469.00]	0.064 [0.001, 0.374]	4.44 [2.46, 10.9]	0.001 [0.001, 0.013]
Island endemic	0.621 [0.01, 54.5]	0.002 [<0.001, 0.049]	3.35 [-0.07, 6.92]	0.002 [0.001, 0.524]
Maximum body mass	1.99 [0.06, 48.3]	0.008 [<0.001, 0.154]	4.29 [2.09, 7.97]	0.001 [0.001, 0.026]

Chapter 4 - Morphological convergence despite genetic and vocal divergence in the Eurasian Wrens (*Troglodytes troglodytes*) of the British Isles.

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Author contributions

MTJ and WJS conceived the study. MTJ organised permits and planned fieldwork with inputs from WJS and JCD. MTJ, WJS and JCD conducted their respective parts of fieldwork. MTJ performed all laboratory procedures, statistical and genomic analyses, with input from WJS. MTJ wrote the first draft with inputs from WJS. All authors contributed to the edits. WJS supervised the project.

Published as: This paper is currently a work in progress.

Data availability statement

Due to the unpublished nature of this work, I would like to highlight the eventual data destinations. All morphological and vocal data needed to recreate the morphological analyses is contained within the Supplementary Material. Raw vocal data, composed of recordings and selections tables, will eventually be available on xeno-canto.org (see https://xeno-canto.org/set/8192 for a sample), and Dryad, respectively. All genomic data will be deposited in NCBI, as per agreed standards. The code necessary to recreate each step of this work will be published in a Dryad repository.

St Kilda Wren (*Troglodytes troglodytes hirtensis*) singing on a rocky outcrop on Hirta, St Kilda Archipelago. © Michał T. Jezierski.

Abstract

Speciation of island-dwelling populations from their nearest mainland relatives is widespread. Islands provide both the geographic isolation that often limits gene flow, while similar ecological conditions across islands worldwide drive evolution in similar directions – known as the island syndrome. Both isolation and change on islands may result in divergence, although the evolutionary relationships among island taxa and their mainland relatives can be unclear. Combined genomic and phenotypic investigations can clarify phylogenetic relationships between taxa, and demonstrate the contribution of known biogeographical patterns to speciation. Here, we leverage diverse sources of data to study genomic, morphological, and vocal variation in the Eurasian Wrens (*Troglodytes troglodytes*) of the British Isles. Different island groups harbour different subspecies, but their interrelationships, and the extent of divergence from one another, was previously unclear. We identify three apparently distinct phylogenetic lineages: (1) 'British' and Hebridean Wrens; (2) St Kilda Wrens; and (3) Shetland Wrens. Furthermore, we demonstrate that the St Kilda Wren originated from Hebridean Wrens and has undergone significant genetic divergence, whilst the Shetland Wren is phylogenetically distinct from the British/Hebridean/St Kilda clade. The Wrens of St Kilda and Shetland show similarity in body mass, which in both is higher than expected for the latitude, consistent with the island rule. However, other patterns of morphological and vocal divergence do not exactly follow the island syndrome, but show notable divergence from other subspecies, particularly in the case of St Kilda Wrens.

Introduction

Marine islands contribute disproportionally to both the world's biodiversity (Fernández-Palacios et al., 2021) and our understanding of biological evolution (Whittaker et al., 2017). Despite occupying less than 7% of Earth's emergent land mass (Fernández-Palacios et al., 2021), island species represent up to 20% of all species across major groups such as birds and flowering plants (Tershy et al., 2015), and harbour 41% of the most threatened vertebrate species (Spatz et al., 2017). Their tendency towards endemism has made island species central to studies of speciation (Gillespie & Roderick, 2002; Price, 2008), whilst their relatively simple ecosystems (Whittaker, Fernández-Palacios, et al., 2023) have made islands important systems in the study of evolutionary and ecological principles (Clutton-Brock & Pemberton, 2004; Losos & Ricklefs, 2009). Speciation is common, as geographic separation often results in reduced gene flow from the original stock (Papadopulos et al., 2011; Phillimore et al., 2008). At the same time, island colonisers face 'simpler' island communities, which are species-poor and disharmonic, which manifests as niche vacancy (Simberloff, 1995). These conditions are experienced on islands worldwide, and originate from the limitations imposed by area, geology, and isolation (Ali, 2017; MacArthur & Wilson, 1967). This similarity of conditions is thought to drive the apparently worldwide pattern of repeated directional change in morphology, behaviour, and life history of island species from their mainland relatives. This so-called 'island syndrome' (Adler and Levins, 1994; Jezierski et al., 2023) involves changes such as a 'slower' life history (Jezierski, 2024), a tendency to increase in body size if your ancestors are small-bodied (and vice versa) (Clegg & Owens, 2002), or in singing birds, fewer 'aggressive' song elements such as rattles and buzzes (Morinay et

al., 2013). Whether the island syndrome represents adaptation, or can be brought about by e.g. genetic drift following relaxed selection is uncertain (Biddick & Burns, 2021; Lomolino et al., 2012). Regardless of its causes, the island syndrome differentiates the colonists from their source population (Whittaker, Fernández-Palacios, & Matthews, 2023), and is an important aspect of island species divergence.

An integrated approach, using both genomic and phenotypic data, can help to delineate divergence between island populations, and describe how island conditions lead to the accumulation of traits related to the island syndrome. Both divergence and trait evolution are important topics in the study of the Eurasian Wrens (*Troglodytes troglodytes*; hereafter Wren) of the islands of the north-east Atlantic, which offer a tractable mosaic of island and mainland populations. The Wren is an abundant passerine that is traditionally associated with low ground cover and thick vegetation (Cramp, 1988; Shirihai & Svensson, 2018). Wrens have extensive infraspecific diversity, with up to 29 recognised subspecies across their large Afro-Eurasian range (del Hoyo & Allen, 2020) (albeit with largely dubious taxonomic justifications (Shirihai & Svensson, 2018)). They are members of a wider clade known for fast diversification within the Troglodytidae (Imfeld et al., 2024), and have been split based on genetic divergence from their Nearctic relatives (Drovetski et al., 2004), which themselves have been split into the Winter (*T. hyemalis*) and Pacific (*T. pacificus*) Wrens (Toews & Irwin, 2008). A total of 16 Wren subspecies are 'island forms' (Gill et al., 2023), and the island diversification of Wrens is particularly notable in the north-east Atlantic. Subspecies have been identified in Iceland (*islandicus*) and the Faroe Islands (*borealis*), which may be very genetically distinct from the neighbouring European and

British populations (Amouret et al., 2016). In the British Isles, five subspecies are thought to be native (Shirihai & Svensson, 2018) (**Fig. 1**): (1) the 'British Wren' (*indigenus;* Great Britain, Ireland, and most of their surrounding islands); (2) the 'Hebridean Wren' (*hebridensis*; the Outer Hebrides excluding St Kilda), (3) the 'St Kilda Wren' (*hirtensis*; St Kilda), (4) the 'Shetland Wren' (*zetlandicus*; Shetland, excluding Fair Isle), and (5) the 'Fair Isle Wren' (*fridariensis*; Fair Isle) (Cramp, 1988). Furthermore, the continental nominate subspecies (*troglodytes*; hereafter 'European Wren'), which is dubiously distinct from the British Wren (Vaurie, 1955), is often described as occurring in southern Britain (Clancey, 1943; Cramp, 1988), although this has been disputed (Shirihai & Svensson, 2018; Vaurie, 1955). The taxonomic relationships and the extent of divergence of the Wren subspecies in the British Isles are unclear (Albrecht et al., 2020; Amouret et al., 2016; Shannon et al., 2014). These Wrens have complex biogeographic histories, including in relation to their formerly conspecific Nearctic relatives (Drovetski et al., 2004), and may be undergoing widespread divergence (Amouret et al., 2016). From the perspective of the 'island subspecies' (i.e. the Hebridean Wren, St Kilda Wren, Shetland Wren, and Fair Isle Wren), Great Britain is the geographically closest 'mainland', due to its size and continental history. Therefore, the British Wren is the likely original 'stock', although previous work based on the *ND2* gene suggested that St Kilda, Hebridean and Fair Isle Wrens may hail from separate branches of the Wren phylogenetic tree, albeit with very weak bootstrap support (Shannon et al., 2014).

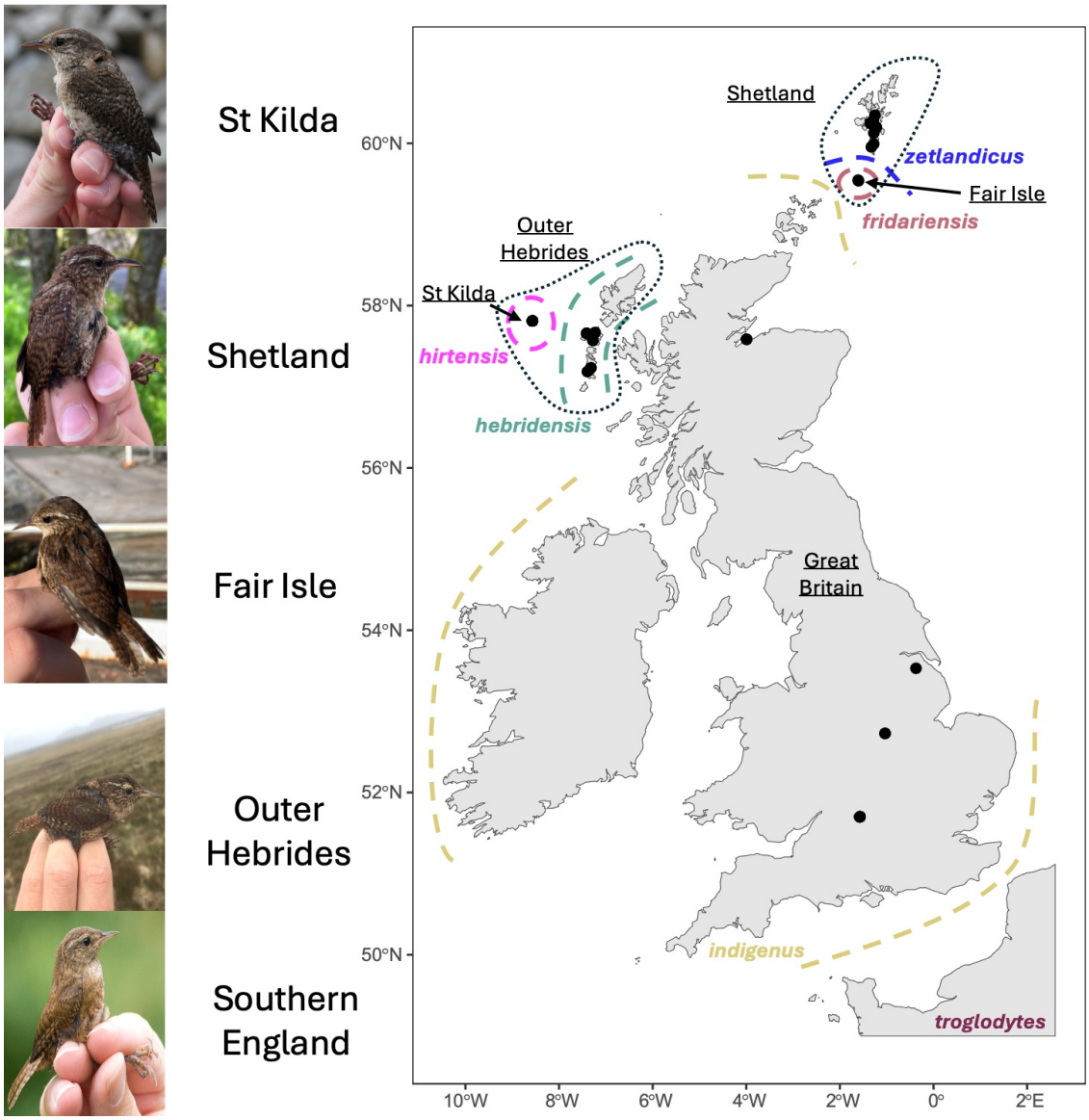

Fig. 1. The Wrens (*Troglodytes troglodytes*) of the British Isles. Each colour-coded dashed line shows the separations of the putative ranges of each subspecies considered in this manuscript, and is labelled with a colour-coded subspecific name. Black dotted lines demarcate the archipelagos of Shetland and Outer Hebrides, with arrows pointing to Fair Isle and St Kilda. Circles correspond to morphological and genetic sampling locations for live birds (n = 45). For equivalent maps of museum data and song recordings see **Fig. S1** and **Fig. S2**. For details of sampling per site see Methods and **Table S1**). Each picture shows a bird from the corresponding location, corresponding to each of the considered subspecies. NB: the continental European

subspecies *troglodytes* is sometimes considered to breed in 'southern Great Britain' (variously up to western Scotland (Shirihai & Svensson, 2018), or only in southern England (Shannon et al., 2014)), with all our sampling sites, except for the northern-most samples from Highland, included in its possible distribution. NB: there is point overlap for sites sampled at finer scale. © of Wren photos Michał T. Jezierski, Oliver J. L. Fox, all used with permission.

Although the British Wren is largely similar (and probably essentially identical) in form and ecology to the European Wren (Vaurie, 1955; Cramp, 1988; Shirihai & Svensson, 2018) each of the other subspecies shows considerable morphological, ecological, and behavioural differentiation (Cramp, 1988; Shirihai & Svensson, 2018). Although the Outer Hebrides might had been partially forested in the past (Fossitt, 1996), each subspecies today inhabits land with limited vegetation beyond human gardens or plantations, if present at all. The islands are characterised by moorland, meadows, plains, pastures, and coastal habitats. The archipelago of St Kilda and the island of Fair Isle have very small land areas (8.5 km^2 and 7.7 km^2, respectively) and harbour very small Wren populations (68-233 (Miles, 2011), and 10-83 territories (Aspinall & Aspinall, 2011), respectively). The Outer Hebrides and Shetland are larger archipelagos (3,056 km^2 and 1,466 km^2), harbouring more Wrens (1,000 – 10,000 (McGowan et al., 2003), and 3,000 – 6,000 pairs (McGowan et al., 2003), respectively), although still much smaller than the island of Great Britain (209,331 km^2). Each island subspecies is larger than the British Wren (Cramp, 1988; Shirihai & Svensson, 2018). They have different colouration, with birds either becoming duller (progressively greyer and duller colouration between British, Fair Isle, and St Kilda Wrens (Cramp, 1988),

Fig. 1) or darker (progressively darker brown between British, Hebridean, and Shetland Wrens (Cramp, 1988), **Fig. 1**). They occupy different habitats, and are associated with coasts and moorland, instead of more garden-like and forested habitats on mainland Great Britain. On St Kilda and Fair Isle, they primarily inhabit cliffs, and can even be seen holding territories on sea stacks such as Stac an Armin (MTJ, WJS, pers. obs.). They are known to hold larger territories (Cody & Cody, 1972) and have smaller clutch sizes (Cody & Cody, 1972) than the British Wren, and it has been suggested that their songs are distinct even to the unaided ear (Cramp, 1988; Shirihai & Svensson, 2018). The Wrens' geographic arrangement, coupled with multiple differences described by generations of natural historians (Clancey, 1943; Vaurie, 1955; Waters, 1964; Cody & Cody, 1972; Cramp, 1988), are strongly suggestive of both; i) geographic isolation with some degree of divergence, potentially from the same mainland stock (the British Wren); and ii) similar phenotypes in island subspecies, of which morphological, colouration, life history and ecological traits are all within the scope of the avian island syndrome (Jezierski et al., 2023). Here we use both genomic and phenotypic data to investigate the evolution of the Wrens of the British Isles. Firstly, we i) examine their divergence and population genetic structure, to infer their interrelationships and degree of genetic distinctiveness; ii) examine various aspects of morphology and songs to quantify phenotypic divergence and consider their consistency with the island syndrome; and iii) we examine signals of evolution in the genomes of each population, to lay the grounds for investigation of the processes that make the Wren subspecies distinct.

Methods

Data collection – live birds

We sampled individuals across the ranges of all five Wren subspecies thought to be endemic to the British Isles. We assumed that subspecies identity conformed to their proposed geographic ranges (Cramp, 1988; Shannon et al., 2014). All Wrens sampled in Great Britain were treated as belonging to the subspecies *indigenus* (the British Wren), as the assertion of European Wrens breeding in southern Great Britain is uncertain (and probably incorrect) due to dubious criteria for morphological separation (Vaurie, 1955). During May and June 2022, MTJ and WJS sampled Wrens across a diversity of sites (**Fig. 1**, **Table S1**). Additional British Wren samples for genome sequencing (three) were collected by JCD in Lincolnshire between 2020-2022 (**Fig. 1**). Our sampling represents much of the latitudinal range of the species in Britain (**Fig. 1**, **Table S1**). All birds were captured under license from the British Trust for Ornithology (BTO), using mist-nets placed within the territories of singing birds. Wrens were lured using a recording of the song of the subspecies appropriate to the area. Each individual was marked with an individually-coded BTO metal leg ring. Before each bird was released, we measured wing length using a butted wing ruler (± 1mm); bill length (to the front of the nares), bill width (at the front of the nares), bill depth (at the front of the nares), tarsus length (from the tibial joint to the foot), and tarsus width (at mid-length) with dial callipers (± 1mm); and tail length (from the uropygial gland) using an avian tail ruler (± 1mm). The data on birds were not separated by age, due to the difficulty of accurately ageing island subspecies (pers. obs. WJS, MTJ; pers. comm. Ian Thompson). Blood samples were taken under Home Office licence PB0AED9B7 by WJS. Samples were taken from the brachial vein using a 0.4 x 20 mm needle. Blood samples were stored using Whatman® FTA cards™ (Whatman, Maidstone, United

Kingdom) at ambient temperature in the field and then at –20°C prior to DNA extraction.

Data collection – museum specimens

To collect additional data on the morphology of each Wren subspecies, we used museum collections of Wren skins from the National Museum of Scotland (NMSZ). This dataset cannot be compared to the morphological data from the live birds directly, due to differences in the handling of live and dead birds and changes to the size of museum skins with time (Knox, 1980; Kuczynski et al., 2002). However, by taking the same measurements, this dataset can be used to support assessments of morphological differences between Wren subspecies and provides increased sample size and geographic coverage. For the museum data, measurements (except mass as that would represent a stuffed skin) were taken as above for all undamaged specimen skins aged as adult for each island subspecies available in NMSZ (**Table S2**) and for 31 specimens from Great Britain. We focused on regions in Great Britain that had not been sampled in the live dataset (**Fig. S1**). We extracted the geographical coordinates associated with each specimen using Google Maps™, to the nearest city and/or centroid of the county, depending on the detail of the label (**Table S2**).

Morphometric analysis

All data was processed and analysed in R v. 4.2.1 (R Core Team, 2020) using *tidyverse* v. 1.3.2 (Wickham et al., 2019) for data wrangling, and *ggplot2* v. 3.3.6 (Wickham & Sievert, 2016), *ggrepel* v. 0.9.1 (Słowikowski, 2023) and *ggpubr* v. 0.4.0 (Kassambara, 2023) for plotting. Data from live Wrens was analysed using linear regression to test whether subspecies affiliation was significantly associated with differences in each selected trait. For each morphological measurement a separate linear model was fit, using *lm()* function in base *stats* package in R in the form of: *trait ~ subspecies + mass + latitude*. The traits examined were wing length, bill length, bill width, bill depth, tarsus length, tarsus width, and tail length, all measured in mm. The p-values from the models were adjusted using the Bonferroni correction using function *p.adjust()* in the package *stats* to correct for multiple comparisons. Mass and latitude were included in the model to control for expected allometric (Huxley, 1932) and latitudinal (Salewski & Watt, 2017) scaling in bird traits. Mass was examined separately using a model in the form of *mass ~ subspecies + latitude*. For both models, the explanatory variables were examined for collinearity using variance inflation factors, with a threshold of two based on previous recommendations (Zuur et al., 2010). All variables had VIF values lower than two and were therefore retained in analyses. We applied the same analysis framework to the museum specimen dataset, except for modelling of mass which is not available for stuffed skins.

To summarise variation across all traits, we used principal component analysis (PCA), as implemented in the function *prcomp()* in the base *stats* R package. All data was scaled and centred, by subtracting the mean and dividing by standard deviation, using

the internal flag *scale* = *T*. All morphological measurements, except for mass for the live wren dataset were used, to maintain comparability with the museum dataset. Specimens with missing data were removed so that we did not need to impute missing trait values (n=6 for live dataset; n = 7 for museum dataset). To further examine whether morphological distinctiveness can be used to distinguish the different subspecies, we conducted a linear discriminant analysis (LDA) using the function *lda()* from the R package MASS (Venables et al., 2002). Data was scaled again using the function *scale()*, using the same parameters as above. We used only the museum dataset for these analyses due to its larger sample size (n=117), and removed individuals with missing variables (n=7). The model was first trained on a random sample of 60% of the data, which was then used to predict the remaining 40% of the data.

Data collection – song data

New song data was collected during May and June 2022, during site visits for bird capture and blood sampling. All new recordings were collected by MTJ using a Zoom F3 (Zoom Corporation) sound recorder and a RØDE NTG5 (RØDE) microphone. As Wrens sing throughout the day, songs were collected during dedicated morning walks or drives (between 3am and 10am), but also opportunistically during fieldwork at any time of the day. Birds were recorded using a hand-held device, either by approaching within a distance that did not cause an observable change in behaviour (e.g. alarm calling, flying away), or from a car. To avoid resampling individuals, songs were recorded either in: i) known territories of birds that have been previously observed (St Kilda, Fair Isle, Outer Hebrides) or at least 1 km apart during the same week. This was deemed far enough based on known territory sizes (Cody & Cody, 1972; Cramp, 1988).

Recordings were made to capture at least three singing bouts of each Wren. A 'bout' is defined here as one complete song (**Fig. S3**), which is a contained singing behaviour followed by a clear, two or more second pause.

Our sampling represents the majority of available songs for each of the island subspecies, as public databases such as xeno-canto.org hold no recordings of comparable length and quality. However, more songs are available of the British Wren, and we collected those across the geographic spread of the subspecies. We have filtered for songs of quality 'A' (highest quality with no interruption) that were at least 30 seconds long in the United Kingdom and the Republic of Ireland. Songs were manually selected to take only .wav files or .mp3 files with a bit rate of 320 mbps, to ensure comparable recording quality. All songs were also listened to, to ascertain quality. Songs were only included if they were not filtered in any way by the uploader, as verified by song description and listening to the song. In total, we collected 55 songs with at least three singing bouts (**Table S3**).

Song analysis

To analyse vocal variation among Wren subspecies (**Table S3**), we segmented fragments of song recordings using RavenPro v. 1.6 (Cornell Lab of Ornithology, 2014). As Wren songs are complex and consist of diverse syllables, including within individuals (Cramp, 1988), we followed the description of elements used by Hall-Craggs, presented in the *Handbook of the Birds of Europe, the Middle East and North Africa* (Cramp, 1988). This classification recognises four element types (**Table S4**, **Fig. S3**), which follow similar structure, even though individual syllables may be highly

variable. There are few clear predictions as to how songs vary in terms of the island syndrome (Jezierski et al., 2023; Morinay et al., 2013), partly due to a significant degree of 'cultural' bottlenecks involved in loss of song diversity (Lachlan et al., 2013). Taking that into consideration, as well as the diversity of syllables used by Wrens, we focused on reproducibly quantifiable aspects of song that are useful in species delimitation (Alström et al., 2021; Martínez-Gómez et al., 2023). We examined: (1) peak frequency, (2) centre frequency, (3) aggregate entropy (distribution of energy between given frequencies), (4) frequency bandwidth (5% to 95% of frequencies), and (5) total duration of an element. These measurements were assessed for the three longest songs in each recording. All songs were segmented by MTJ to ensure correct recognition of Wren syllables and avoid observer bias. We avoided analysing songs that were significantly impacted by intrusion from other species' vocalisations (in particular, Skylarks *Alauda arvensis*, Starlings *Sturnus vulgaris* and House Sparrows *Passer domesticus*).

Due to high variation within each individual, even between the defined elements (**Fig. S3**) we have focused the analysis on average measurements per segment type per individual. Additionally, we have derived the measurements only for elements A and B, as not all subspecies present with elements C and D. We analysed this discrepancy of song structure by including average number of elements C and D per song. This resulted in a total of 12 variables (two measures per A and B + mean numbers of C and D per song) per individual bird. To summarise variation across all song measurements, we used PCA and LDA, with the same protocol as for morphological measurements. We additionally compared the differences between individual song elements, by fitting

a linear model using the function *lm()* per measured song trait, in the form of *lm(song trait ~ ssp + latitude)*. We included latitude, as bird songs are known to vary with latitude, and particularly some of the measures we use (e.g. number of rattles and buzzes) are known to vary with latitude in the closely related House Wrens (*Troglodytes aedon*) (Kaluthota et al., 2016). The p-values from the models were adjusted using the Bonferroni correction using the function *p.adjust()* in the package *stats* to correct for multiple comparisons.

DNA extraction and sequencing

DNA extraction from blood samples was carried out using a phenol-chloroform protocol, as described in Smith et al. (2023). A 5x1 mm section of sample on the FTA card™ was inserted into 180 μL of QIAGEN buffer ATL, with 20 μL of QIAGEN Proteinase K. These were digested at 56°C for six hours. Following incubation, 400 μL of phenol:chloroform:isoamyl alcohol (25:24:1) was added and the samples were centrifuged at 15,000 rpm for 15 minutes. Half of the aqueous layer was transferred to a new microcentrifuge tube containing 35 μL of 3 M sodium acetate, vortexed for 10 seconds and chilled for 10 minutes at -20°C. DNA was precipitated with 700 μL of ice-cold 100% ethanol, and 2 μL of glycogen was added. The sample was then chilled overnight at -20°C. The following day, samples were centrifuged for 30 minutes at 15,000 rpm, and the supernatant was removed. The precipitate was rinsed with 900 μL of ice-cold 70% ethanol, and placed in a refrigerated centrifuge at 4°C for 30 min at 15,000 rpm, twice. The supernatant was then removed, and the precipitated DNA left to dry at room temperature. Once dried, DNA was resuspended in 40 μL of QIAGEN AE buffer. DNA quality and quantity was assessed using gel electrophoresis and Qubit HS

dsDNA. The 29 highest quality samples were sent for Illumina 6000 paired-end 150 bp sequencing by Novogene (Cambridge, UK).

Genomic data preparation

We sequenced 11Gb for each of 29 individuals of the five Wren subspecies. The genomic data was checked for quality using FASTQC v. 0.11.9 (Andrews, 2010). All sequences were flagged as 'good' by FASTQC across all individuals, and adapters had been trimmed by the sequencing company. FASTQC reports indicated poorer sequence quality in the first 10 bp of each read, and we used Trimmomatic v. 1.8 (Bolger et al., 2014) to remove the first 10 bp of each read using 'HEADCROP:10'. Reads from a Carolina Wren (*Thryothurus ludovicianus*; NCBI SRR9946695) were used as an outgroup in the relevant analyses, and these were also processed with Trimmomatic. We then mapped each sequence to the reference genome. For the reference, we used the scaffold-based genome ASM1339724v1 of the Carolina Wren, a high coverage annotated genome from the B10K initiative (Feng et al., 2020), which is the only available reference genome for the Troglodytidae. We indexed the reference genome using samtools v. 1.16.1 (Li et al., 2009) using the command *faidx*, and proceeded to make a build for Bowtie2 v. 2.4.5 (Langmead & Salzberg, 2012) with the command *bowtie2-build*. We then mapped the read data to the reference using paired-end mode. The resultant SAM files were sorted and indexed as BAM files. Duplicate reads were removed using GATK v. 4.1.8 (McKenna et al., 2010) with the command *MarkDuplicatesSpark*. Processed BAM files were used for variant calling using the GATK *HaplotypeCaller* (Van der Auwera et al., 2013). Variant recalibration was not possible due to lack of high-quality reference libraries, so we followed the protocol

used in population genomics of non-model organisms (as described in Howard-McCombe et al., 2023) involving hard filtering using both GATK and VCFtools v0.1.16 (Danecek et al., 2011). Filters used were QD < 2.0; QUAL < 30.0; SOR > 3.0; FS > 60.0; MQ < 40.0; MQRankSum < -12.5; ReadPosRankSum < -8.0 for GATK filtering. Using VCFtools we removed indels (--remove-indels) and retained only biallelic sites (--min-alleles 2, --max-alleles 2), sites where the minor allele count was ≤5% (--maf 0.05), sites where genotype quality was >20 (--minGQ 20), and sites where genotypes were called in 100% of individuals (--max-missing 1). This dataset yielded 2,619,325 SNPs. For population genetic structure analyses, the dataset was additionally filtered using PLINK v. 2.0.0 (Purcell et al., 2007) with an R^2 threshold of 0.1 (meaning that loci with higher correlation than that were removed) in 50 kb windows with 10 kb steps (--indep-pairwise 50 10 0.1). After this hard-filtering, we retained a total of 174,271 SNPs. Finally, we examined all individuals and sites using VCFtools to determine: i) missingness; ii) relatedness; iii) heterozygosity, and iv) read depth, to confirm that all filters were applied correctly and that the data contained no siblings.

Genomic analysis – population genetic structure and gene flow

To examine population genetic structure among the Wren subspecies, we performed multiple analyses to visualise and quantify genetic relationships between individuals, their variation, and their patterns of gene flow. For this, we used the LD-filtered VCF unless specified otherwise. We summarised population genetic structure within our sample using principal component analysis of genomic data, as implemented in plink v. 1.9.0 (Purcell et al., 2007). We explore patterns of genome-wide divergence using global weighted F_{ST}, comparing each of the five subspecific populations, plus splitting

the populations from Great Britain according to county. We calculated these using VCFtools with the function -weir-fst-pop, which calculates F_{ST} with the Weir estimator (Weir & Cockerham, 1984), to make pair-wise comparisons between each population.

To assess levels of hybridisation among the different subspecies, we performed two different analyses. First, we ran ADMIXTURE v.1.3.0 (Alexander et al., 2009) to examine patterns of genetic ancestry for each individual, with the default 5-fold cross-validation error. We ran the analysis for K values from 1 to 7 (to allow for each subspecies having a specific genetic ancestry component, and to include potential unsampled ancestry, e.g. from the European Wren (Shannon et al., 2014)), repeated 10 times. We merged different runs using CLUMPP v. 1.1.2 (Jakobsson & Rosenberg, 2007) to generate estimates of average ADMIXTURE proportions. Second, we used the D-statistic (Patterson et al., 2012) calculation on the non-LD filtered VCF, as applied in the programme Dsuite (Malinsky et al., 2021), to test for historical introgression. The D-statistic calculates the pattern of shared and derived alleles between branches (P1, P2, and P3, where P1 and P2 are sisters) of the phylogenetic tree, along an explicitly modelled phylogeny, to accommodate for patterns consistent with introgression. We used the function Dtrios, with the software reconstructing a phylogenetic tree containing all populations, to calculate patterns of the D-statistic and f_4-ratio, the latter of which describes the fraction of introgression. We ran Dtrios with a clustering test for patterns expected of discordant alleles derived from introgression, rather than homoplasy, which can bias D-statistic estimates (Malinsky et al., 2021). We used the threshold of significance whereas p-value must be significant at <0.05 and the Z-score must be higher than 3 (Zheng and Janke, 2018) We report only significant D-statistics

with topologies that were independently obtained in the phylogenetic analysis below, as Dtrios will output all possible combinations.

To infer phylogenetic relationships among Wren individuals, we used IQTREE v. 2.2.2.6 (Minh et al., 2020), specifying data as DNA, using model finder (with flag -MFP (Kalyaanamoorthy et al., 2017)), and correcting for ascertainment bias among variable sites (with flag +ASC) (Lewis, 2001). IQTree modelfinder reported TVM (transversion model) + F (empirical base frequencies) + ASC (model ascertainment bias correction) + R2 (two rate parameters) as the best model (ΔBIC = 8.55). We specified the Carolina Wren as an outgroup. IQTREE results were bootstrapped 10,000 times.

Genome analysis – patterns of evolution along the genome.

We used window-based approaches to investigate patterns of signals of evolution in the Wren populations. To this end we used: i) d_{xy}, a measure of absolute sequence divergence (Nei & Li, 1979); ii) F_{ST}, a measure of relative genomic differentiation (Weir & Cockerham, 1984); iii) π, a measure of nucleotide diversity (Nei & Li, 1979); and iv) f_d, a measure of introgression based on the D-statistic, which is suitable for use in a window-based context, unlike the D-statistic itself (Malinsky et al., 2021). These measures have been widely used in population genomic studies, including those focussing on avian evolution (Elgvin et al., 2017; Irwin et al., 2018), and their patterns, in combination, can be used to infer evolutionary processes affecting the genome. Dsuite was used to calculate f_d, and the remaining measures were calculated using the software pixy v. 1.2.7 (Korunes & Samuk, 2021). All analyses pertaining to this section have been performed using the non-LD filtered VCF, as linkage disequilibrium

itself can be an important evolutionary pattern (Slatkin, 2008). We determined a window size of 100 kb following calculation of the decay of linkage disequilibrium with distance from loci, using PopLDdecay v. 3.42 (Zhang et al., 2018). Due to the scaffold-based nature of the reference genome, many scaffolds are smaller in size than 100 kb, making the window size inconsistent along large tracts of the genome. To this end, we retain in the analysis only scaffolds larger than 100 kb (n = 2,201), and only fully covered windows (n = 7,760). This approached allowed us to retain SNPs along 78.55% of the length of the reference genome. For F_{ST}, d_{xy} and f_d we considered as significant sites those which fell within the upper 1% of the distribution of values (e.g. Elgvin et al., 2017; Irwin et al., 2018). We then used the Carolina Wren's genome annotation files to extract those genes present within the windows we found to be significantly different. As F_{ST}, d_{xy} and f_d are calculated between two populations, our analyses have focused on two main comparison sets, based on the results of the analyses described above. Following the main phylogenetic splits, we tested the following comparisons: St Kilda to British Wrens; St Kilda to Hebridean Wrens; Hebridean to British Wrens; and Shetland to British Wrens. Additionally, in the Supplementary Material we present the comparisons of: Fair Isle and British Wrens; and Fair Isle and Shetland Wrens. Gene Ontology enrichment analysis was performed using the default settings on https://geneontology.org/, using the reference list of the chicken (*Gallus gallus*) as the closest available species in the Panther database (Mi et al., 2013). We extracted Panther's GO-slim biological process annotations of the genes of interest (Mi et al., 2018). We used Fisher's exact test to check for significant enrichment, and used the false discovery rate < 0.05 as the significance threshold.

Results

The genetic distinctiveness and population structure of Wren populations in the British Isles

The maximum-likelihood phylogeny revealed two main splits among the sampled individuals, with robust bootstrap support: a British, Hebridean and St Kilda clade; and a Shetland and Fair Isle clade (**Fig. 2A**). Within the British, Hebridean, and St Kilda clade, Hebridean birds were nested within the British clade, and St Kilda birds were nested within the Hebridean clade, albeit with a very high branch length. St Kilda Wrens have historically small population sizes, and we find notable degrees of inbreeding in this subspecies (F_{mean}=0.413), compared to the second highest measure of F_{mean}=0.243 among the Fair Isle Wrens (**Fig. S4**). The Wren populations show considerable genetic differentiation. In a genomic PCA, each subspecies forms its own genetic cluster that does not overlap with any of the other subspecies, although the Hebridean and British subspecies are close to one another, and the Hebridean group shows a split into two subgroups on the second principal component axis (**Fig. 2B**). Shetland, Fair Isle and St Kilda Wrens occupy their own space, with Fair Isle Wrens located in-between the British and Shetland clusters. This pattern of genomic differentiation was further supported by weighted genome-wide F_{ST} estimates (**Table S5**), which reveal strong differentiation between island Wren populations and the British population. Relative to the 'mainland' British Wren samples, the weighted genome-wide mean F_{ST} values were 0.11 for St Kilda Wrens; 0.01 for Hebridean Wrens; 0.09 for Shetland Wrens and 0.02 for Fair Isle Wrens, confirming that Shetland and St Kilda Wrens are more highly differentiated from their 'mainland' relative than Hebridean and Fair Isle Wrens.

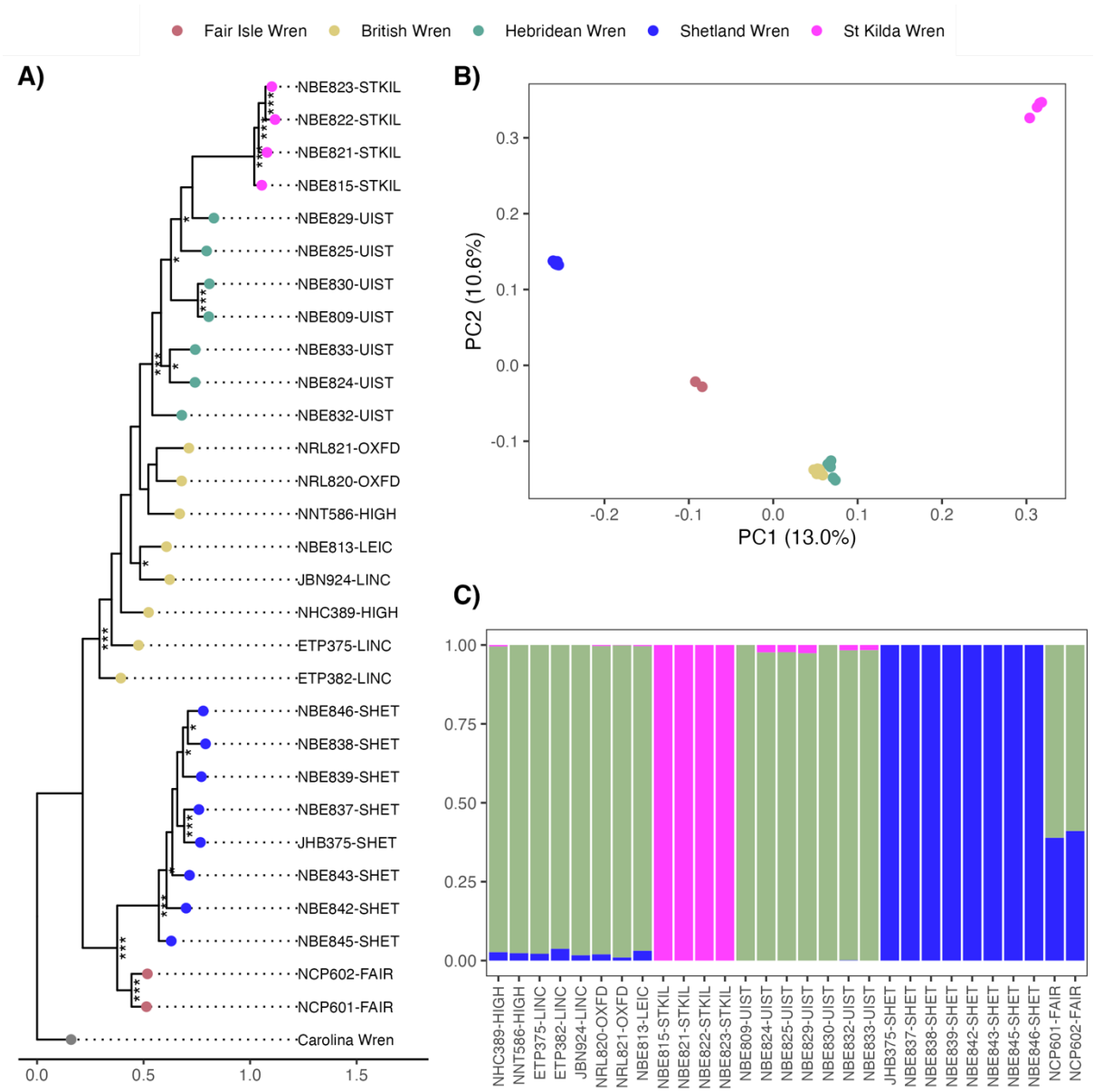

Fig. 2. The population structure and phylogeny of Wrens in the British Isles. **A)** phylogenetic relationships among the sampled individuals, showing there is robust support for a split between the British/Hebridean/St Kilda Wrens, and the Shetland/Fair Isle Wrens. The IQTree phylogeny suggests an origin for the Hebridean Wren in Great Britain, and, in turn, an origin for the St Kilda Wren in the Outer Hebrides. A single asterisk represents >70% bootstrap support and a triple asterisk represents

100% bootstrap support. Additional region codes point to the sampling location of birds: STKIL – St Kilda; UIST – Outer Hebrides; OXFD – Oxfordshire; HIGH – Highland; LEIC – Leicestershire; LINC – Lincolnshire; SHET – Shetland; FAIR – Fair Isle. **B)** Genomic principal component analysis showing the first two axes of variation. Together, these axes of variation separate individuals by geography, with British and Hebridean Wrens weakly differentiated from each other. St Kilda and Shetland Wrens are both distinctive from the British/Hebridean cluster, but in different directions in the first principal component. Fair Isle Wrens fall in a position that is intermediate between the Shetland and British Wrens. **C)** ADMIXTURE results at K=3 for all samples excluding the outgroup. This analysis highlights a split between the St Kilda Wrens, Shetland Wrens, and the British/Hebridean Wrens (also see **Fig. S5** and **S6**). The Fair Isle Wren appears to have Shetland-British admixed ancestry. The region codes for each individual are reported as in A).

With respect to gene flow patterns among the Wren populations, ADMIXTURE results revealed similar levels of error between K=1 and K=3, with a breakpoint after K=4 onwards (see **Fig. S5**), with K=3 (**Fig. 2C**) showing the most biologically-plausible (cf. phylogeny, PCA, and F_{ST} results) grouping. It recognises individual clusters for both St Kilda and Shetland, and a cluster common to the Hebridean and British Wrens. The Fair Isle Wrens have ancestry components common to both the Shetland and British/Hebridean groups. D-statistic tests show that, in addition to potential recent mixing (**Fig.2**), there is a significant degree of introgression between i) Fair Isle and British populations; and ii) St Kilda and British, Shetland, and Fair Isle populations

(**Table 1**). All introgression comparisons, bar the OH – SK – SH combination, show statistically significant clustering patterns, indicating origin from introgression.

Table 1. The results of the Dtrios test performed using in Dsuite. P1, P2 and P3 represent the populations examined for potential patterns of historical introgression. The subspecies codes are: FI = Fair Isle; GB = British; OH = Hebridean; SH = Shetland; SK = St Kilda. D refers to Patterson's D statistic, with positive values indicating introgression between P2 and P3, while negative values would indicate introgression between P1 and P3. The Z-score and p-value infer the significance of Patterson's D (Z > 3, p-value < 0.05). The f_4-ratio indicates the proportion of introgression between the populations exchanging genes.

P1	***P2***	***P3***	***D***	***Z***	***p-value***	***f_4 ratio***	***clustering p-value***
SH	**FI**	**GB**	0.00500	3.860	1.133x10e-4	0.0492	3.981x10e-5
OH	**SK**	**FI**	0.00617	4.630	3.663x10e-6	0.0098	2.382x10e-3
OH	**SK**	**GB**	0.00510	4.382	1.178x10e-5	0.0570	0.0138
GB	**SK**	**SH**	0.00719	5.028	4.952x10e-7	0.0159	3.758x10e-3
OH	**SK**	**SH**	0.00547	4.725	2.307x10e-6	0.0120	0.616

Morphological convergence and vocal divergence among Wren populations.

PCA analysis of the 'live' and 'museum' datasets (**Fig. 3A, Fig. S7, Tables S8 and S9**) showed weak morphological differentiation amongst subspecies. The St Kilda and Shetland Wrens morphological datasets show near-complete overlap in the museum dataset (**Fig. 3A**), but in the live dataset are separated by longer tails, wings and wider bills and tarsi (**Fig. S7**) although the differences in those measurements are not significant once mass and latitude are accounted for (**Table S6**). British and Hebridean Wrens occupy their own morphospace in both datasets, which transitions smoothly into the St Kilda and Shetland morphospace (**Fig. 3A, Fig. S7)**. Finally, Fair Isle Wrens show overlap of the morphospace with both St Kilda/Shetland group and British Hebridean group in both datasets (**Fig. 3A**, **Fig. S7**). In comparisons of individual measurements, St Kilda and Shetland Wren show significant differences from British and Hebridean populations, but similarity between each other (**Fig. S8** and **S9**, **Tables S6** and **S7**). In a linear discriminant analysis (LDA), a similar pattern to the PCA is repeated (**Fig. S10**), wherein there is considerable overlap between St Kilda/Shetland and the British/Hebridean groups, which are separate, but transition smoothly into each other, with Fair Isle Wrens morphologically overlapping both former clades. LDA could accurately predict subspecies designation only 27.3% of the time in general, and only 29.4% between St Kilda and Shetland Wren, and only 25.9% of the time between British, Hebridean and Fair Isle Wrens. However, both the St Kilda and Shetland Wren can be distinguished from the mainland relatives, and from each other by plumage, which we did not quantify (**Fig. 1**). In the live dataset, mass could be included, and it was found that both the St Kilda (β = 2.78), and Shetland Wrens (β = 2.34), are

statistically significantly heavier than expected for the latitude, and that latitude is also a significant predictor of bird mass ($\beta = 0.32$) (**Table S6**).

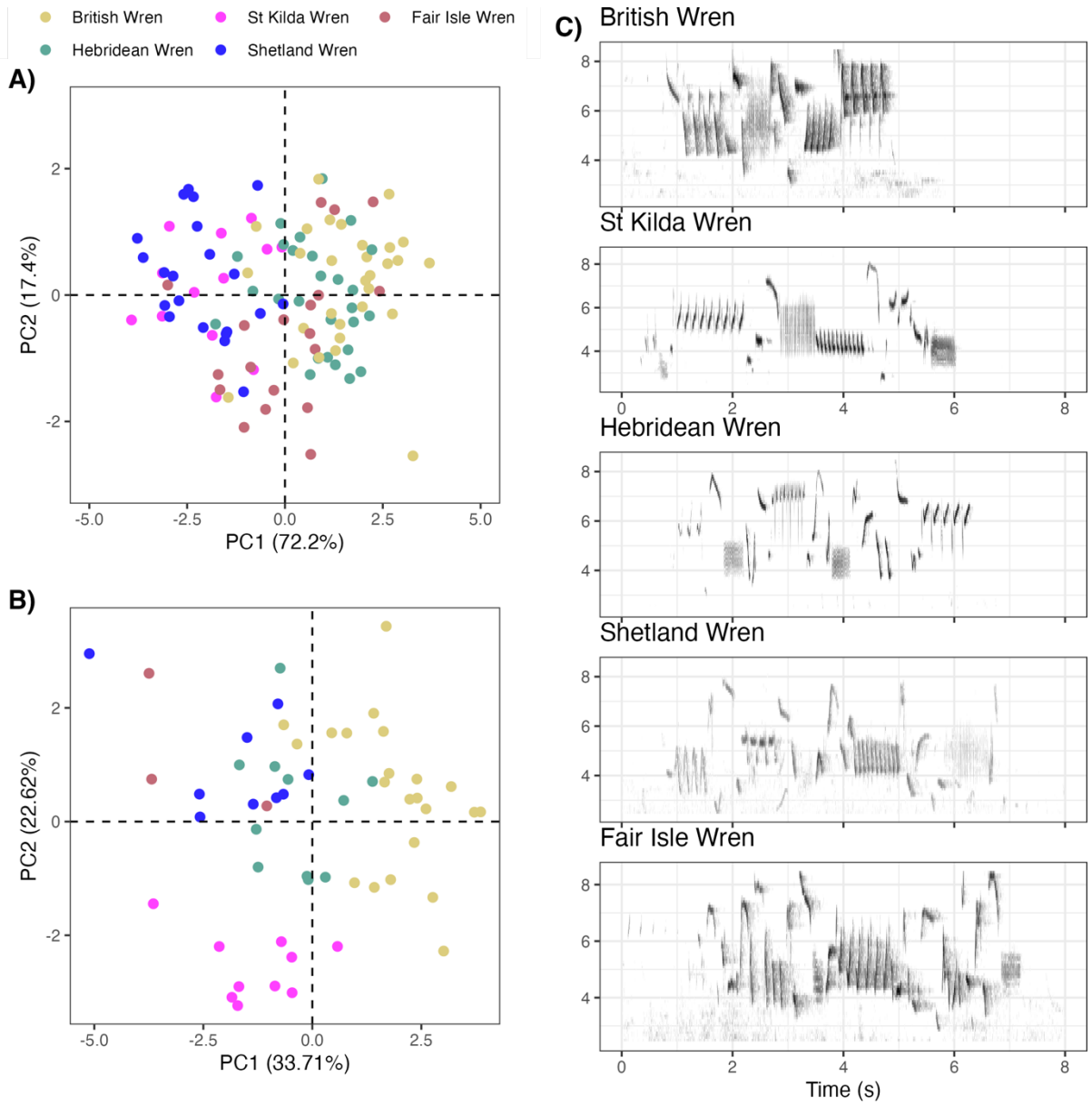

Fig. 3. Morphological convergence despite vocal divergence in the Wrens of the British Isles. Island subspecies of Wren show similarity in **A)** morphology (museum dataset, n = 117), with notable overlap between St Kilda/Shetland and between British/Hebridean populations, and overall smooth transitioning between the two groups. This is based on principal component analysis of 110 individuals using seven measurements of morphological traits. Loadings of individual axes are shown in **Table S9.** However, these morphological similarities co-occur with differences in **B)** song structure, visualised here using a PCA of twelve metrics of Wren song across 55

individuals. Loadings of individual axes are shown in **Table S11** St Kilda Wrens form their own cluster, separated from the other Wrens. Within the larger group, there is a smoothly transitioning difference between the remaining island subspecies, and the British Wren. **C)** a typical song from each subspecies, showing the differences between subspecies summarised in a PCA. St Kilda Wren songs rarely span above 6 kHz, compared to the songs of all other subspecies, with fewer cases of large changes in frequency between neighbouring elements (lower bandwidth).

Comparison of Wren songs has shown considerable differences among subspecies (**Fig. 3B** and **C**). St Kilda Wrens are separated from the remainder of subspecies, with the others forming a continuous group, albeit with smooth separation between island and British Wrens. The differentiation of St Kilda Wrens stems from multiple differences of their songs from other subspecies (**Fig. 3C**, **Table S10**). Foremostly, St Kilda Wrens show the lowest bandwidth of both elements A (average difference to British = -652.77 Hz) and B (avg. diff. = -741.58 Hz), with low centre (avg. diff. = -810.92 Hz) and peak frequencies (avg. diff. = -978.04 Hz) of element A, and the longest (avg. diff. = 0.31 s) and the least entropic B (avg. diff. = -0.89 bits) elements, resulting in what appears to be a 'neater' song (**Fig. 3C**). All of these differences are statistically significant, whilst the other island subspecies show largely insignificant differences from the British Wren (**Table S10**). Not much is significantly different and shared by all island subspecies, except for peak frequency of element A, which is lower in all subspecies, and the number of buzzes (element D), which are absent from the British Wren, but present in all island subspecies (**Table S10**). The Shetland Wren additionally differs in having the most entropic (avg. diff = 0.69 bits) and longer (avg. diff. = 0.34 bits)

elements A. This results in a ‘messier’ song than the St Kilda Wren (**Fig. 3C**), although that is characteristic of nearly all other subspecies. Only peak frequency of element A and the bandwidth of the element B have shown significant correlation with latitude. Owing to these much larger differences than found in morphology, LDA can assign the subspecies correctly 77% of them time, with St Kilda Wren and British Wren forming clusters of their own (**Fig. S12**), while the remaining island subspecies show overlap. These clusters are distinctive enough that an LDA model has assigned St Kilda Wrens’s and British Wren’s song to subspecies correctly 100% of the time.

Genome-wide patterns of Wren divergence

We found significant linkage disequilibrium (LD) in the genome of St Kilda Wrens compared to other populations (**Fig. S13**), where correlation between sites is >0.3 even at distance of 300 kb. The other populations (except Fair Isle, which could not be estimated due to small sample size) would have LD decay to background level of 0.15 at 1000 bp (British), 3,500 bp (Hebridean) and 53,000 bp (Shetland). F_{ST} values revealed multiple highly divergent windows between all of the Wren subspecies (**Fig. 4**). In the main comparisons examined (focusing on the distinction between St Kilda and Shetland Wren from the British Wren), nucleotide diversity was always lower in significantly differentiated windows: British and St Kilda Wren ($P < 2.2 \times 10^{-16}$, two-tailed Mann-Whitney test); British and Shetland Wren ($P < 2.2 \times 10^{-16}$); British and Hebridean Wren ($P < 2.1 \times 10^{-7}$); and Hebridean and St Kilda Wren ($P < 2.2 \times 10^{-16}$). However, in the case of the Hebridean Wren, that difference was smaller (**Fig. 4A, B, C**), as this subspecies was on average much less differentiated from British Wrens that the others (**Fig. 4A**). Manhattan plots of the F_{ST} reveal multiple highly differentiated peaks along the comparisons of each subspecies (**Fig. 4D**).

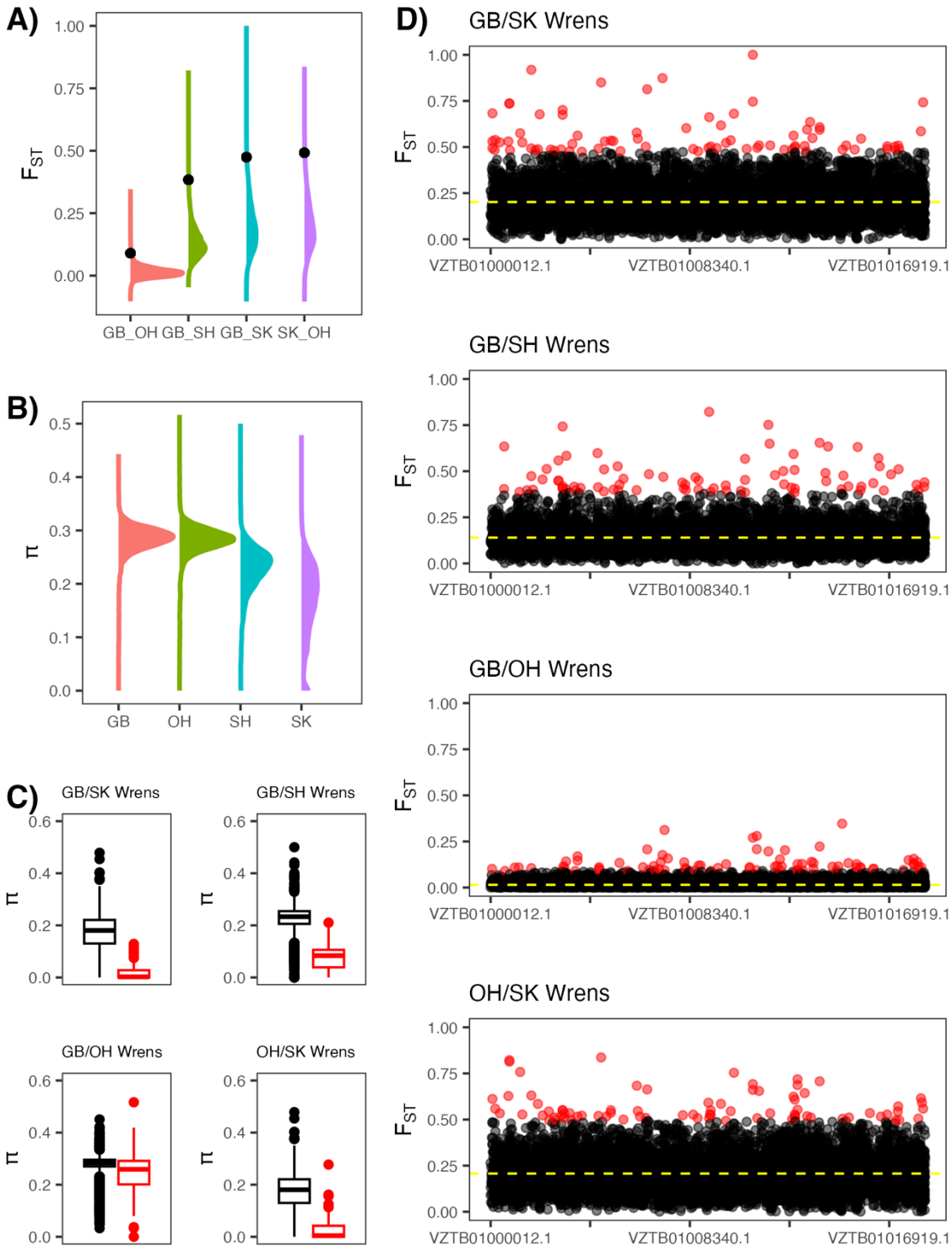

Fig. 3. Wrens from St Kilda and Shetland show considerable genetic differentiation with respect to their closest-related populations. **A)** Large F_{ST} found along 100 kb windows in both St Kilda (relative to both British and Hebridean) and Shetland (relative to British) subspecies. The Hebridean population shows much lower F_{ST}, in agreement

with results of population structure. The codes signify compared population: GB_OH = British to Hebridean; GB_SH = British to Shetland; GB_SK = British to St Kilda; OH_SK = Hebridean to St Kilda. **B)** Patterns of nucleotide diversity show the reverse pattern, with St Kilda and Shetland Wrens showing lower diversity in 100 kb windows than either the Hebridean and British Wrens. Subspecies codes: GB = British Wren; OH = Hebridean Wren; SK = St Kilda Wren; SH = Shetland Wren. **C)** The highly differentiated windows show significant differences in nucleotide diversity (Mann-Whitney test). **D)** F_{ST} along the genome reveals windows at or near fixation in the St Kilda Wren compared to the British Wren, and considerable differentiation in the Shetland Wren.

We have also found notable absolute divergence (d_{xy}) between the Wren subspecies (**Fig. S14**), but d_{xy} was not showing notable differences in nucleotide diversity between significantly and not-significantly divergent sites. Fair Isle Wrens have shown considerable differentiation relative to both Shetland and British Wrens (**Fig. S15)**, mirroring most patterns seen in the differentiation of St Kilda and Shetland Wren (**Fig. 4**). However, they do show overall higher nucleotide diversity than e.g. St Kilda Wrens which have comparable population size, and one that has a distinctly flatter distribution. The f_d statistics' distribution along the genome indicates significant degree of introgression from the British Wren into St Kilda Wren, with many windows showing very high values of f_d (**Fig. S16**). However, despite detectable introgression between St Kilda and British Wren (**Table 1**), there are no windows along the genome of the former showing significant introgression in any set of P1/P2/P3 values tested.

We examined gene occurrence patterns on genomic windows which were significantly differentiated from British Wrens in terms of F_{ST}, and found 32 genes in the St Kilda Wren (**Table S12**) and 62 in the Shetland Wren (**Table S13**). Notably, we have found that five genes are shared between the St Kilda and Shetland Wren, only (**Table 2**).

Table 2. Genes present in significantly differentiated (see Methods) 100kb windows in both the Shetland and St Kilda Wrens. Windowed F_{ST} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus*). NB: original spelling of GO-Slim terms maintained.

Gene name	Panther GO-Slim biological process	Window Fst (Shetland)	Window Fst (St Kilda)	Scaffold
Abca1_1	phospholipid transport	0.65	0.59	VZTB01013939.1
Lpl	multicellular organismal process; fatty acid biosynthetic process; regulation of biological process; protein-containing complex organization; triglyceride catabolic process	0.74	0.70	VZTB01003133.1
Nipsnap3a	unclassified	0.65	0.61	VZTB01013939.1
Psd3	mismatched	0.41	0.68	VZTB01003133.1
Tspan3	unclassified	0.47	0.92	VZTB01001724.1

In gene ontology enrichment analysis relative to the known set of the chicken (*Gallus gallus*) these genes have not shown significant enrichment (but bear in mind small sample sizes), but among the five, the two characterised genes are related to lipid metabolism (*Lpl, Abca1_1*), while one of the uncharacterised genes (*Nipsnap3a*) is a paralogue of the gene *Nipsnap3b* which is involved in lipoprotein metabolism and signalling. The set of highly differentiated genes in St Kilda Wrens (**Table S12**) did not

produce a significant GO enrichment results, whereas Shetland Wrens show enrichment in genes related to: regulation of bone remodelling (fold enrichment (EN) = 59.7, false discovery rate (FDR) = 0.022); response to nicotine (EN = 58.65, FDR = 0.006); positive regulation of neuroblast proliferation (EN = 49.16, FDR = 0.025); cholinergic synaptic transmission (EN = 55.72, FDR = 0.005); membrane depolarisation (EN = 31.84, FDR = 0.015); central nervous system differentiation (EN = 18.27, FDR = 0.034); regulation of plasma membrane bounded cell projection organization (EN = 8.19, FDR = 0.040); and tissue development (EN = 4.82, FDR = 0.024) (for all see **Table S13**). A set of further seven genes is highly differentiated in both Hebridean and St Kilda Wrens, indicating possible step-wise acquirement of mutation by St Kilda Wrens (**Table S14**). This set produces significant GO enrichment results for two top-GO biological processes: axon regeneration (EN = >100, FDR = 0.013); and regulation of TGF-β receptor signalling pathway (EN = >100; FDR = 0.005). Genes showing absolute divergence were largely overlapping with significantly differentiated genes (**Table S15, S16, S17** and **S18**). In particular, the *Lpl* gene has shown evidence of absolute divergence and relative differentiation of in both the Shetland and the St Kilda Wrens.

Discussion

Our investigation has, for the first time, comprehensively assessed Wren subspecies of the British Isles with respect to their phylogeny, population genetic structure, and phenotypic differences (Vaurie, 1955; McGowan et al., 2003; Shannon et al., 2014; Albrecht et al., 2020).

Two clades of Wrens in the British Isles

Our work clarifies the relationships among the subspecies, which were until now poorly resolved (Shannon et al., 2014; Albrecht et al., 2020). Contrary to what was previously shown in genetic studies (Shannon et al., 2014), the St Kilda and Hebridean Wrens originate from within the British subspecies, but show clear genetic differentiation from it, particularly in the case of St Kilda Wrens. Shetland and Fair Isle Wrens represent an entirely distinct lineage, separate from the British/Hebridean/St Kilda clade. Although the placement of the Fair Isle Wren may be somewhat dubious, due to the nearly 50/50 genetic ancestry split in ADMIXTURE analyses, we have identified the Shetland Wren as a distinct lineage. Furthermore, the genetic differences (genetic distance, unique ancestry assignment in ADMIXTURE, distance in genetic PCA) of the St Kilda Wren from all the other subspecies, support the St Kilda Wren as a divergent and monophyletic group (although not reciprocally with the Hebridean/British Wrens). This relationship suggests that both the St Kilda and Shetland Wrens represent independent island colonisations, with the possible source population for the Shetland Wren being the European subspecies. There are known influxes of non-local Wrens on Scottish islands (Rintoul and Baxter, 1917), and these individuals may contain continental European, rather than British, birds.

Morphological and vocal distinctiveness of island Wrens

We have found complex patterns of morphological differentiation among the Wren subspecies. All Scottish island subspecies are larger than most individuals of the British Wren, but this difference can be mostly accounted for by latitude. Wrens in our sample follow the expected pattern of being larger with latitude, which is thought to occur due to potential thermoregulatory benefits (Salewski & Watt, 2017). Such a pattern has been demonstrated previously in Wrens, where a 5% body mass difference was found between eastern Scotland (higher) and the southwest of England (lower) (Morrison et al., 2016). However, we found no latitudinal trends in morphological metrics, such as bill or tarsus length, in the museum dataset, while the reported differences were accounted for by weight differences in the live data.

In the case of the Shetland and St Kilda Wrens, we found these populations to be significantly heavier than the other subspecies, even when latitude is considered, with longer wings, tarsi, and tails, as well as thicker bills and tarsi. The only trait that differed between them, in terms of the direction of change relative to the British Wren, was bill length, with St Kilda Wrens having shorter, and Shetland Wrens having longer bills than their mainland British relatives. Overall, the morphological differences between Wrens are subtle. PCA and LDA identified a single cluster incorporating all subspecies. However, within the clusters in both analyses, there is a strong separation, with St Kilda/Shetland Wrens on one side, and Hebridean/British Wrens on the other (with Fair Isle possibly spanning both sides). As a result of this apparent convergence between St Kilda and Shetland Wrens, they are difficult to distinguish in the field. Nonetheless, geographical distribution and plumage characteristics, (not yet quantified, but darker

Shetland birds cf. to greyer St Kilda Wrens (Cramp, 1988)), are of major help. With respect to the Fair Isle Wren, the patterns of both genomic divergence and morphology are consistent with a hybrid origin, as such patterns are repeated e.g. in Scottish populations of Rock Doves (*Columba livia*) hybridising with feral pigeons (Smith et al., 2022). Fair Isle is a major flyway, and it has been suggested that populations of both the Rock Dove (Smith, 2023) and Starling (*Sturnus vulgaris*) (McGowan et al., 2003) on this island are also intermediate in phenotype between populations on Shetland, and those in more southerly locations.

Our analysis of songs reveals further evidence of subspecies differentiation, particularly in the St Kilda Wrens. PCA and LDA both identified St Kilda Wrens as a distinct song cluster, which in linear comparisons is characterised by more repeated and variable song (i.e. with respect to frequency changes and entropy). Other subspecies also differ consistently from the mainland British individuals on some axes (e.g. lower peak frequencies across all subspecies, which are likely due to larger size), yet not as consistently as St Kilda Wrens. Interestingly, we also found structural differences, such as absence of the element D (the buzz) in the mainland subspecies. Elements such as buzzes are thought to be rare on islands as they are considered aggressive (Morinay et al., 2013). Such elements have been found to correlate with latitude, where the number of trill elements increases, in the closely related House Wrens (*Troglodytes aedon*) (Kaluthota et al., 2016). As a result, both PCA and LDA present the subspecies in three clusters: St Kilda Wrens; other island subspecies, and British and Irish birds (although with some overlap amongst the other island subspecies). Both morphological and vocal characteristics allow for the distinction of

the St Kilda Wren from its relatives, and make it a diagnosable taxonomic unit showing considerable genetic distinctiveness. The metrics we use are important and commonly used in species delimitation (Alström et al., 2021; Martínez-Gómez et al., 2023). Whilst the Wren songs do not show notable convergence, as with morphology, the degree of vocal divergence raises the question of whether songs are a possible mechanism of reproductive isolation in this system, at least between St Kilda Wrens and migrants or dispersing individuals from elsewhere. This would assist geographic isolation in maintaining the distinctiveness of this population.

The consistency of phenotypic evolution in island Wrens with the island syndrome.

Our analysis has revealed that both subspecies of Wrens on the most isolated archipelagos with respect to mainland Great Britain – those of St Kilda and Shetland – have become larger than expected for their latitude. This pattern is consistent with the island rule, which posits that small organisms should become larger, and large organisms should become smaller (Clegg & Owens, 2002; Benítez-López et al., 2022 Jezierski et al., 2023). Both the St Kilda and Shetland Wrens averaged near 14g in our live dataset, relative to the 10g of British subspecies (~40% increase in body mass). The phylogeny of the subspecies indicates that these differences are convergently acquired by both the St Kilda and Shetland Wrens, consistent with the expected pattern as part of the island syndrome (Clegg & Owens, 2002; Jezierski et al., 2023). Patterns of morphological change, that can be accounted by weight alone, are less apparent and not readily visible in bills, legs or flight apparatus. Our analysis has not focused significantly on flight apparatus, i.e. we have not measured traits related to

flight performance such as Kipp's distance, but the observed higher weight of St Kilda and Shetland Wrens also co-occurs with increased wing length.

With respect to songs, the island syndrome is not yet fully explored (Jezierski et al., 2023), although most commonly it is reported to result in lower song complexity (such as no. of syllables, or their variation). Due to the diversity of syllables in Wren songs (Cramp, 1988), syllable classification would be difficult to assess, and therefore we did not quantify comparable metrics of syllable diversity. Our results do show a drop in both bandwidth and entropy in the St Kilda Wren, which may be correlated with complexity (although see Benedict and Najar, 2019). This pattern is not repeated in other island subspecies, and it is unclear if our results represent convergence in songs (although island subspecies, exclusive of the St Kilda Wren, show overlap in songs). Further patterns of bird song evolution on islands remain uncertain. For example, bandwidth has been shown to decrease in island species (Morinay et al. 2013), but in other studies an increase has been reported (Robert et al., 2021). Curiously, this inconsistency is exactly what we observe between the St Kilda (low bandwidth) and Shetland (high bandwidth) Wrens. Another prediction of the island syndrome would be a decrease in 'aggressive' song elements (Morinay et al., 2013), such as buzzes and rattles, and we find completely the opposite effect, of either no difference or a significant increase in elements C and D. Overall, it does not appear that the vocal differences in the island subspecies of Wren show evidence of the island syndrome.

Patterns of song change in the island syndrome are further obscured by the fact that aspects of song variation are lost culturally along colonisation gradients, similar to genetic diversity (Lachlan et al., 2013, Potvin and Clegg, 2015). Further investigations

on a wider sample of songs could explore relationships of such 'cultural loss', for example by focusing on song evolution in the triad of British-Hebridean-St Kilda Wrens.

The genomic patterns of differentiation of island Wrens

The phenotypic evolution of the Wren subspecies, particularly those of St Kilda and Shetland, is associated with notable divergence patterns across the genome, both in terms of relative and absolute sequence divergence. We also show notable sharing of some of those differentiated genes, either through possible step-wise acquisition (St Kilda and Hebridean Wren), or through independent acquisition (Shetland and St Kilda Wren). The complete evolutionary story cannot be resolved without better understanding the basal part of the Shetland/Fair Isle clade, but our results still indicate that both unique and shared genetic adaptations are participating in the divergence of St Kilda and Shetland Wrens, similarly to previous results in e.g. white-eyes (Zosteropidae) (Estandía et al., 2023).

The gene ontology enrichment analyses have revealed that, both in the case of the Shetland Wren, and the differentiated genes shared between Hebridean and St Kilda Wrens, there is notable enrichment of genes associated with nervous systems. Furthermore, in the presumably independently differentiated genes shared between St Kilda and Shetland, three of the five genes may be key in lipid metabolism. Although they have limited annotation and known function in birds, human mutations of these genes are associated with a severe disease which involves abnormal fat concentration in the blood, and deposition throughout the body (Santamarina-Fojo, 1998). These may be indicative of further, convergent adaptations between the St Kilda/Hebridean

and Shetland groups. However, both the behavioural and the metabolic aspects of the island syndrome are particularly understudied (Jezierski et al., 2023). With the added uncertainty of function, particularly with respect to nervous system-related genes, these results alone cannot be used to invoke island syndrome-like adaptations in the Wrens. However, the lipid-related findings are particularly noteworthy, as overall it is thought that metabolic difference constitute a part of the island syndrome (McNab, 1994) due to pervasive resource limitation typical of islands (Lomolino et al., 2012). This has been shown in the Red-billed Chough (*Pyrrhocorax pyrrhocorax*) of the Canary Islands, which has highly elevated blood triglycerides, in relation to overall poorer diet on islands, compared to mainland relatives (Blanco et al., 2014).

Limitations and opportunities in the full understanding of Wren biogeography

Our results currently show that Wrens in the British Isles are composed of two lineages, both of which have colonised a remote island archipelago and become differentiated. These differences may, at least partially, be explained by anagenetic changes caused by the island syndrome. However, full understanding of the steps involved in Wren divergence cannot be achieved without resolving the relationships of the subspecies in the British Isles within a wider European, and perhaps North American, context. Currently, it seems most parsimonious to assume that the Shetland Wren separately originates from within the European subspecies, with the rest of the British Isles being an independent colonisation. However, the relationships of the British Isles' subspecies are unclear with regards to Icelandic (ssp. *islandicus*) and Faroese (ssp. *borealis*) (Amouret et al., 2016) subspecies, as well as the nearest *Troglodytes* species, from which the Eurasian Wren was previously split (Drovetski et

al., 2004). This brings possibilities of more complex colonisation paths, or unexpected inclusion of one of those unsampled populations within the current phylogenetic groupings. Nonetheless, the observed differences in body mass are indicative of island syndrome-like adaptations, regardless of the presumed origin of either St Kilda or Shetland Wrens. Even if their origin involved other routes, e.g. Iceland birds colonising either archipelago, then our results still indicate they are larger than expected for their latitude, which in this system would be expected of the island syndrome.

Once these phylobiogeographic relationships are fully understood, and bearing in mind the evidence already presented here, it might be poignant to revisit the specific designations for St Kilda, and possibly, Shetland Wren, depending on the full scope of divergence and distinctiveness from other populations (Tobias et al., 2010). Our results indicate that these distinct lineages could benefit from further protection, particularly in case of the St Kilda Wren, due to high inbreeding and limited population size, which often threatens island populations (de Villemereuil et al., 2019). In small island populations, where many natural history events can be tracked, investigating the drivers of the island syndrome could be particularly fruitful, compared to previous efforts mostly focused on describing patterns (Jezierski et al., 2023; Lomolino et al., 2012; Whittaker, Fernández-Palacios, et al., 2023). Particularly on St Kilda, the role of predation in the evolution of the island syndrome could be explored, due to the history of cat predation across centuries, and collecting effort in the past few hundred years, which all ceased after the islands were abandoned in 1930s (Love, 2009). Therefore, many specimens are available to represent a time series of varying selective pressures, where the effects of predation on phenotype and genetics may be

observable, as has already been leveraged to investigate how island species cope with predation (Vanderwerf, 2012).

Conclusion

Our integrative study of genomic and phenotypic data has reconstructed the population genetic structure and pattern of phenotypic differences between Wren populations in the British Isles. The phylogenetic relationships suggest independent colonisations of remote archipelagos by St Kilda and Shetland Wren, with phenotypic convergence consistent with the island rule. The rest of their morphology, as well as vocal traits, did not strictly follow island syndrome patterns, but in the case of the St Kilda Wren both axes of phenotypic variation have shown strong divergence from other Wren populations. Both St Kilda and Shetland Wrens also show evidence of genomic divergence in different parts of the genome, except for genes related to lipid metabolism, which appear very divergent compared to the British subspecies in both populations. Together, this evidence suggests there are three genetically distinct and phenotypically-identifiable lineages of Wrens, prompting the need to reassess their differences and similarities in context of possible elevation to species status. Their evolution is at least partially consistent with the island syndrome, even if brought about by distinct genetic mechanisms.

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Table S1. Data on live Wrens collected for this study. For details of sampling see Methods. RING denotes the metal British Trust for Ornithology ring number. SSP column denotes presumed subspecies (see Methods) using the following codes: GB = British; SK = St Kilda; OH = Hebridean; SH = Shetland; FI = Fair Isle. The remaining columns denoted morphological measurements (in mm, except for mass, which is in grammes): WL = wing length; BL = bill length; BW = bill width; BD = bill depth; TL = tarsus length; TW = tarsus width; TAL = tail length. LON and LAT correspond to longitude and latitude. Column SEQ denotes if the individual's genome is featured in the study (Y = Yes; N = No).

RING	SSP	WL	BL	BW	BD	TL	TW	TAL	MASS	DATE	LON	LAT	SEQ
NBE812	GB	51	11.4	2.2	2.5	20.4	NA	NA	10.6	29/04/2022	-1.03	52.73	N
NBE813	GB	51	11.1	2.2	2.4	20.7	NA	NA	10.5	29/04/2022	-1.03	52.73	Y
NHC389	GB	50	10.7	2.2	2.3	18.8	1.5	32	10.2	19/05/2022	-3.99	57.58	Y
NNT586	GB	49	12.3	2.5	2.5	20.9	1.8	31	11.5	19/05/2022	-3.99	57.58	Y
NRL803	GB	48	11.2	2.5	2.5	19.8	1.4	30	8.1	26/07/2022	-1.57	51.70	N
NRL804	GB	46	NA	NA	NA	NA	NA	NA	8.6	26/07/2022	-1.57	51.70	N
NRL817	GB	50	10.5	2.3	2.6	NA	NA	NA	9.9	26/07/2022	-1.57	51.70	N
NRL818	GB	48	NA	NA	NA	NA	NA	NA	8.3	26/07/2022	-1.57	51.70	N
NRL820	GB	50	10.3	2.5	2.4	20.3	1.6	33	9.8	26/07/2022	-1.57	51.70	Y
NRL821	GB	48	10.6	2.2	2.3	18.3	1.4	30	8.2	26/07/2022	-1.57	51.70	Y
NRL822	GB	51	10.5	2.1	2.3	21	1.5	34	9.9	26/07/2022	-1.57	51.70	N
NBE815	SK	56	11.4	2.7	2.8	21.7	1.7	36	14.6	02/05/2022	-8.57	57.81	Y
NBE816	SK	54	10.8	2.2	2.8	21.1	1.6	36	NA	02/05/2022	-8.57	57.81	N
NBE817	SK	55	12.2	2.8	2.7	21.1	1.6	39	13.8	02/05/2022	-8.57	57.81	N
NBE818	SK	56	10.6	2.8	2.9	22.2	1.4	39	14.2	02/05/2022	-8.57	57.81	N
NBE819	SK	51	11.2	2.1	2.8	20.5	1.4	32	13.3	03/05/2022	-8.57	57.81	N
NBE820	SK	55	12	2.9	2.4	21.5	1.5	36	NA	03/05/2022	-8.57	57.81	N
NBE821	SK	55	11.6	2.5	2.9	21.5	2	37	15.2	04/05/2022	-8.57	57.81	Y

NBE822	SK	51	10.5	2.4	2.7	20.8	1.7	32	12.8	04/05/2022	-8.57	57.81	Y
NBE823	SK	56	11.4	2.2	2.9	21.4	1.7	36	13.5	05/05/2022	-8.57	57.81	Y
NBE824	OH	53	11.1	NA	NA	21.1	NA	36	11.8	11/05/2022	-7.32	57.23	Y
NBE825	OH	51	10.3	2.2	2.7	21.3	1.5	37	11	11/05/2022	-7.32	57.23	Y
NBE829	OH	51	10.8	3	2.7	20.7	1.5	32	12.9	13/05/2022	-7.28	57.57	Y
NBE830	OH	49	9.6	2	2.2	20.6	1.2	30	12	14/05/2022	-7.41	57.66	Y
NBE831	OH	52	11.4	2.1	2.8	20.9	1.6	35	12.1	15/05/2022	-7.41	57.66	N
NBE809	OH	52	12.6	2	2.7	21.7	1.6	30	12.5	15/05/2022	-7.41	57.66	Y
NBE832	OH	54	11.8	2.5	2.8	21	1.4	34	12.4	15/05/2022	-7.23	57.69	Y
NBE833	OH	47	10	1.9	2.3	20.1	1.3	29	11.9	16/05/2022	-7.40	57.19	Y
NBE834	SH	54	13.4	2.5	3	21.7	1.8	35	14.1	21/05/2022	-1.29	60.27	N
NBE835	SH	54	13.9	2.4	3	22.3	1.6	36	13.9	22/05/2022	-1.29	60.27	N
NBE836	SH	53	14.3	2.3	3.3	21.3	1.3	34	13.7	22/05/2022	-1.29	60.27	N
NBE837	SH	53	12.1	2.4	2.7	20.9	1.7	34	14.6	22/05/2022	-1.28	59.99	Y
JHB375	SH	54	13.1	2.4	2.8	22.3	1.5	34	14.2	23/05/2022	-1.33	59.95	Y
NBE838	SH	50	12.7	2.2	2.8	20.4	1.5	33	14.4	24/05/2022	-1.36	60.25	Y
NBE839	SH	53	14.9	2.6	3.3	21.3	1.6	34	14.4	24/05/2022	-1.29	60.27	Y
NBE840	SH	54	13.7	2.4	2.7	21.6	1.4	30	13.6	24/05/2022	-1.29	60.27	N
NBE841	SH	52	14.7	2.7	3.1	22	1.7	34	14.7	24/05/2022	-1.29	60.27	N
NBE842	SH	54	13.7	2.6	2.9	22.5	1.4	34	NA	26/05/2022	-1.29	60.28	Y
NBE843	SH	53	12.1	2.2	2.9	21.9	1.6	34	14.4	26/05/2022	-1.29	60.28	Y
NBE844	SH	52	12.3	2.2	2.7	21.9	1.6	33	13.8	27/05/2022	-1.22	60.20	N
NBE845	SH	52	13.9	2.4	2.9	22.8	1.6	32	14.6	27/05/2022	-1.22	60.20	Y
NBE846	SH	54	13.5	2.5	2.8	22.7	1.6	34	14.3	28/05/2022	-1.28	60.13	Y
NBE847	SH	52	14.2	2.4	2.9	21.6	1.6	32	14.5	29/05/2022	-1.25	60.35	N
NCP601	FI	53	11.6	2.1	2.5	21.1	1.4	35	11.7	31/05/2022	-1.60	59.54	Y
NCP602	FI	54	12.6	2.2	2.6	21.6	1.5	34	12.8	01/06/2022	-1.61	59.55	Y

Table S2. Data on museum specimens of Wrens measured for this study. All specimens come from the zoological collections of the National Museums, Scotland (NMSZ). For details of sampling see Methods. SSP column denotes presumed subspecies (as identified on the label, see Methods) using the following codes: GB = British; SK = St Kilda; OH = Hebridean; SH = Shetland; FI = Fair Isle. The remaining columns denoted morphological measurements (in mm): WL = wing length; BL = bill length; BW = bill width; BD = bill depth; TL = tarsus length; TW = tarsus width; TAL = tail length. LON and LAT correspond to longitude and latitude, taken to the nearest settlement/country centroid if not given more precisely. Specimens highlighted in bold are the type specimens of the subspecies. NB: the St Kilda holotype is not in the dataset, as it is not stored in NMSZ.

ACCESSION	SSP	WL	BL	BW	BD	TW	TL	TAL	DATE	LON	LAT
1915.44.29	FI	51	11.3	3.1	2.8	20.1	1.9	29	07/08/1914	-1.63	59.53
1915.44.28	FI	48	10.1	2	2.4	17.5	1.7	29	14/01/NA	-1.63	59.53
1931.50.101	FI	NA	9.3	2.6	3	19.3	2.1	28	04/09/1921	-1.63	59.53
1905.126.58	FI	47	10.2	2.8	3.2	18.7	1.7	25	04/09/1905	-1.63	59.53
1905.126.54	FI	48	10.6	2.2	2.5	18.7	1.7	32	20/09/1905	-1.63	59.53
1910.4.35	FI	48	9.4	2.3	2.9	17	1.7	33	17/09/2006	-1.63	59.53
1905.126.56	FI	49	10.4	2.5	2.7	19	1.8	26	16/09/1905	-1.63	59.53
1907.4.36	FI	53	11	2.5	3.3	21.7	1.9	33	27/09/2006	-1.63	59.53
1913.56.29	FI	49	10.2	3	2.7	19.44	1.6	27	02/10/2002	-1.63	59.53
1931.50.02	FI	51	10.9	3	3.1	19.4	1.9	30	01/10/1921	-1.63	59.53
1905.126.53	FI	48	10.4	2.4	2.8	19.2	1.7	29	16/09/1905	-1.63	59.53
1913.50.31	FI	49	11.3	3	2.9	18.7	1.8	30	04/10/1912	-1.63	59.53
1953.1.7	FI	48	10.6	2.7	2.8	18.4	1.9	30	20/10/1952	-1.63	59.53
1913.50.32	FI	45	10.3	2.5	2.4	17.5	1.6	29	02/10/2012	-1.63	59.53
1905.126.57	FI	48	10.9	3	3.2	18.4	1.7	29	20/09/1905	-1.63	59.53
NA	FI	51	11.2	2.7	2.7	19.9	1.9	29	28/12/1911	-1.63	59.53

1905.126.55	FI	50	11.6	2.9	3	17.4	1.7	27	15/09/1905	-1.63	59.53
1927.74.9	FI	48	10.4	2.9	2.9	21	2.1	27	24/05/2027	-1.63	59.53
1905.126	FI	52	9.4	3	2.4	17.6	1.7	30	12/07/1910	-1.63	59.53
NMSZ 1913.050.030	**FI**	**47**	**9.7**	**2.5**	**3**	**20.1**	**1.6**	**30**	**25/09/1912**	**-1.63**	**59.53**
1952.19.1185	OH	49	10.3	2.4	2.8	17.2	1.8	29	12/10/1941	-7.31	57.16
1968.80.20	OH	46	9.7	3	2.5	17.3	1.7	28	29/04/1924	-6.68	56.97
1968.80.21	OH	47	10.5	2.5	2.5	19.3	1.7	32	06/11/1925	-6.68	56.97
1952.19.1186	OH	46	10.2	2.8	2.7	18.5	1.7	29	12/10/1941	-7.31	57.16
1968.80.22	OH	45	10	2.6	2.4	18.6	1.6	29	07/04/2023	-6.68	56.97
1956.65.4765	OH	42	8.6	2.2	2.4	19	2	NA	25/06/1947	-7.31	57.16
1914.168.27	OH	47	10.4	2.4	2.4	18.5	1.7	28	03/10/1914	-6.26	58.52
NA	OH	50	10	2.2	2.7	17.8	1.6	33	03/01/1907	-6.39	58.21
1914.168.26	OH	47	9.9	3.1	2.5	17.6	1.6	32	06/10/1914	-6.26	58.52
1914.168.24	OH	48	9.5	2.5	3.2	18	1.8	31	06/10/1914	-6.26	58.52
1970.76.1523	OH	50	10.4	2.8	3	17.4	2	32	06/02/1933	-7.31	57.16
NA	OH	51	11.2	2.9	2.9	20.2	1.8	32	01/11/1906	-6.39	58.21
1970.76.1525	OH	47	10.3	2.8	3	18.5	1.6	29	02/02/1933	-7.31	57.16
1952.19.1187	OH	49	9.8	2.6	3	18.6	1.9	31	13/10/1941	-7.31	57.16
NA	OH	49	10.1	2.2	2.5	18	1.6	30	20/10/1906	-7.37	57.33
1970.76.1524	OH	55	9.8	3	3	17.5	1.7	34	06/02/1933	-7.31	57.16
1970.76.1531	OH	50	9.9	2.6	2.9	18.5	1.6	35	08/10/1936	-6.96	57.74
1956.65.4766	OH	50	10.1	2.5	3.1	17.4	1.7	33	19/06/1947	-7.31	57.16
1970.76.315	OH	52	10.7	2.4	2.7	18.6	1.6	30	11/12/1933	-7.22	57.68
1950.6.46	OH	46	10.4	3	2.6	17.2	1.5	30	25/10/1926	-6.68	56.97
1970.76.1529	OH	46	10.4	2.5	2.5	18	1.8	30	02/01/1934	-7.22	57.68
1970.76.1527	OH	45	10.4	2.7	2.9	18	1.5	28	20/01/1934	-7.22	57.68
1956.65.4767	OH	47	10.2	2.7	2.7	19.4	1.5	28	19/06/1947	-7.31	57.16
1970.76.1526	OH	46	9.2	2.5	2.8	18.5	1.7	29	10/02/1933	-7.31	57.16
1970.76.1386	OH	49	11.4	2.5	2.3	17.3	2	30	17/09/1933	-7.22	57.68
1970.76.1530	OH	45	11	2.7	2.7	17.8	1.9	28	08/10/1936	-6.96	57.74
1970.76.314	OH	48	10	2.6	2.5	17.6	1.7	28	11/12/1933	-7.22	57.68

NMSZ 1914.168.023	**OH**	**47**	**9.5**	**2.1**	**2.6**	**18.7**	**1.6**	**29**	**01/10/1914**	**-6.26**	**58.52**
200 10 2	SK	51	11.8	2.9	2.9	20.1	1.8	34	18/08/1999	-8.57	57.81
1910 165 46	SK	52	11.6	2.6	2.8	20.9	2.1	35	24/09/2010	-8.57	57.81
1910 165 49	SK	51	10.1	2.6	2.8	18.2	2	34	09/09/2010	-8.57	57.81
2007 78	SK	53	12	2.9	2.8	20.4	2	34	7/NA/2007	-8.57	57.81
1965.38.453	SK	51	10.6	2.4	2.6	18.7	1.9	30	28/08/1911	-8.57	57.81
1953.53.13	SK	50	11.5	2.5	3.2	19.6	1.7	33	19/NA/11	-8.57	57.81
1965.38.454	SK	50	11	2.5	2.8	20.1	2	34	06/10/1911	-8.57	57.81
NA	SK	49	11	3	2.9	19	1.8	30	24/09/1911	-8.57	57.81
NA	SK	52	11.5	2.9	3.2	19.7	2.1	33	21/09/1911	-8.57	57.81
NA	SK	52	NA	NA	NA	18.5	1.8	33	28/09/1911	-8.57	57.81
1910.168.48	SK	51	12.1	2.6	3.1	20.4	1.9	26	03/09/1910	-8.57	57.81
NA	SK	50	11	2.5	2.8	18.4	1.8	32	23/09/1911	-8.57	57.81
NA	SK	49	11.5	2.7	3.1	19.8	2	31	14/09/1911	-8.49	57.87
1910.165.43	SK	53	11.3	3.2	3	21.3	2.1	35	19/09/2010	-8.57	57.81
1956.65.4689	GB	46	10.1	2.8	2.8	17.4	1.6	30	06/10/1946	-2.57	53.86
1956.65.4706	GB	50	10.4	3	2.5	16.9	2.1	35	06/10/1946	-2.57	53.86
1934.61.1067	GB	49	11.2	2.4	2.7	18.4	1.6	31	31/10/1908	1.73	52.61
1934.61.1070	GB	50	10.8	2.7	2.9	18.9	1.8	33	26/08/2019	0.96	52
1956.65.4700	GB	47	10.1	2.2	2.3	17.1	1.5	31	12/01/1947	-2.63	53.56
2000.221	GB	48	10.4	2.5	2.5	19	1.7	NA	04/05/2000	-3.22	55.79
1992.41.2	GB	47	9.7	2.2	2.8	18.7	1.8	30	26/08/1990	-3.19	55.95
1956.65.4821	GB	48	10.7	2.5	2.7	17.4	1.7	33	29/10/1948	-5.57	56.03
1956.65.4705	GB	45	9	2.2	2.5	17.2	2	28	09/11/1946	-2.57	53.86
2003.26.2	GB	46	9.9	2.6	2.8	17.4	1.8	29	28/01/2003	-6.81	56.5
1994.22.2	GB	45	10.2	3	2.6	19.3	1.7	33	23/02/1993	-3.2	55.84
1956.65.4825	GB	49	10.6	2.5	2.4	17	1.7	34	8/NA/1948	-5.57	56.03
2004.33.1	GB	47	10.5	2.1	2.4	19.4	1.5	29	02/01/2000	-2.72	56.06
1934.61.1065	GB	44	9.8	2.5	2.6	17.6	1.5	29	16/10/1908	1.73	52.61
1992.73.1	GB	47	9.9	2.4	2.6	17.2	1.6	29	27/05/1999	-2.78	55.96
1953.53.15	GB	46	10	2.3	2.6	16	1.4	30	22/10/1915	-2.93	58.69

1956.65.4790	GB	42	8.9	2.7	2.8	18.5	1.6	24	05/08/1935	-4.24	55.79
2009.55.3	GB	44	10.6	2.8	2.3	19	1.8	31	22/11/2003	-3.9	55.01
1970.76.311	GB	47	9.9	2.8	2.7	19.2	1.7	29	12/06/1926	-6.19	55.63
1970.76.1521	GB	49	10.3	3.2	2.8	20.2	2.1	30	08/03/1935	-3.83	55.08
1970.76.312	GB	50	10	2.6	2.4	17.5	1.5	32	NA/NA/NA	-1.51	52.41
1956.65.4789	GB	49	9.6	2.5	2.6	18	1.6	33	29/03/1946	-4.24	55.79
1956.65.4793	GB	45	10.3	2.6	2	16.2	1.4	29	17/01/1945	-4.24	55.79
1956.65.4782	GB	46	9.7	2.3	2.3	17.5	1.7	29	11/07/1946	-4.24	55.79
1970.76.1522	GB	48	10.5	2.8	2.9	18.8	1.7	29	02/03/1935	-3.83	55.08
1970.76.1387	GB	44	9.6	2.6	2.8	18.8	1.9	29	08/02/1934	-2.01	51.82
1970.76.1514	GB	44	10	2.5	2.5	18.9	1.5	31	07/03/1935	-3.62	55.15
1965.38.452	GB	47	9.6	2.6	2.2	17.5	1.8	30	21/09/1912	-2.56	56.19
1965.38.450	GB	46	9.8	2.6	2.5	17.8	1.7	29	11/10/1910	-2.56	56.19
1965.38.451	GB	45	10	2.2	2.5	19.7	1.6	29	01/05/1912	-2.56	56.19
NA	GB	44	9.2	2.4	2.3	19.1	1.5	31	23/10/2016	-2.02	57.36
NMSZ 1956.065.4768	**GB**	**44**	**NA**	**NA**	**NA**	**19.5**	**1.5**	**28**	**24/04/1937**	**-4.24**	**55.79**
NA	SH	52	11.5	2.7	3.2	19.3	2.1	32	12/12/1906	-1.3	59.92
1911.18.1	SH	52	11.9	2.4	3	20.3	1.7	36	31/01/1911	-1.15	60.15
1953.53.14	SH	52	11.1	2.8	NA	19.5	1.9	32	NA/NA/NA	-1.15	60.15
NA	SH	52	11.6	2.6	3	18.8	1.9	37	28/11/1907	-1.15	60.15
NA	SH	49	12.2	2.5	2.6	20.4	1.7	29	05/01/1911	-1.34	60.5
NA	SH	49	11.2	2.6	2.8	18.5	1.7	30	19/03/1911	-1.15	60.15
NA	SH	53	12.2	3	3.1	18.5	2	33	30/03/1911	-1.15	60.15
1934.61.1072	SH	49	12.6	2.8	2.8	19.8	1.7	31	NA/NA/NA	-1.34	60.5
2011.27.4	SH	49	10.6	2.1	2.6	20.2	2.1	33	22/10/2008	-1.09	60.14
1926.102.3	SH	50	11.1	2.5	3	19.4	1.9	32	02/08/1926	-1.06	60.6
1926.104.4	SH	48	12	3.2	2.9	19	1.6	31	31/07/1926	-1.06	60.6
NA	SH	48	10.5	2.8	2.6	21.7	2.2	31	19/03/1911	-1.15	60.15
1965.38.456	SH	52	11.2	2.8	3	22.3	1.9	33	1910/NA/NA	-1.34	60.5
NA	SH	51	11	2.9	3.1	20.2	1.6	32	22/04/1911	-1.15	60.15
1956.65.4763	SH	52	10.4	2.4	3.1	21	1.9	33	07/07/1949	-1.18	60

NA	SH	53	11.1	3	2.7	18.6	2	38	20/10/NA	-2.08	60.13
1970.76.316	SH	52	11.5	2.4	3.1	21.3	2.2	32	21/04/1914	-1.15	60.15
2003.28.4	SH	53	11.2	2.9	2.9	19.4	1.8	NA	22/10/2002	-1.22	60.04
NA	SH	52	11.7	2.7	2.8	19.4	1.9	35	19/03/1911	-1.15	60.15
1965.38.455	SH	52	11.5	3.1	2.8	19.2	2.1	35	31/01/1911	-1.15	60.15
1934.61.1071	SH	54	11.8	3	3.1	19.2	2	36	NA/NA/NA	-1.34	60.5
1911.15.2	SH	51	11.7	2.8	3	20.9	1.7	32	31/01/1911	-1.15	60.15
NMSZ 1919.004	**SH**	**54**	**12**	**2.7**	**3**	**20.5**	**2.1**	**35**	**12/12/1906**	**-1.3**	**59.92**

Table S3. Data on song recordings of Wrens measured for this study (n = 55). Samples come either from our sampling (ID as numbers) or from xeno-canto.org (ID as XC song identifier). For details of sampling see Methods. SSP column denotes presumed subspecies using following codes: GB = British; SK = St Kilda; OH = Hebridean; SH = Shetland; FI = Fair Isle. The remaining columns represent mean value per element (in subscript), or count per song in case of columns 'C' and 'D': BW = bandwidth (in Hz); EN = aggregate entropy (in bits); PK = peak frequency (in Hz); Δ = duration (in seconds); CT = centre frequency (in Hz); C = number of elements C per song; D = number of elements D per song. LON and LAT correspond to longitude and latitude. For description of song elements and measurements see **Table S4**, **Fig. S3** and Methods.

ID	SSP	BW_A	BW_B	EN_A	EN_B	PK_A	PK_B	Δ_A	Δ_B	CT_A	CT_B	C	D	DATE	LON	LAT
1	SK	1850	968.75	3.39	3.48	5006.25	5354.17	0.5	1.07	5325	5437.5	1	1	05/05/2022	57.81	-8.57
2	SK	1637.5	677.08	3.33	2.89	5118.75	5635.42	0.45	0.91	5450	5614.58	1	1	06/05/2022	57.81	-8.57
3	SK	1571.69	801.14	3.29	3.27	5233.46	5071.02	0.38	0.95	5294.12	5198.86	1	3.33	06/05/2022	57.82	-8.57
4	SK	1450.37	786.06	3.22	3.17	4681.99	5350.96	0.48	0.95	4863.97	5322.12	1	2	06/05/2022	57.81	-8.56
5	SK	2015.62	642.86	3.55	2.92	4535.16	4714.29	0.83	1.09	4570.31	4700.89	1	0.66	07/05/2022	57.81	-8.57
6	SK	1781.25	593.75	2.96	2.85	5270.83	4468.75	0.46	0.93	5020.83	4375	1	0	07/05/2022	57.81	-8.57
7	SK	1635.42	687.5	3.49	2.82	4760.42	5171.88	0.39	1.18	4916.67	5218.75	1	1	07/05/2022	57.81	-8.57
8	SK	1381.25	864.58	3.35	3.32	5575	5114.58	0.32	0.7	5575	5114.58	1	2	07/05/2022	57.82	-8.57
9	SK	1870.07	758.52	3.18	2.87	5353.62	5122.16	0.33	0.83	5309.21	5130.68	2	2	07/05/2022	57.81	-8.57
10	SK	1818.75	1281.25	3.56	3.69	4996.88	5937.5	0.39	0.98	5118.75	5890.62	1	0.66	07/05/2022	57.81	-8.57

11	OH	2407.89	1056.82	3.83	3.18	5911.18	5855.11	0.43	0.76	6315.79	5880.68	0	2.33	12/05/2022	57.33	-7.32
12	OH	2821.02	2468.75	4.29	4.7	5335.23	5375	0.85	1.06	5659.09	4843.75	0	1	14/05/2022	57.23	-7.33
13	OH	2650	1270.83	4.13	3.55	4662.5	5500	0.62	0.79	4737.5	5625	1	1	14/05/2022	57.23	-7.32
14	OH	2460.94	1089.84	3.77	3.53	4833.98	5589.84	0.33	0.62	4980.47	5683.59	1	0.66	17/05/2022	57.24	-7.35
15	OH	2631.25	1115.62	4.23	3.42	5875	5671.88	0.41	0.53	6087.5	5606.25	0.66	1	17/05/2022	57.24	-7.34
16	OH	2507.81	1281.25	4	3.88	5921.88	5197.92	0.59	0.99	6023.44	4979.17	0	1	14/05/2022	57.2	-7.39
17	OH	1613.84	1078.12	3.48	3.71	5276.79	4781.25	0.54	0.54	5055.8	4718.75	1	1	15/05/2022	57.66	-7.41
18	OH	1916.67	925.78	3.95	3.33	5541.67	5367.19	0.36	0.46	5817.71	5355.47	1	2	15/05/2022	57.66	-7.41
19	OH	2867.19	1392.86	3.96	3.88	4546.88	5303.57	0.8	0.69	5109.38	5263.39	0.66	1	17/05/2022	57.63	-7.41
20	OH	2918.75	1143.75	4.07	3.7	5287.5	4856.25	0.63	0.62	5368.75	5175	2	1	17/05/2022	57.57	-7.28
21	OH	2890.62	1531.25	3.81	4.26	5835.94	5843.75	0.54	0.69	5867.19	5750	1	1	14/05/2022	57.41	-7.25
22	SH	2636.25	1304.69	4.17	3.73	5437.5	5250	0.48	0.67	5523.75	5226.56	1	2.33	24/05/2022	60.27	-1.29
23	SH	2581.25	1523.44	3.92	4.02	5343.75	5074.22	0.55	0.76	5375	5039.06	1.33	0	24/05/2022	60.27	-1.29
24	SH	3328.12	718.75	4.41	2.8	5381.25	4187.5	1.19	0.5	5437.5	4125	0	2	24/05/2022	60.13	-1.21
25	SH	2573.86	2183.04	3.95	4.38	5250	4446.43	0.6	0.76	5829.55	4513.39	1	1	26/05/2022	60.03	-1.22
26	SH	2710.94	921.88	4.51	3.5	5390.62	5656.25	0.53	0.87	5781.25	5562.5	0	1	29/05/2022	60.13	-1.28
27	SH	2517.19	1476.56	3.98	3.81	5123.44	5003.91	0.43	0.66	5339.06	5109.38	0.33	2.33	29/05/2022	60.13	-1.21
28	SH	2602.94	1052.08	3.9	3.41	4306.99	4708.33	0.54	0.66	4687.5	4750	1	0.66	29/05/2022	60.14	-1.21
29	SH	2806.64	937.5	4.31	3.43	5841.8	4727.68	0.62	0.66	5771.48	4580.36	1	1	30/05/2022	60.1	-1.28
30	SH	2476.56	1031.25	4.17	3.63	4695.31	4851.56	0.75	0.71	4539.06	5027.34	1	1	29/05/2022	60.01	-1.22

31	FI	3165.87	1281.25	4.37	3.89	4500	4734.38	0.99	0.49	4911.06	4734.38	0	2	01/06/2022	59.54	-1.61
32	FI	2370.54	1166.67	3.91	3.76	5444.2	5177.08	0.59	0.78	5477.68	5145.83	0	1	03/06/2022	59.55	-1.61
33	FI	2575	1104.17	3.8	3.46	4581.25	4541.67	0.71	0.39	4600	4541.67	0	2	04/06/2022	59.53	-1.63
34	GB	2963.54	1843.75	4.1	3.93	5531.25	5206.25	0.48	0.55	5364.58	5287.5	1	0	01/05/2022	57.29	-6.44
35	GB	2835.94	1957.03	3.96	4.2	6453.12	5343.75	0.37	0.71	6000	5402.34	0	0	01/05/2022	57.3	-6.35
36	GB	2669.41	1379.46	3.8	3.89	5866.78	5752.23	0.24	0.71	5758.22	5645.09	2.33	0	01/05/2022	57.3	-6.35
37	GB	1904.61	1239.58	3.01	3.89	6064.14	5177.08	0.27	0.43	5911.18	5166.67	1.33	0	01/05/2022	57.29	-6.17
38	GB	1937.5	1468.75	3.66	4.06	7226.56	5625	0.33	0.61	7218.75	5572.92	1	0	20/05/2022	57.47	-3.23
39	GB	1445.31	2171.88	2.78	4.37	6015.62	5312.5	0.27	0.7	6015.62	5445.31	1	0	20/05/2022	57.47	-3.24
XC145562	GB	2878.27	1971.48	4.14	4.35	4780.37	4919.14	0.67	1.01	5282.81	4785.16	2	0	08/07/2012	54.94	-1.94
XC206775	GB	2142.86	2250	3.67	4.48	5845.98	5105.77	0.32	0.6	6127.23	5293.27	1.67	0	19/05/2009	54.12	-0.54
XC313805	GB	2316.02	1424.06	4.15	4.13	6105.86	5449.34	0.4	0.71	6067.58	5478.05	1	0	23/04/2016	52.94	1.11
XC441561	GB	2952.01	2363.87	4.31	4.6	6115.43	5072.27	0.6	0.49	6593.08	5167.97	0.67	0	26/10/2018	53.12	-1.92
XC492792	GB	2583.98	2058.57	3.68	4.14	5326.98	4332.48	0.35	0.65	5340.23	4384.16	1.33	0	29/07/2019	52.3	0.27
XC544337	GB	2350.45	2854.17	3.41	4.75	5330.36	4927.08	0.3	0.68	5337.05	5427.08	1	0	10/04/2020	54.12	-0.56
XC741439	GB	2526.56	1751.37	3.89	4.37	5620.17	4952.64	0.48	0.59	5993.41	4952.64	1	0	07/06/2022	52.94	1.12
XC788818	GB	2737.11	1138.18	3.94	3.86	6125	5826.27	0.37	0.55	6244.63	5727.83	1.3	0	08/04/1990	55.23	-2.59
XC788820	GB	2531.25	1586.54	3.94	4.24	6036.06	5653.85	0.35	0.76	5963.94	5855.77	2	0	06/04/2015	55.23	-2.01
XC788822	GB	2601.56	1533.48	3.25	3.87	4859.38	5631.7	0.3	0.68	5031.25	5712.05	1.33	0	04/05/2020	54.33	-0.52
XC791053	GB	1283.38	1985.16	2.91	4.18	5469.43	5639.65	0.22	0.55	5443.59	5881.64	2	0	19/03/2023	52.2	-6.46

XC811329	GB	2927.88	3107.14	3.96	4.62	5343.75	5223.21	0.58	1	5314.9	5263.39	2.33	0	27/05/2023	51.72	-0.14
XC812091	GB	1894.92	1501.94	3.85	4.2	6352.29	5329.47	0.33	0.51	6459.96	5221.8	1.33	0	16/06/2022	51.87	-5.23
XC813828	GB	2062.4	1536.04	3.17	3.86	5445.51	5392.87	0.3	0.58	5464.65	5617.77	1	0	24/06/2023	55.87	-4.28
XC814301	GB	2428.57	2250	3.71	4.25	5973.21	5460.94	0.42	0.44	5941.96	6062.5	2.33	0	17/05/2023	51.15	-2.79
XC815154	GB	1860.99	2613.8	3.62	4.56	6172.85	5495.94	0.39	0.67	6144.14	5717.89	3	0	16/04/2022	52.6	-2.13

Table S4. The elements of Eurasian Wren song as described by Hall-Craggs (Cramp 1988), and used in this study. See **Fig. S3** for graphical representation of each element.

Element type	Description
Element type A	A series of heterogenous units characterised by a lack of uniformity in duration and acoustic structure of adjacent units.
Element type B	A series of repeated units, which show marked uniformity of unit structure, duration.
Element type C	A series of rapidly repeated clicks, sounding like a rattle.
Element type D	A single continuous buzz.

Table S5. Genome-wide F_{ST} estimates (see Methods) for each subspecies, and also separated for each of the British Wren populations sampled. Codes correspond to the subspecific designation/sampling location of birds: SK – St Kilda Wren; OH – Hebridean Wren; SH – Shetland Wren; FI – Fair Isle Wren; GB – British Wren (British Wrens are further split into OXFD – Oxfordshire; HIGH – Highland; LEIC – Leicestershire; LINC – Lincolnshire).

Mean F_{ST}	**SK**	**OH**	**SH**	**FI**	**GB**	**OXFD**	**LEIC**	**LINC**	**HIGH**
SK		0.12	0.21	0.24	0.11	0.19	0.20	0.16	0.19
OH			0.10	0.04	0.01	-0.01	-0.10	0.00	-0.01
SH				0.10	0.09	0.12	0.05	0.11	0.12
FI					0.02	0.05	0.04	0.04	0.05
GB									
OXFD							-0.12	-0.03	-0.03
LEIC								-0.13	-0.12
LINC									-0.03
HIGH									

Table S6. Differences in the morphological measurements between the subspecies in the live Wren dataset (n=45). Each row corresponds to a trait that was tested using the function *lm(trait ~ subspecies + weight + latitude*). See Methods for more details. First data column represents the intercept values for *indigenus* subspecies. β represents the coefficient as reported by the output of *summary(lm*) and corresponds to: i) difference between that subspecies and *indigenus*; or ii) the slope of the gradient (for weight and latitude). Sample sizes for each comparison are provided for each model examined, as they varied due to data missingness. Significance levels for α are coded as follows: *** - p-value < 0.001; ** - p-value < 0.01; * - p-value <0.05; . – p-value < 0.1; ns – non-significant. P-values are reported after Bonferroni correction for multiple comparisons.

Trait tested	**British Wren**	**Hebridean Wren**	**St Kilda Wren**	**Shetland Wren**	**Fair Isle Wren**	**weight**	**latitude**
Wing length	50.41	β = 0.09	β = 1.25	β = 0.01	β = 2.73	β = 1.13	β = -0.23
(N = 42)		α ns	α ns	α ns	α ns	α .	α ns
Bill length	3.44	β = -0.99	β = -1.21	β = 0.70	β = -0.08	β = 0.27	β = 0.09
(N = 40)		α ns	α ns	α ns	α ns	α ns	α ns
Bill width	2.23	β = -0.22	β = -0.14	β = -0.23	β = -0.29	β = 0.11	β = 0.02
(N = 39)		α ns	α ns	α ns	α ns	α .	α ns
Bill depth	2.61	β = 0.12	β = 0.26	β = 0.38	β = 0.09	β = 0.05	β = -0.01
(N = 39)		α ns	α ns	α ns	α ns	α ns	α ns
Tarsus length	23.84	β = 0.43	β = -0.07	β = 0.62	β = 1.11	β = 0.51	β = -0.17
(N = 39)		α ns	α ns	α ns	α ns	α *	α ns
Tarsus width	0.81	β = -0.35	β = -0.36	β = -0.45	β = -0.35	β = 0.12	β = -0.01
(N = 36)		α *	α ns	α ns	α ns	α *	α ns
Tail length	41.25	β = 0.59	β = 2.32	β = 0.48	β = 2.72	β = 0.73	β = -0.31
(N = 37)		α ns	α ns	α ns	α ns	α ns	α ns

Weight	-7.09	β = 1.05	β = 2.78	β = 2.34	β = 0.58	NA	β = 0.32
(N = 42)		α ns	α ***	α **	α ns		α **

Table S7. Differences in the morphological measurements between the subspecies in the museum Wren dataset (n=117). Each row corresponds to a trait that was tested using the function *lm(trait ~ subspecies + latitude*). See Methods for more details. First data column represents the intercept values for *indigenus* subspecies. β represents the coefficient as reported by the output of *summary(lm*) and corresponds to: i) difference between that subspecies and *indigenus*; or ii) the slope of the gradient (for latitude). Sample sizes for each comparison are provided for each model examined, as they varied due to data missingness. Significance levels for α are coded as follows: *** - p-value < 0.001; ** - p-value < 0.01; * - p-value <0.05; . – p-value < 0.1; ns – non-significant. P-values are reported after Bonferroni correction for multiple comparisons.

Trait tested	**British Wren**	**Hebridean Wren**	**St Kilda Wren**	**Shetland Wren**	**Fair Isle Wren**	**latitude**
Wing length	β = 61.19	β = 1.96	β = 5.22	β = 6.12	β = 3.62	β = -0.27
(N = 116)		α .	α ***	α ***	α *	α ns
Bill length	β = 12.33	β = -0.20	β = -1.38	β = 1.63	β = 0.62	β = -0.04
(N = 115)		α ns	α ***	α ***	α ns	α ns
Bill width	β = 4.35	β = 0.13	β = 0.25	β = 0.34	β = 0.27	β = 0.03
(N = 115)		α ns	α ns	α ns	α ns	α ns
Bill depth	β = 4.26	β = 0.22	β = 0.49	β = 0.52	β = 0.41	β = -0.03
(N = 115)		α *	α ***	α ***	α ***	α ns
Tarsus length	β = 18.96	β = 0.05	β = 1.53	β = 1.80	β = 0.85	β = -0.01
(N = 117)		α ns	α **	α *	α ns	α ns
Tarsus width	β = 3.32	β = 0.11	β = 0.33	β = 0.38	β = 0.24	β = -0.03
(N = 117)		α .	α ***	α **	α *	α .
Tail length	β = 41.19	β = 0.52	β = 2.74	β = 3.88	β = -0.25	β = -0.20
(N = 114)		α ns	α *	α *	α ns	α ns

Table S8. Loadings of the morphological PCA of the live Wren dataset (see **Fig. S7**).

Trait tested	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Wing length	0.46	-0.24	0.31	-0.1	0.09	-0.56	0.55
Bill length	0.35	0.62	-0.12	0.14	-0.05	-0.51	-0.44
Bill depth	0.43	0.33	-0.01	-0.06	-0.62	0.45	0.34
Bill width	0.3	-0.27	-0.27	0.86	0.1	0.13	0.05
Tarsus length	0.43	0.2	0.26	-0.15	0.69	0.46	-0.1
Tarsus width	0.27	-0.21	-0.82	-0.43	0.13	-0.03	0.03
Tail length	0.37	-0.54	0.26	-0.15	-0.33	0.05	-0.61

Table S9. Loadings of the morphological PCA of the museum Wren dataset (see **Fig. 3**).

Trait tested	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Wing length	-0.46	0.28	-0.12	0.19	-0.07	-0.2	-0.78
Bill length	-0.42	-0.03	0.01	0.14	0.68	-0.47	0.33
Bill depth	-0.38	-0.31	0.15	0.59	-0.55	-0.05	0.29
Bill width	-0.25	-0.59	-0.7	-0.19	0.07	0.24	-0.07
Tarsus length	-0.37	-0.21	0.59	-0.12	0.26	0.6	-0.15
Tarsus width	-0.39	0.03	0.15	-0.74	-0.39	-0.32	0.16
Tail length	-0.33	0.65	-0.32	0.04	-0.04	0.47	0.37

Table S10. Differences in the vocal measurements between the subspecies in the song dataset (n=55). Each row corresponds to a trait that was tested using the function *lm(trait ~ subspecies + latitude*). See Methods for more details. First data column represents the intercept values for *indigenus* subspecies. β represents the coefficient as reported by the output of *summary(lm*) and corresponds to: i) difference between that subspecies and *indigenus*; or ii) the slope of the gradient (for latitude). NB: all sample sizes equal in this table. Significance levels for α are coded as follows: *** - p-value < 0.001; ** - p-value < 0.01; * - p-value <0.05; . – p-value < 0.1; ns – non-significant. P-values are reported after Bonferroni correction for multiple comparisons.

Trait tested	British Wren	Hebridean Wren	St Kilda Wren	Shetland Wren	Fair Isle Wren	latitude
Bandwidth A	β = 2391.39	β = 162.68 α ns	β = -652.77 α *	β = 340.17 α ns	β = 350.95 α ns	β = -0.65 α ns
Bandwidth B	β = 7828.26	β = -287.56 α ns	β = -741.58 α **	β = -56.71 α ns	β = -176.41 α ns	β = -108.64 α .
Entropy A	β = 5.79	β = 0.39 α ns	β = -0.22 α ns	β = 0.69 α *	β = 0.54 α ns	β = -0.03 α ns
Entropy B	β = 7.50	β = -0.30 α ns	β = -0.89 α ***	β = -0.24 α ns	β = -0.21 α ns	β = -0.06 α ns
Duration A	β = 1.22	β = 0.22 α **	β = 0.13 α ns	β = 0.34 α *	β = 0.46 α **	β = -0.02 α ns
Duration B	β = 0.74	β = 0.07 α ns	β = 0.31 α ***	β = 0.06 α ns	β = -0.08 α ns	β = 0.00 α ns
Peak A	β = 2368.92	β = -638.90 α *	β = -978.04 α **	β = -981.61 α *	β = -1298.67 α **	β = 63.35 α **
Peak B	β = 3377.65	β = -18.87 α ns	β = -234.13 α ns	β = -632.13 α ns	β = -671.65 α ns	β = 35.47 α ns

Centre A	β = 4374.23	β = -396.51	β = -810.92	β = -653.89	β = -1006.21	β = 27.35
		α ns	α **	α ns	α .	α ns
Centre B	β = 4930.14	β = -85.12	β = -241.24	β = -580.63	β = -649.56	β = 8.85
		α ns	α ns	α ns	α ns	α ns
C	β = 7.90	β = -0.35	β = 0.04	β = -0.05	β = -0.86	β = -0.12
		α ns	α ns	α ns	α ns	α ns
D	β = -0.14	β = 1.17	β = 1.36	β = 1.24	β = 1.65	β = 0.00
		α ***	α ***	α **	α **	α ns

Table S11. Loadings of the vocal PCA of Wren recordings. The tested traits were averaged per element and individual (see Methods). C and D refer to the mean number of either element per song.

Trait tested	*PC1*	*PC2*	*PC3*	*PC4*	*PC5*	*PC6*	*PC7*	*PC8*	*PC9*	*PC10*	*PC11*	*PC12*
Bandwidth A	-0.1	0.51	-0.11	-0.26	0.2	-0.18	-0.12	0.32	-0.64	0.2	-0.02	-0.06
Bandwidth B	0.29	0.32	0.36	-0.12	-0.13	0.38	0.23	0.01	-0.17	-0.53	-0.13	0.35
Entropy A	-0.12	0.47	-0.3	-0.25	0.05	-0.25	0.14	0.24	0.64	-0.25	0.05	0.04
Entropy B	0.32	0.35	0.25	-0.1	-0.11	0.37	0.11	-0.03	0.26	0.58	0.22	-0.3
Peak A	0.37	0.11	-0.29	0.35	-0.26	-0.22	0.06	-0.06	-0.19	-0.15	0.67	0.05
Peak B	0.31	-0.19	-0.36	-0.46	0.07	0.06	-0.08	-0.17	0.03	0.31	0.01	0.62
Duration A	-0.36	0.31	-0.02	-0.13	-0.09	-0.09	0.07	-0.85	-0.09	-0.02	0.04	-0.03
Duration B	-0.12	-0.21	0.14	-0.47	-0.77	-0.22	0.07	0.17	-0.08	0.01	0.04	-0.12
Centre A	0.35	0.16	-0.35	0.28	-0.31	-0.15	0.14	-0.09	-0.03	0.12	-0.68	-0.13
Centre B	0.35	-0.2	-0.25	-0.42	0.25	0.12	0	-0.15	-0.08	-0.36	0.02	-0.6
C	0.26	-0.11	0.41	-0.08	0.31	-0.6	0.52	-0.08	-0.01	0.1	-0.01	0.04
D	-0.32	-0.14	-0.34	0.03	0.03	0.34	0.77	0.13	-0.15	0.1	0.08	0

Table S12. Genes present in significantly differentiated (see Methods) 100kb windows in the genomes of St Kilda Wrens. Windowed F_{ST} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	Panther GO-Slim biological process	Window F_{ST}	Scaffold
Abca1_2	phospholipid transport	0.61	VZTB01013939.1
Adamtsl1	proteolysis extracellular matrix organization	0.47	VZTB01003828.1
Adipor2	cytokine-mediated signalling pathway hormone-mediated signalling pathway	0.48	VZTB01003382.1
Ankra2	regulation of gene expression	0.49	VZTB01002497.1
Btf3_0	*uncharacterised*	0.49	VZTB01002497.1
C2cd5	regulation of protein localization to membrane; regulation of intracellular protein transport; protein localization to plasma membrane; positive regulation of protein transport; intracellular protein transmembrane transport; regulation of vesicle-mediated transport; positive regulation of organelle organization; positive regulation of transmembrane transport	0.49	VZTB01000027.1
Clta	clathrin-dependent endocytosis	0.53	VZTB01004974.1
Cps1	alpha-amino acid metabolic process	0.48	VZTB01000056.1
Eva1c_0	*uncharacterised*	0.48	VZTB01001861.1
Gne	*uncharacterised*	0.53	VZTB01004974.1
Gpatch4	*uncharacterised*	0.48	VZTB01005215.1
Grm7_0	*unmapped*	0.48	VZTB01008522.1
Iqgap3	epidermal growth factor receptor signalling pathway; actomyosin contractile ring assembly; ameboidal-type cell migration; actin filament organization;	0.48	VZTB01005215.1

	positive regulation of protein kinase activity; mitotic cytokinetic process		
Lamtor2	cellular response to organonitrogen compound; positive regulation of TOR signalling; cellular response to oxygen-containing compound; response to amino acid	0.48	VZTB01005215.1
Map1a	regulation of protein depolymerization; axonogenesis; regulation of supramolecular fiber organization; regulation of microtubule polymerization or depolymerization; microtubule cytoskeleton ;organization dendrite development	0.55	VZTB01013398.1
Mex3a	*uncharacterised*	0.48	VZTB01005215.1
Nans	glycosylation	0.53	VZTB01004974.1
Naxe	*unmapped*	0.48	VZTB01005215.1
Nipsnap3a	*uncharacterised*	0.61	VZTB01013939.1
Ppip5k1	alcohol biosynthetic process; organophosphate biosynthetic process; phosphate-containing compound metabolic process	0.55	VZTB01013398.1
Rab11a_0	pigmentation; exocytosis; protein localization to plasma membrane; establishment of vesicle localization; intracellular protein transport; neurotransmitter receptor transport to postsynaptic membrane; endocytic recycling	0.48	VZTB01005215.1
Rab25	exocytosis	0.48	VZTB01005215.1
Rorb_2	*unmapped*	0.49	VZTB01010727.1
Serpina1_0	*unmapped*	0.49	VZTB01012398.1
Serpina1_1	*unmapped*	0.49	VZTB01012398.1
Serpina5	*unmapped*	0.49	VZTB01012398.1

Serpina7	*unmapped*	0.49	VZTB01012398.1
St8sia1	*unmapped*	0.53	VZTB01000027.1
Ttc24	*uncharacterised*	0.48	VZTB01005215.1
Ubqln4	ubiquitin-dependent protein catabolic process	0.48	VZTB01005215.1
Utp15	rRNA processing; positive regulation of transcription by RNA polymerase I	0.49	VZTB01002497.1
Wnt5b	neuron differentiation; cell fate commitment; canonical Wnt signaling pathway	0.48	VZTB01003382.1

Table S13. Genes present in significantly differentiated (see Methods) 100kb windows in the genomes of Shetland Wrens. Windowed F_{ST} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	Panther GO-Slim biological process	Window F_{ST}	Scaffold
Abca1_2	phospholipid transport	0.65	VZTB01013939.1
Abhd5	*unmapped*	0.39	VZTB01010561.1
Abra_1	regulation of Rho protein signal transduction; positive regulation of DNA-binding transcription factor activity; positive regulation of transcription by RNA polymerase II; positive regulation of Ras protein signal transduction	0.45	VZTB01010714.1
Arl15	*unmapped*	0.63	VZTB01014370.1
Arsg	*uncharacterised*	0.41	VZTB01012743.1
Brinp3	cellular response to lipid; cellular response to oxygen-containing compound; nervous system development; negative regulation of mitotic cell cycle	0.63	VZTB01000544.1
Cdc37l1_0	protein stabilization; protein folding	0.51	VZTB01002440.1
Chrna6	monoatomic ion transmembrane transport; chemical synaptic transmission; nervous system process; regulation of membrane potential; signal transduction	0.41	VZTB01003133.1
Chrnb3	monoatomic ion transmembrane transport; response to chemical; chemical synaptic transmission; nervous system process; regulation of membrane potential;	0.41	VZTB01003133.1

	signal transduction		
Dennd1a	endocytosis;	0.41	VZTB01004456.1
	endocytic recycling		
Dmrt3	regulation of transcription by RNA polymerase II;	0.4	VZTB01008526.1
	male sex differentiation		
Eys_2	*unmapped*	0.4	VZTB01006079.1
Fnta	cellular metabolic process;	0.53	VZTB01016552.1
	protein modification process		
Fut10	glycosylation	0.53	VZTB01016552.1
Gab3	signal transduction	0.4	VZTB01014845.1
Gak_0	*unmapped*	0.42	VZTB01003133.1
Glis3	regulation of transcription by RNA polymerase II	0.46	VZTB01005252.1
Gna13	Rho protein signal transduction;	0.41	VZTB01012743.1
	positive regulation of phospholipase activity;		
	adenylate cyclase-activating G protein-coupled receptor		
	signaling pathway		
Grem1	animal organ morphogenesis;	0.41	VZTB01012906.1
	negative regulation of BMP signaling pathway		
Gys2	glycogen biosynthetic process	0.4	VZTB01004976.1
Ibsp	extracellular matrix organization;	0.45	VZTB01014358.1
	bone mineralization		
Ichy	*unmapped*	0.4	VZTB01003263.1
Inpp4b	*uncharacterised*	0.43	VZTB01012397.1
Kif24	*unmapped*	0.39	VZTB01001008.1
Ld	*uncharacterised*	0.41	VZTB01012906.1
Lpl	multicellular organismal process;	0.74	VZTB01003133.1
	fatty acid biosynthetic process;		
	regulation of biological process;		
	protein-containing complex organization;		
	triglyceride catabolic process		
Lrmp	*uncharacterised*	0.4	VZTB01004976.1

Mast4_0	cytoskeleton organization; intracellular signal transduction; peptidyl-serine phosphorylation	0.45	VZTB01002881.1
Mast4_1	cytoskeleton organization; intracellular signal transduction; peptidyl-serine phosphorylation	0.44	VZTB01018233.1
Mgat4c_1	protein N-linked glycosylation	0.41	VZTB01007850.1
Musk	multicellular organism development; positive regulation of cellular component organization; transmembrane receptor protein tyrosine kinase signalling pathway; positive regulation of phosphatidylinositol 3-kinase signalling; positive regulation of kinase activity; regulation of neuron projection development	0.49	VZTB01014293.1
Nfib	regulation of transcription by RNA polymerase II	0.42	VZTB01018219.1
Nipsnap3a	*uncharacterised*	0.65	VZTB01013939.1
Npr1_0	enzyme-linked receptor protein signaling pathway; cGMP biosynthetic process	0.4	VZTB01016696.1
Ntrk2_0	cellular response to growth factor stimulus; multicellular organism development; regulation of protein kinase B signalling; modulation of chemical synaptic transmission; positive regulation of cellular component organization; transmembrane receptor protein tyrosine kinase signalling pathway; positive regulation of phosphatidylinositol 3-kinase signalling; positive regulation of kinase activity; trans-synaptic signalling; regulation of neuron projection development	0.43	VZTB01005066.1

Nts	*uncharacterised*	0.41	VZTB01007850.1
Nudt2	nucleoside monophosphate metabolic process; ATP biosynthetic process	0.39	VZTB01001008.1
Oc116	biomineral tissue development	0.45	VZTB01014358.1
Osmr	*uncharacterised*	0.43	VZTB01008013.1
Otp	neuron differentiation	0.38	VZTB01012904.1
Oxr1	response to oxidative stress	0.45	VZTB01010714.1
Pcdh17	cell adhesion	0.4	VZTB01003720.1
Picalm_0	synaptic vesicle transport; vesicle budding from membrane; clathrin-dependent endocytosis; synaptic vesicle endocytosis	0.4	VZTB01014845.1
Pik3r1_0	insulin receptor signaling pathway; phosphatidylinositol phosphate biosynthetic process; regulation of phosphatidylinositol 3-kinase activity	0.56	VZTB01002881.1
Pkd2	signaling receptor binding; cytoskeletal protein binding; potassium channel activity; voltage-gated calcium channel activity; calcium ion binding sodium channel activity	0.45	VZTB01014358.1
Psd3	*unmapped*	0.41	VZTB01003133.1
Rcl1	endonucleolytic cleavage of tricistronic rRNA transcript (SSU-rRNA, 5.8S rRNA, LSU-rRNA)	0.51	VZTB01002440.1
Rgs7bp	G protein-coupled receptor signalling pathway	0.41	VZTB01003780.1
Sema3a_2	regulation of cell size; neural crest cell migration; negative regulation of response to external stimulus; negative regulation of locomotion; cell surface receptor signalling pathway; regulation of chemotaxis;	0.39	VZTB01009943.1

	negative regulation of multicellular organismal process; motor neuron axon guidance; positive regulation of cell migration; regulation of neurogenesis; regulation of axonogenesis; regulation of cell growth; negative regulation of cellular component organization		
Sh3gl2	synaptic vesicle endocytosis; protein depolymerization	0.4	VZTB01001747.1
Slc16a6	monocarboxylic acid transport	0.41	VZTB01012743.1
Slc26a1	*uncharacterised*	0.41	VZTB01003133.1
Spp1	*uncharacterised*	0.45	VZTB01014358.1
Spx	*uncharacterised*	0.4	VZTB01004976.1
Ssbp2	positive regulation of transcription by RNA polymerase II	0.42	VZTB01015680.1
Tbca	*uncharacterised*	0.38	VZTB01012904.1
Thap1	*uncharacterised*	0.41	VZTB01003133.1
Tmem215	*unmapped*	0.4	VZTB01016696.1
Tspan3	*uncharacterised*	0.47	VZTB01001724.1
Ubap1_0	ubiquitin-dependent protein catabolic process via the multivesicular body sorting pathway	0.39	VZTB01001008.1
Vcan	central nervous system development; skeletal system development; positive regulation of neurogenesis; positive regulation of transcription by RNA polymerase II; glial cell differentiation; positive regulation of cell population proliferation	0.39	VZTB01009111.1
Wipi1	protein lipidation; autophagy of nucleus; autophagy of mitochondrion; autophagosome assembly; protein localization	0.41	VZTB01012743.1

Table S14. Genes present in significantly differentiated (see Methods) 100kb windows that are shared between Hebridean and St Kilda Wrens. Windowed F_{ST} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	**Panther GO-Slim biological process**	**Window F_{ST} (Hebridean)**	**Window F_{ST} (St Kilda)**	**Scaffold**
Bcl9l	negative regulation of signal transduction; canonical Wnt signalling pathway; regulation of transforming growth factor beta receptor signalling pathway; positive regulation of transcription by RNA polymerase II	0.1	0.6	VZTB01008020.1
Ccdc84	*uncharacterised*	0.1	0.6	VZTB01008020.1
Cxcr5	cell chemotaxis; positive regulation of cytosolic calcium ion concentration; immune response; calcium-mediated signalling	0.1	0.6	VZTB01008020.1
Ddx6	negative regulation of translation; P-body assembly	0.1	0.6	VZTB01008020.1
Nrep	regulation of neuron differentiation; regeneration response to wounding; regulation of transforming growth factor beta receptor signalling pathway; axon development cellular response to stress	0.18	0.87	VZTB01007081.1
Rps25	*uncharacterised*	0.1	0.6	VZTB01008020.1
Stard4	intracellular cholesterol;	0.18	0.87	VZTB01007081.1

transport

lipid storage

Table S15. Genes present in 100kb genomic windows that show significant absolute divergence, and that are shared between St Kilda and Shetland Wren. Windowed d_{xy} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	**Panther GO-Slim biological process**	**Window d_{xy} (Shetland)**	**Window d_{xy} (St Kilda)**	**Scaffold**
Adamtsl1	proteolysis; extracellular matrix organization	0.36	0.54	VZTB01003828.1
Ak6	*uncharacterised*	0.36	0.37	VZTB01007295.1
Ccdc125	*uncharacterised*	0.36	0.37	VZTB01007295.1
Emc4	*unmapped*	0.36	0.37	VZTB01007295.1
Exosc5	*unmapped*	0.36	0.37	VZTB01007295.1
Fam151b	*uncharacterised*	0.36	0.37	VZTB01007295.1
Lpl	multicellular organismal process; fatty acid biosynthetic process; regulation of biological process; protein-containing complex organization; triglyceride catabolic process	0.39	0.39	VZTB01003133.1
Rad17	DNA repair; DNA damage checkpoint signalling; mitotic DNA replication checkpoint signalling	0.36	0.37	VZTB01007295.1
Zfyve16_0	endosomal transport	0.36	0.37	VZTB01007295.1
Zfyve16_1	endosomal transport	0.36	0.37	VZTB01007295.1

Table S16. Genes present in 100kb genomic windows that show significant absolute divergence in St Kilda Wrens. Windowed d_{xy} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	Panther GO-Slim biological process	Window d_{xy}	Scaffold
Bcl9l	negative regulation of signal transduction; canonical Wnt signalling pathway; regulation of transforming growth factor beta receptor signaling pathway; positive regulation of transcription by RNA polymerase II	0.41	VZTB01008020.1
Card19	*uncharacterised*	0.38	VZTB01012128.1
Ccdc84	*uncharacterised*	0.41	VZTB01008020.1
Cenpk	*mitotic sister chromatid segregation*	0.38	VZTB01013327.1
Cxcr5	cell chemotaxis; positive regulation of cytosolic calcium ion concentration; immune response; calcium-mediated signalling	0.41	VZTB01008020.1
Ddx6	negative regulation of translation; P-body assembly	0.41	VZTB01008020.1
Lpl	multicellular organismal process; fatty acid biosynthetic process; regulation of biological process; protein-containing complex organization; triglyceride catabolic process	0.39	VZTB01003133.1
Nfib	regulation of transcription by RNA polymerase II	0.38	VZTB01018219.1
Rps25	*uncharacterised*	0.41	VZTB01008020.1
Sncaip	*uncharacterised*	0.39	VZTB01009797.1
Susd3	*uncharacterised*	0.38	VZTB01012128.1
Wnk2	negative regulation of monoatomic ion transport;	0.4	VZTB01012128.1

positive regulation of monoatomic ion transmembrane transport;

monoatomic ion homeostasis;

intracellular signal transduction;

regulation of potassium ion transmembrane transport;

regulation of sodium ion transport;

protein phosphorylation

Table S17. Genes present in 100kb genomic windows that show significant absolute divergence in Shetland Wrens. Windowed d_{xy} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	Panther GO-Slim biological process	Window d_{xy}	Scaffold
Acr_8	*unmapped*	0.36	VZTB01015045.1
Adamtsl1	proteolysis; extracellular matrix organization	0.36	VZTB01003828.1
Ak6	*uncharacterised*	0.36	VZTB01007295.1
Ccdc125	*uncharacterised*	0.36	VZTB01007295.1
Cdc37l1_0	*unmapped*	0.4	VZTB01002440.1
Dmrt3	regulation of transcription by RNA polymerase II; male sex differentiation	0.39	VZTB01008526.1
Emc4	*unmapped*	0.36	VZTB01007295.1
Exosc5	*unmapped*	0.36	VZTB01007295.1
Eys_2	*unmapped*	0.38	VZTB01006079.1
Fam151b	*uncharacterised*	0.36	VZTB01007295.1
Glis3	regulation of transcription by RNA polymerase II	0.41	VZTB01005252.1
Ichy	*unmapped*	0.37	VZTB01003263.1
Kcnv2_0	*unmapped*	0.36	VZTB01015045.1
Lpl	multicellular organismal process; fatty acid biosynthetic process; regulation of biological process; protein-containing complex organization; triglyceride catabolic process	0.39	VZTB01003133.1
Mast4_0	*unmapped*	0.37	VZTB01002881.1
Musk	multicellular organism development; positive regulation of cellular component organization;	0.41	VZTB01014293.1

	transmembrane receptor protein tyrosine kinase signalling pathway; positive regulation of phosphatidylinositol 3-kinase signalling; positive regulation of kinase activity regulation of neuron projection development		
Pik3r1_0	*unmapped*	0.38	VZTB01002881.1
Plcxd2	*uncharacterised*	0.36	VZTB01000554.1
Pum3	Regulation of translation	0.36	VZTB01015045.1
Rad17	DNA repair; DNA damage checkpoint signalling; mitotic DNA replication checkpoint signalling	0.36	VZTB01007295.1
Rcl1	endonucleolytic cleavage of tricistronic rRNA transcript (SSU-rRNA, 5.8S rRNA, LSU-rRNA)	0.4	VZTB01002440.1
Xrcc4	double-strand break repair via nonhomologous end joining; positive regulation of catalytic activity; response to ionizing radiation	0.41	VZTB01009111.1
Zfyve16_0	*unmapped*	0.36	VZTB01007295.1
Zfyve16_1	*unmapped*	0.36	VZTB01007295.1

Table S18. Genes present in 100kb genomic windows that show significant absolute divergence, and that are shared between St Kilda and Shetland Wrens. Windowed d_{xy} is calculated relative to the British Wren. Scaffolds are the scaffolds of the reference genome of the Carolina Wren (*Thryothurus ludovicianus* ASM1339724v1). NB: original spelling of GO-Slim terms maintained.

Name	**Panther GO-Slim biological process**	**Window d_{xy} (Hebridean)**	**Window d_{xy} (St Kilda)**	**Name**
Adamtsl1	proteolysis; extracellular matrix organization	0.43	0.54	VZTB01003828.1
Ak6	*uncharacterised*	0.36	0.37	VZTB01007295.1
Atp5l	proton motive force-driven ATP synthesis	0.35	0.39	VZTB01013366.1
Ccdc125	*uncharacterised*	0.36	0.37	VZTB01007295.1
Cldn22_1	*unmapped*	0.35	0.39	VZTB01013366.1
Crhbp	negative regulation of multicellular organismal process; regulation of signalling receptor activity; negative regulation of signal transduction; regulation of peptide hormone secretion; negative regulation of transport; hormone-mediated signalling pathway; regulation of system process;	0.36	0.37	VZTB01018021.1

	negative regulation of molecular function			
Emc4	*unmapped*	0.36	0.37	VZTB01007295.1
Exosc5	*unmapped*	0.36	0.37	VZTB01007295.1
F2rl1_1	*unmapped*	0.36	0.37	VZTB01018021.1
Fam151b	*uncharacterised*	0.36	0.37	VZTB01007295.1
Htr3a	*unmapped*	0.35	0.39	VZTB01013366.1
Kcnj5_1	*unmapped*	0.35	0.39	VZTB01013366.1
Kmt2a	histone lysine methylation; positive regulation of DNA-templated transcription	0.35	0.39	VZTB01013366.1
Rad17	DNA repair; DNA damage checkpoint signalling; mitotic DNA replication checkpoint signalling	0.36	0.37	VZTB01007295.1
S100z	*uncharacterised*	0.36	0.37	VZTB01018021.1
Ube4a	protein polyubiquitination; ubiquitin-dependent ERAD pathway	0.35	0.39	VZTB01013366.1
Usp28	protein deubiquitination; regulation of protein stability; DNA damage checkpoint signalling	0.35	0.39	VZTB01013366.1
Zbtb16	*unmapped*	0.35	0.39	VZTB01013366.1
Zbtb16a	*unmapped*	0.35	0.39	VZTB01013366.1
Zfyve16_0	*unmapped*	0.36	0.37	VZTB01007295.1

Zfyve16_1	*unmapped*	0.36	0.37	VZTB01007295.1

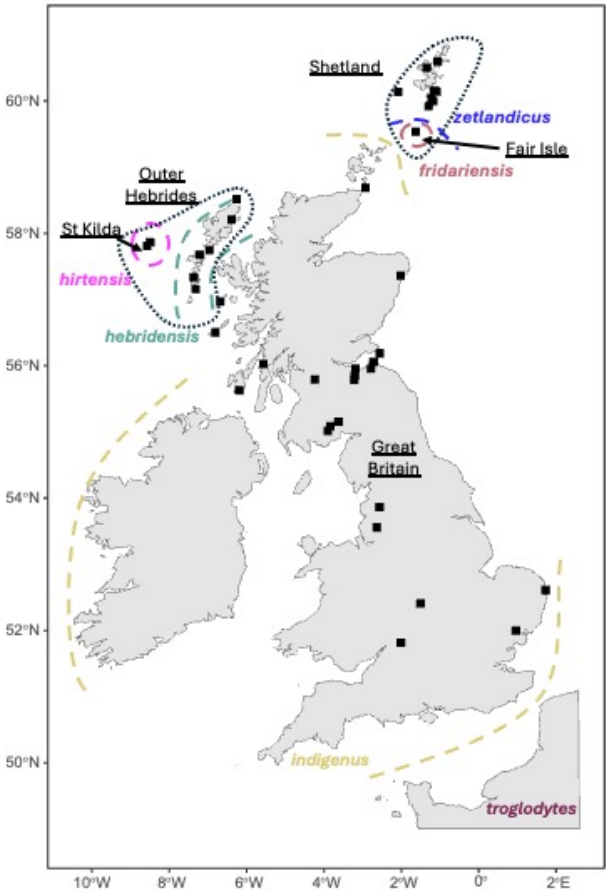

Fig. S1. Sampling locations of morphological data collected from museum specimens. Squares correspond to sampling locations of museum specimens (n = 117), to the nearest settlement or county centroid (see Methods). For equivalent maps of live data and song recordings see **Fig. 1** and **Fig. S2**. For details of sampling per site see Methods and **Table S2**). Each colour-coded dashed line shows the separation of the putative ranges of each subspecies considered in this manuscript, and is labelled with a colour-coded subspecific name. Black dotted lines demarcate the archipelagos of Shetland and the Outer Hebrides, with arrows pointing to Fair Isle and St Kilda. NB: there is point overlap for sites sampled at finer scale.

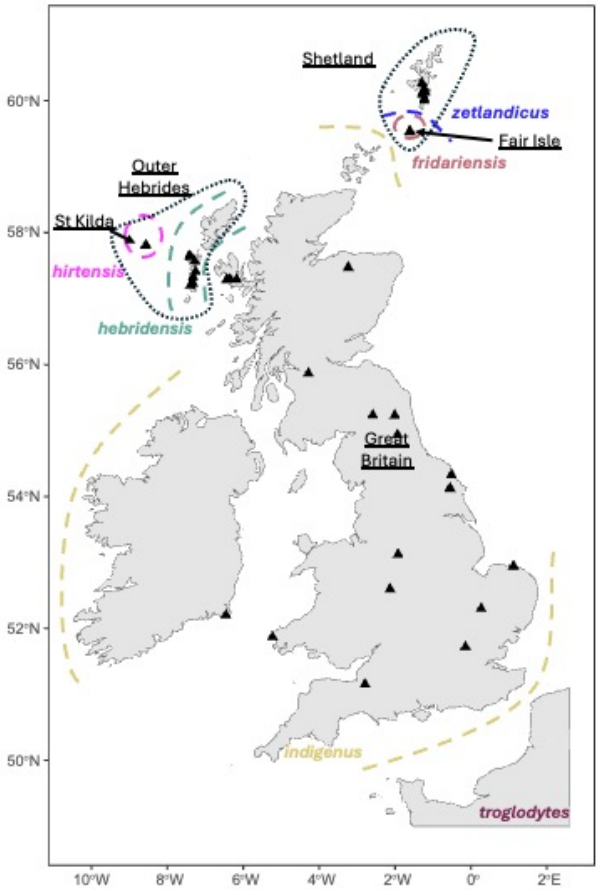

Fig. S2. The distribution of Wren song recording data. Triangles correspond to sampling locations of sound recorded birds (n = 56), (see Methods). For equivalent maps of live data and song recordings see **Fig. 1** and **Fig. S1**. For details of sampling per site see Methods and **Table S3**). Each colour-coded dashed line shows the separation of the putative ranges of each subspecies considered in this manuscript, and is labelled with a colour-coded subspecific name. Black dotted lines demarcate the archipelagos of Shetland and the Outer Hebrides, with arrows pointing to Fair Isle and St Kilda. NB: there is point overlap for sites sampled at finer scale.

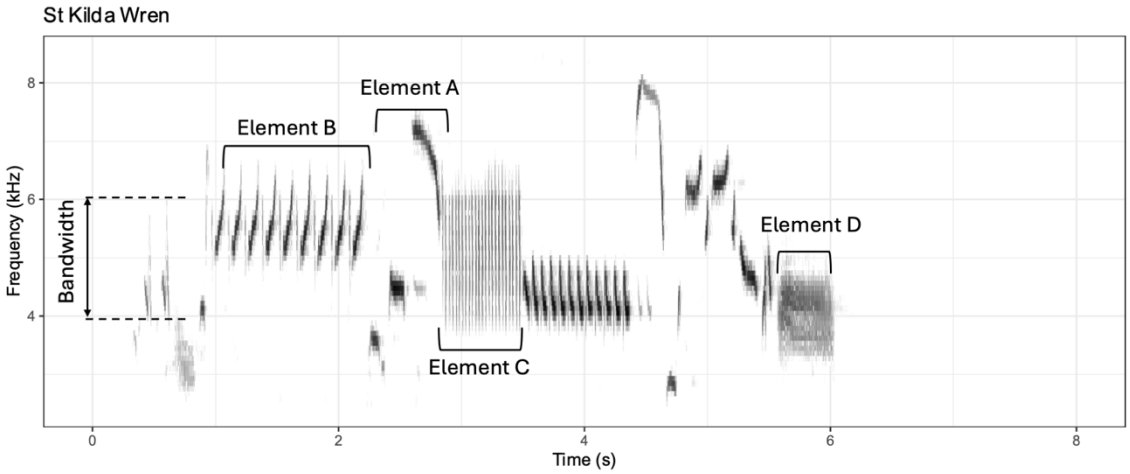

Fig S3. Example of a bout of Wren song (here: St Kilda) showing the four elements of song as defined by Hall-Craggs (Cramp 1988), and used in this study. See **Table S4** for descriptors of each element. In addition, one of the measures – bandwidth – is shown for clarification. It represents the difference between the maximum and minimum frequencies in an element.

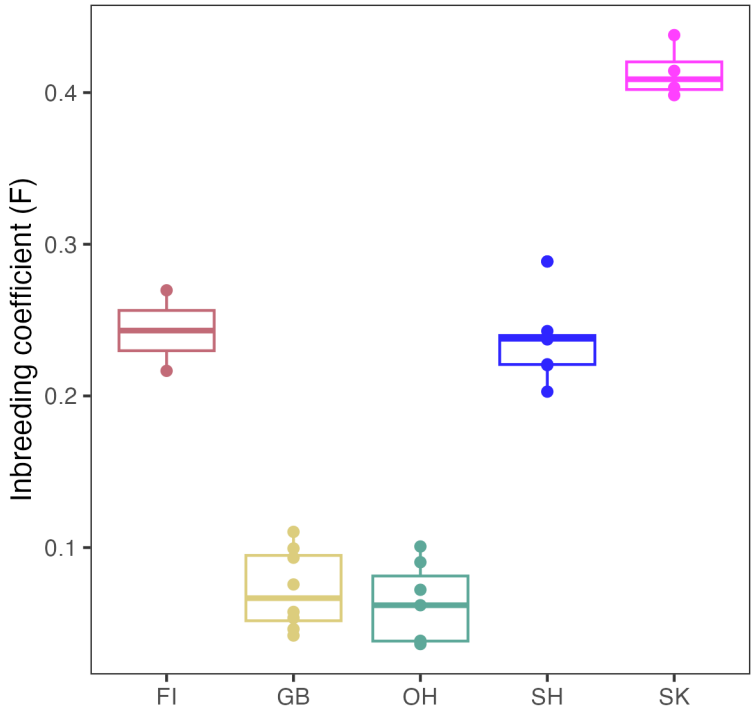

Fig. S4. Patterns of the inbreeding coefficient (see Methods) among the samples of live Wren (n = 29) show that the St Kilda Wren is more inbred than the other subspecies, and that there appears to be little difference in levels of inbreeding between the British and Hebridean Wrens. Population codes of the presumed subspecies: FI = Fair Isle; GB = British; OH = Hebridean; SH = Shetland; SK = St Kilda.

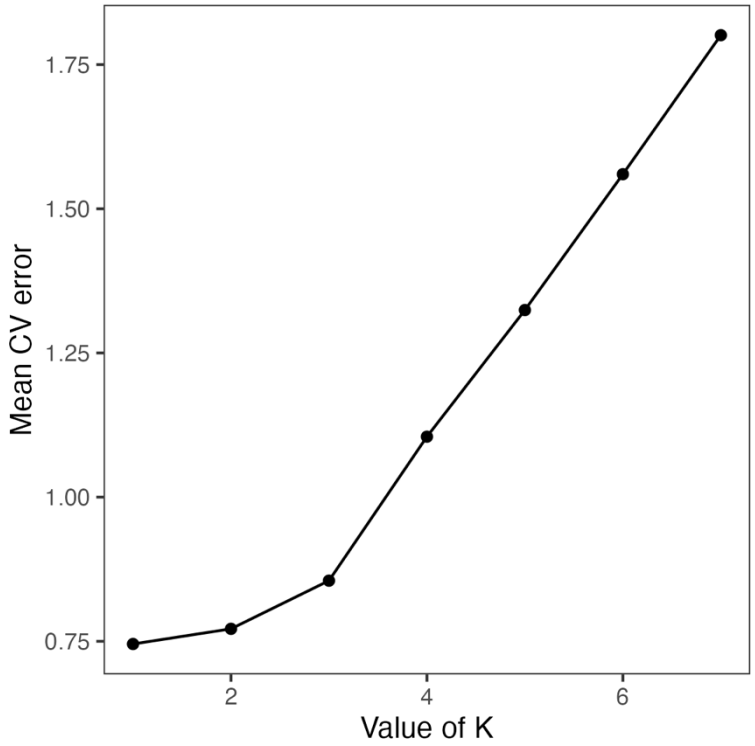

Fig. S5. Values of 5-fold cross-validation error for the ADMIXTURE runs as presented in **Fig. 2** and **Fig. S6**.

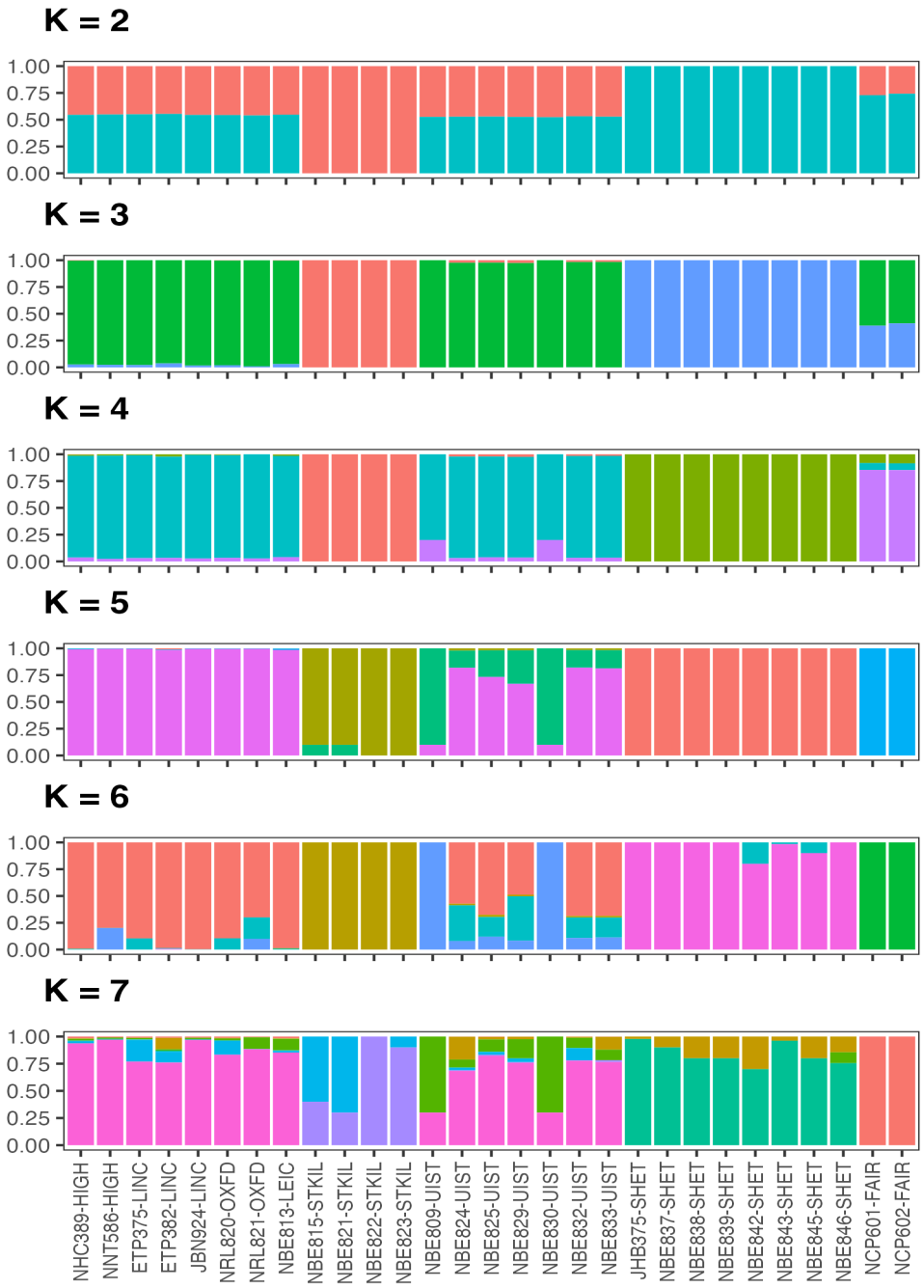

Fig S6. ADMIXTURE results at all tested K-values (K = 2 to K = 7) for all samples excluding the outgroup. For cross-validation error of each K score please refer to **Fig. S5**. Additional site codes point to the sampling location of birds: STKIL – St Kilda; UIST – Outer Hebrides; OXFD – Oxfordshire; HIGH – Highland; LEIC – Leicestershire; LINC – Lincolnshire; SHET – Shetland; FAIR – Fair Isle.

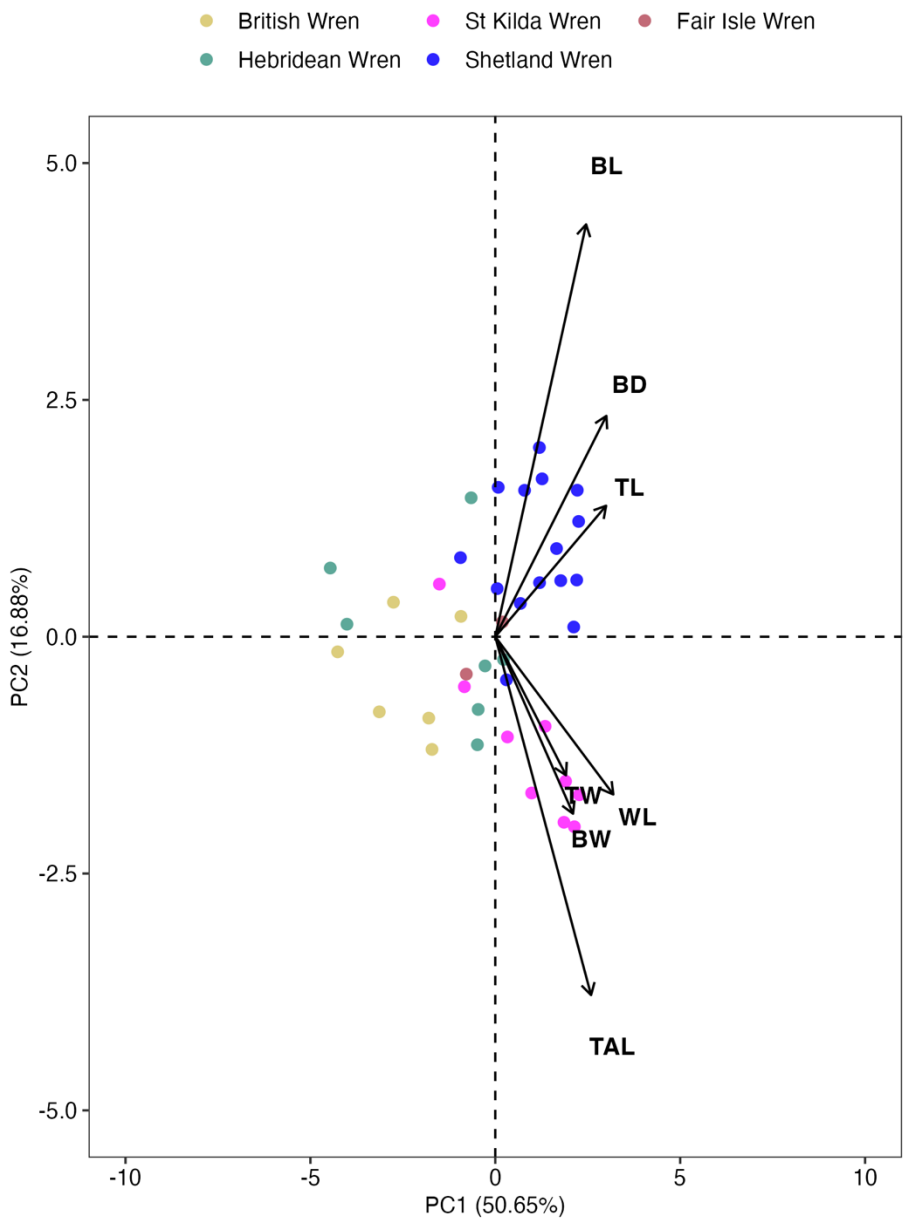

Fig. S7. Principal component analysis of morphology of Wren subspecies based on data from live specimens (n = 39). PC1 is a general body size component (**Table S8**) largely separating St Kilda and Shetland Wrens from the rest. Then along PC2 there is some separation between larger-billed and longer tarsus Shetland Wrens, compared to longer-winged and tailed St Kilda Wrens with wider bills and tarsi.

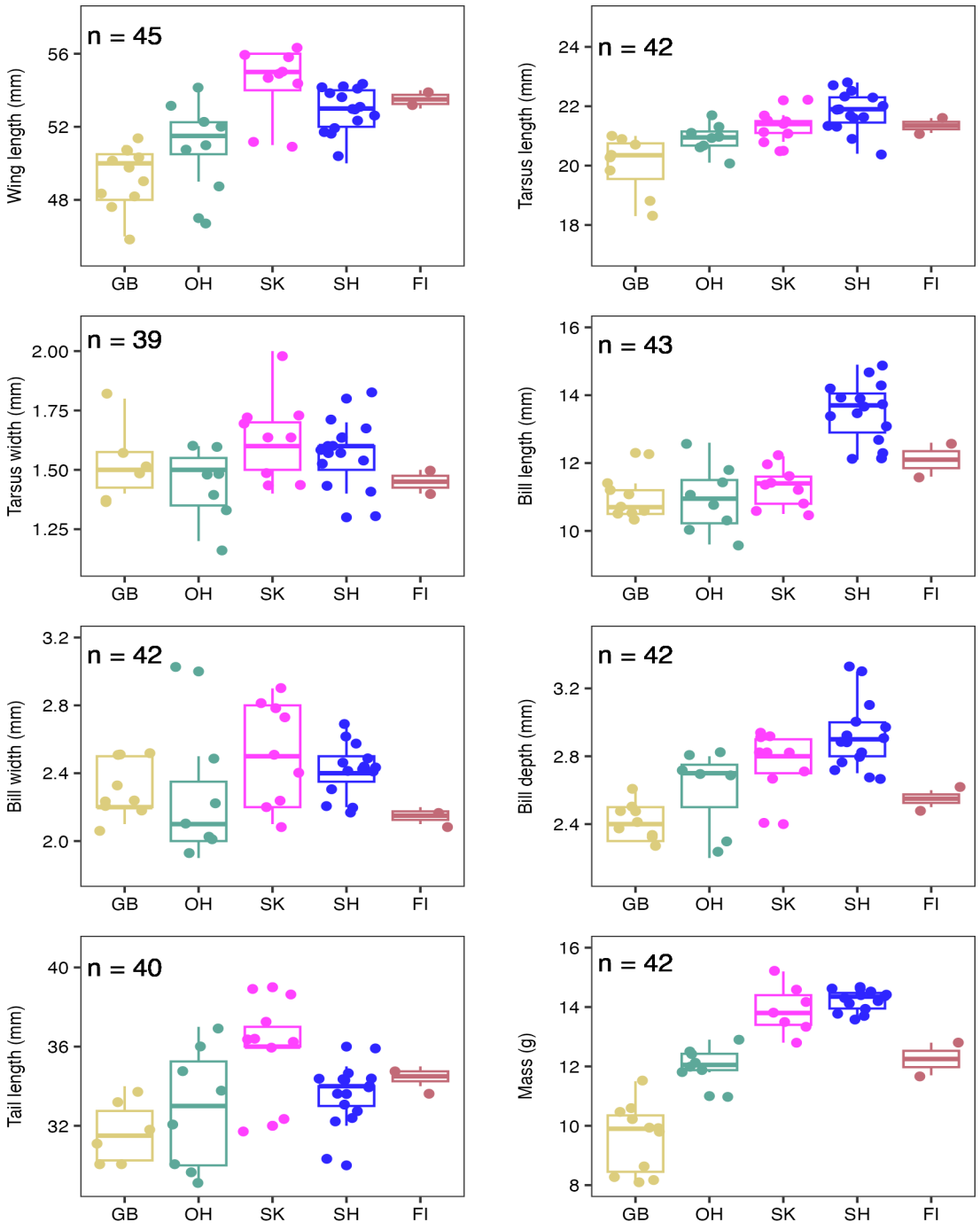

Fig. S8. Morphological comparisons between the Wrens of the live dataset (n = 45). Each of the measured traits is shown, with jitter added for clarity using function *geom_jitter()*. Sample sizes for individual trait comparisons are shown, as they vary due to data missingness (see Methods). For the significance of differences, once mass and latitudinal variation is accounted for, see **Table S6**.

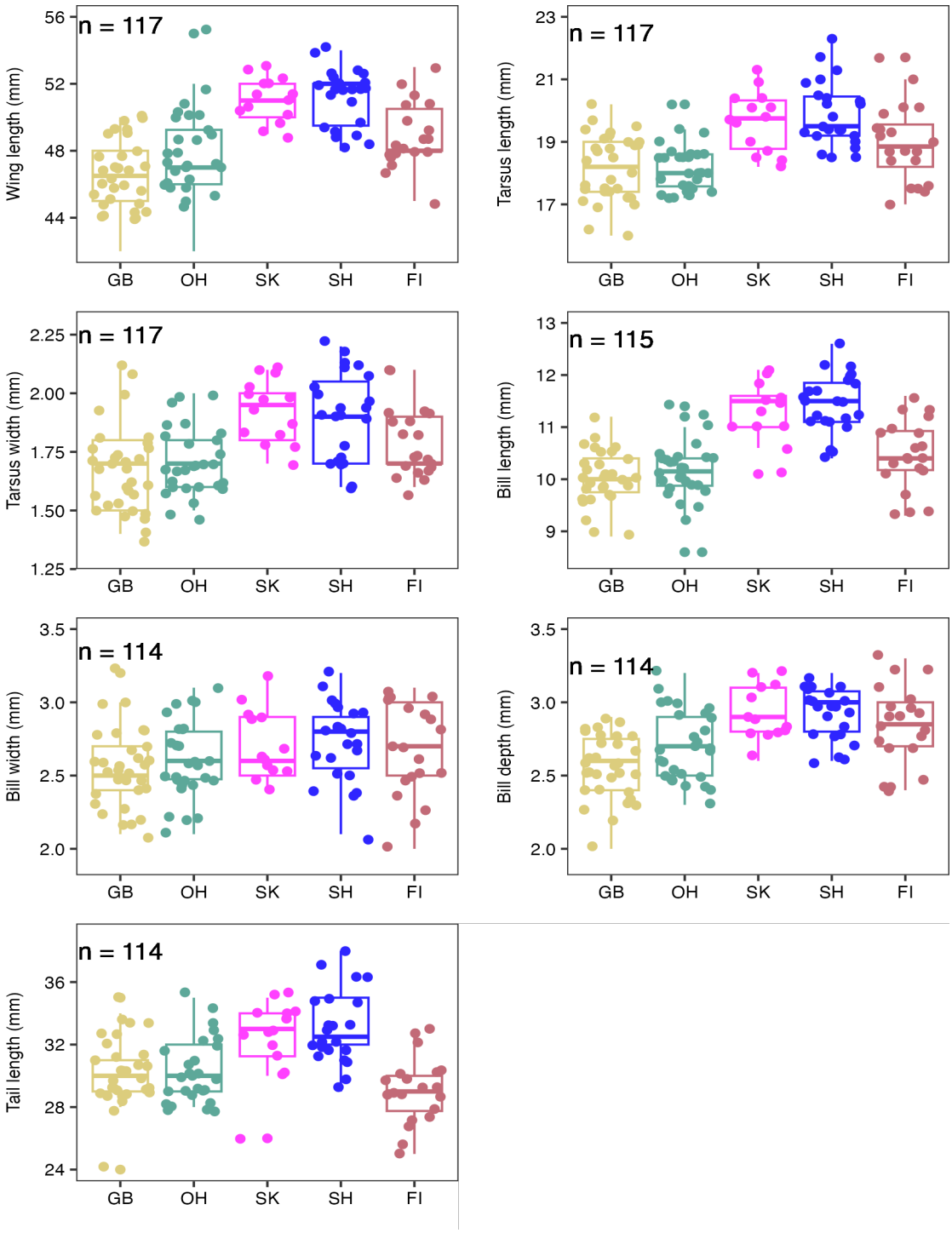

Fig. S9. Morphological comparisons between the Wrens of the museum dataset (n = 177). Each of the measured traits is shown, with jitter added for clarity using function *geom_jitter()*. Sample sizes for individual trait comparisons are shown, as they vary due to data missingness (see Methods). For the significance of differences, once mass and latitudinal variation is accounted for, see **Table S7**.

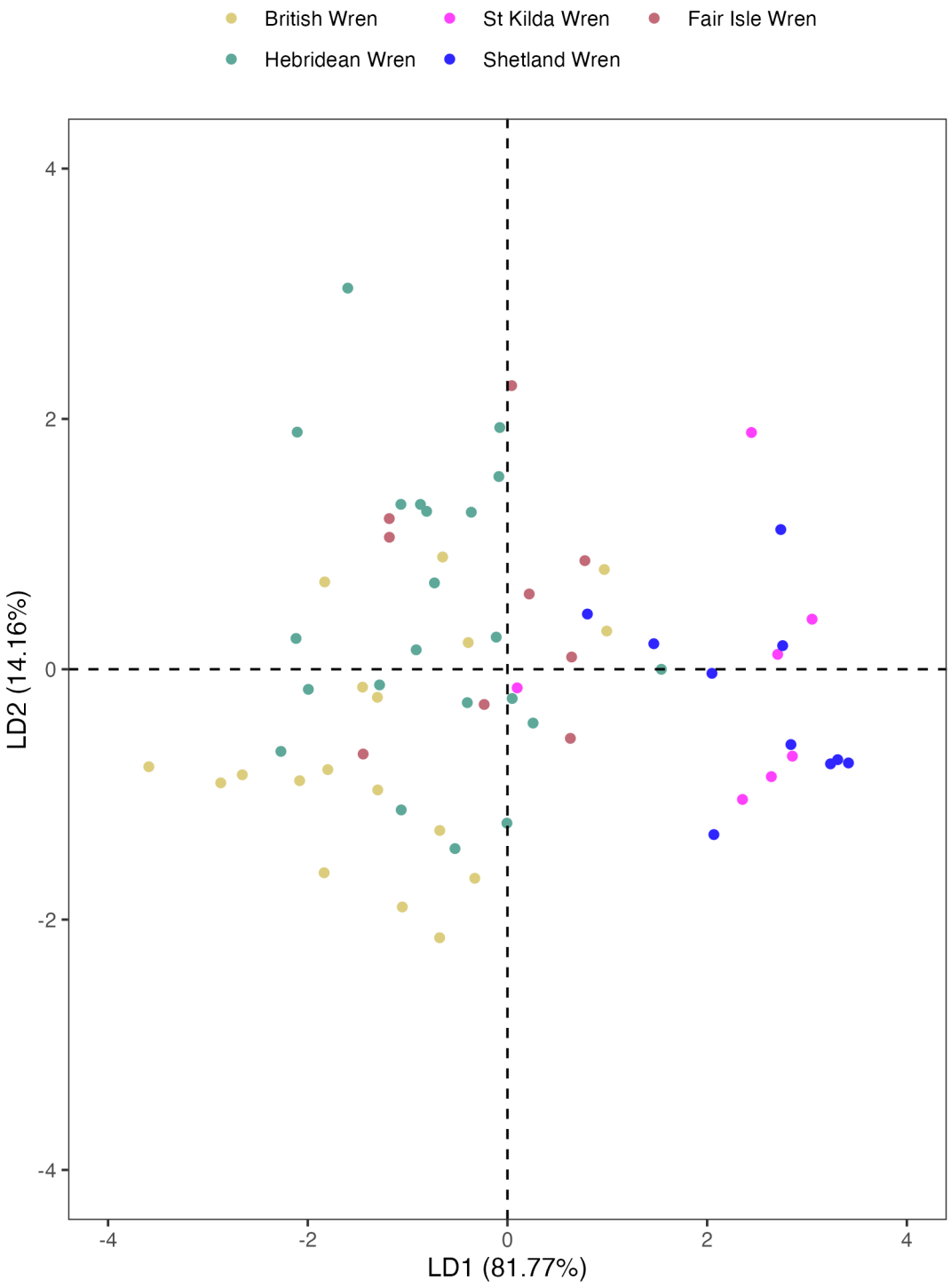

Fig. S10. Linear discriminant analysis of a training subsample (n = 72) of the museum specimen dataset (n = 117). This subsample was used to train the prediction of the LDA model presented in the main text. It shows substantial overlap primarily between Shetland and St Kilda Wrens, and Hebridean and British Wrens.

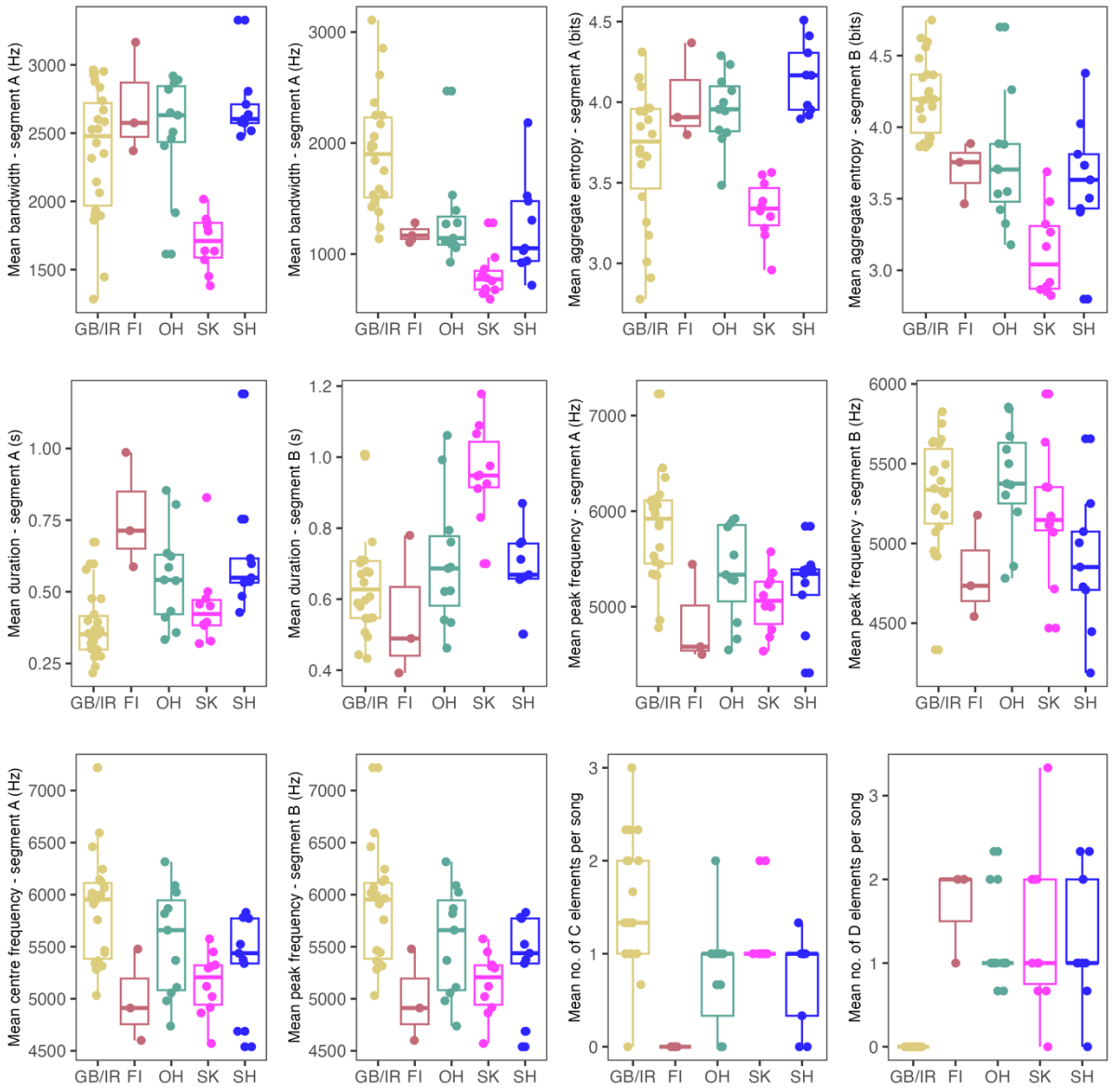

Fig. S11. Vocal comparisons between the Wrens of the song dataset (n = 56). Each of the measured traits is shown, with horizontal jitter added for clarity using function *geom_jitter()*. For the significance of differences, once latitudinal variation is accounted for see **Table S10**.

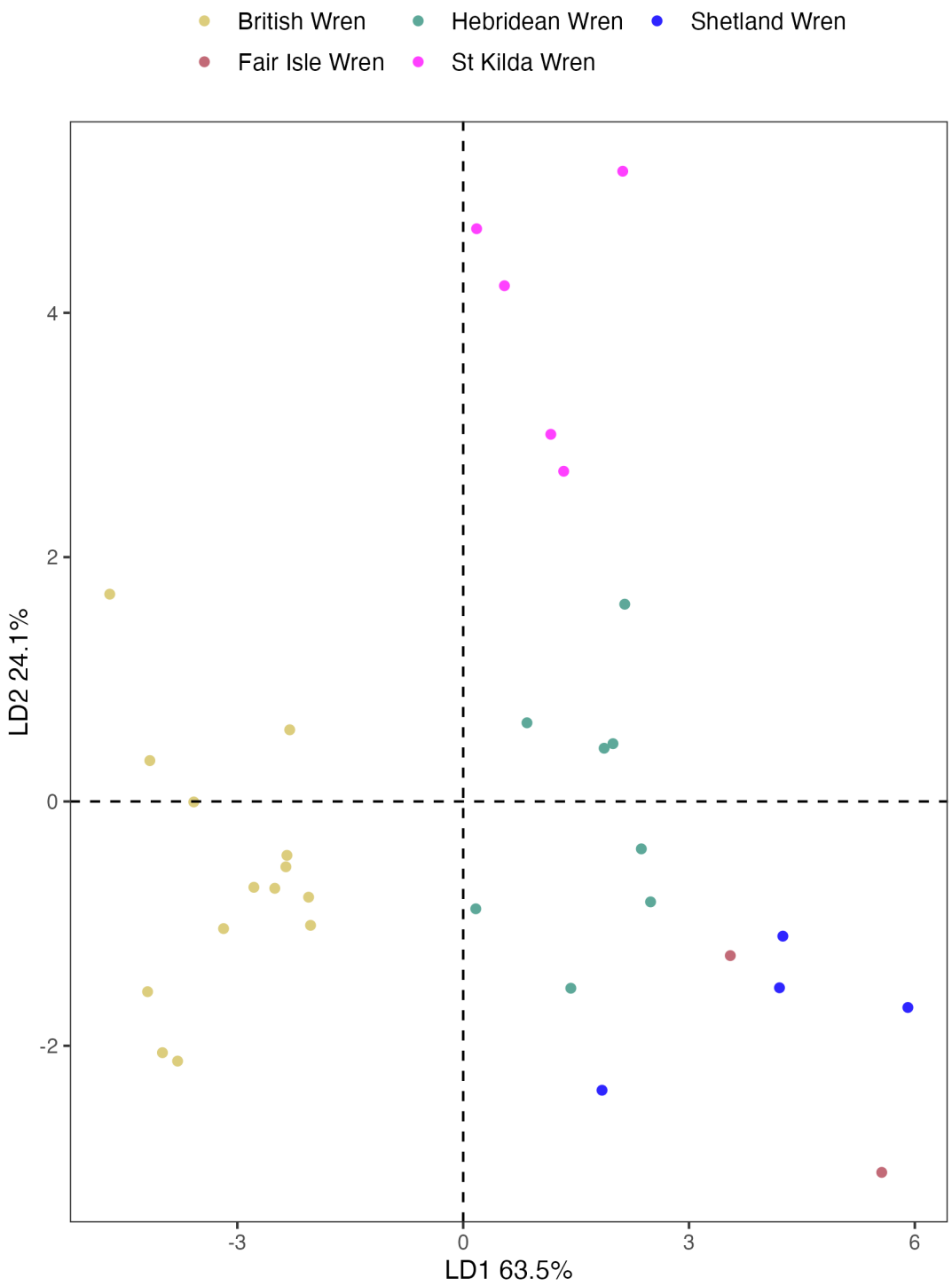

Fig. S12. Linear discriminant analysis of a training subsample (n = 33) of the sound recording dataset (n = 55). This subsample was used to train the prediction of the LDA model presented in the main text.

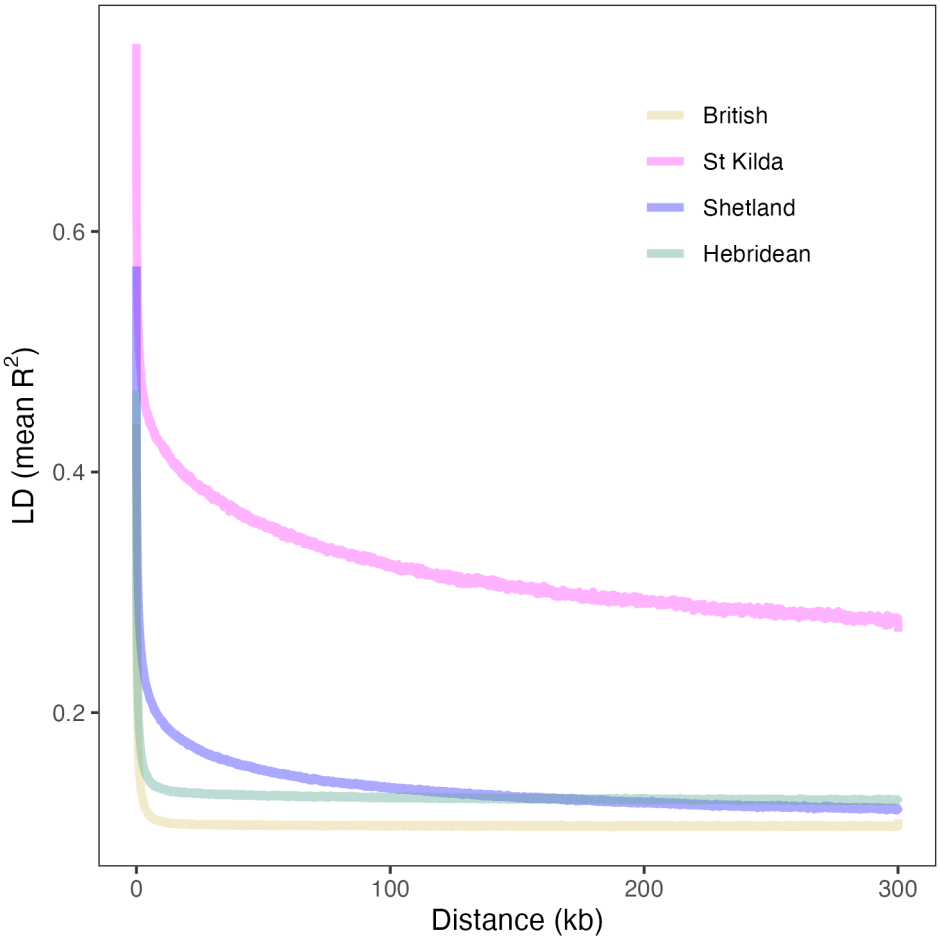

Fig. S13. Patterns of linkage disequilibrium (LD) decay along the genome for four of the Wren subspecies. Linkage disequilibrium is expressed as the correlation between loci per distance from the locus.

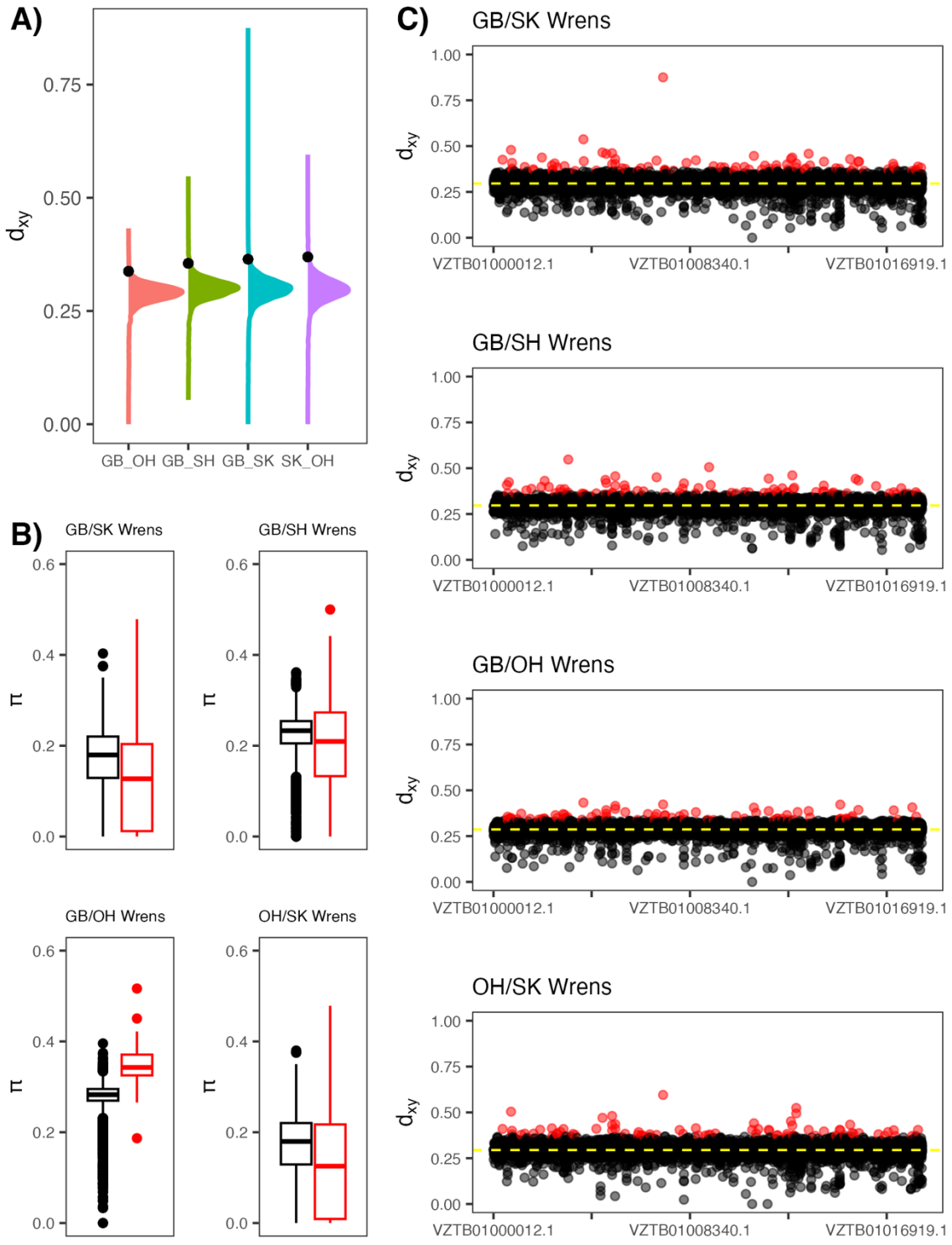

Fig. S14. The statistics of absolute sequence divergence (d_{xy}) between windows in Shetland and St Kilda Wren. **A)** shows the overall pattern of sequence divergence is less contrasting than pattern of F_{ST} (**Fig. 4**). Significant outliers in d_{xy} show less clear-cut differences in nucleotide diversity (**B**), and windowed estimates are less out of the mean.

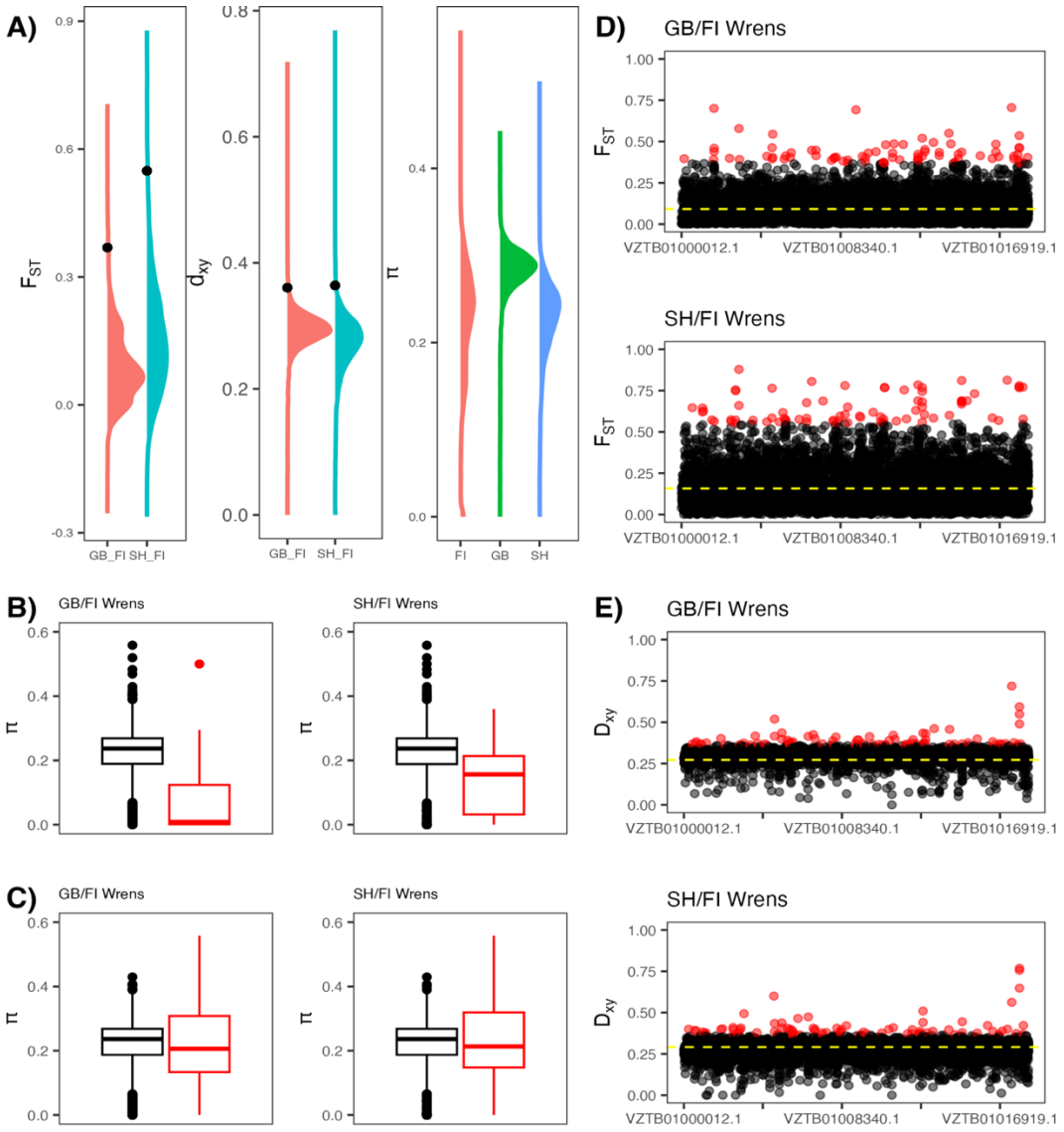

Fig. S15. Patterns of genomic evolution of the Fair Isle Wren. Compared to other populations (see **Fig. 4**) Fair Isle Wrens show similar patterns of genomic evolution, e.g. with respects to patterns of absolute divergence (d_{xy}) in **A)**; patterns of both absolute and relative (F_{ST}) in relation to nucleotide diversity (π) in **B)** and **C)**. However, with respect to F_{ST} and π in **A)** there is a notable 'humped' pattern of distribution, similar to St Kilda (see **Fig. 3**). Patterns of window-based F_{ST} in **D)** show a considerable degree of differentiation both with respect to British and Shetland Wren. However, patterns of absolute divergence in **E)** show a focused peak of molecular evolution.

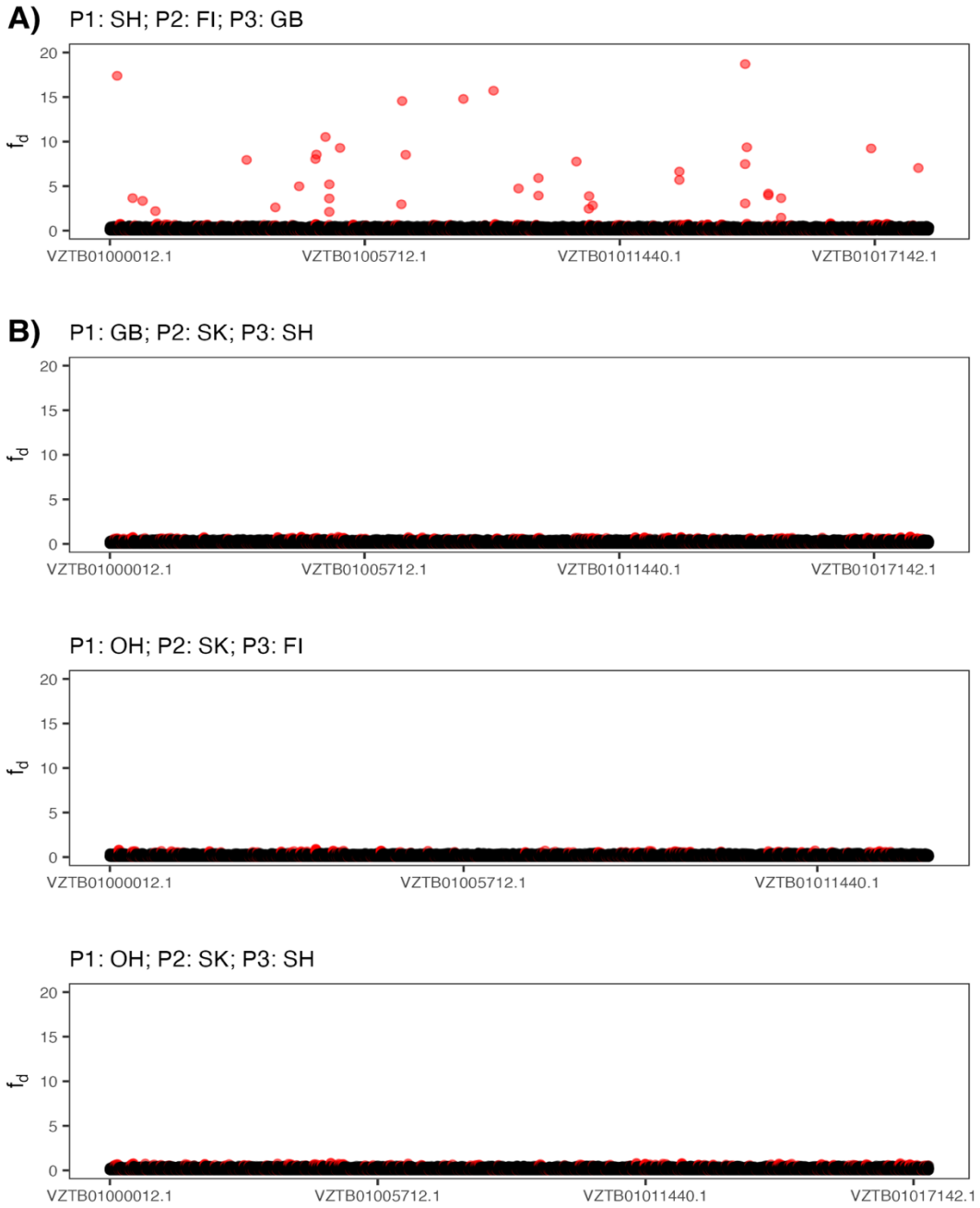

Fig. S16. Patterns of introgression along genome windows in comparisons found to have significant overall D-statistics (**Table 1**). The comparisons include assessment of **A)** introgression between Fair Isle and Shetland populations, showing widespread large introgression in some parts of the genome. **B)** introgression does not reveal larger introgression in any part of the genome. Significant (red) windows represent top 1% of the scores in the genome (see Methods).

Discussion

The study of populations and species on islands can enhance our understanding of a diversity of biological phenomena, including speciation (Gillespie & Roderick, 2002; Jønsson et al., 2012; Landis et al., 2018), natural selection (Clutton-Brock & Pemberton, 2004; Grant & Grant, 2006), and the pattern of trait similarity known as the island syndrome (Clegg & Owens, 2002; Covas, 2012; Wright et al., 2016). Unfortunately, many island populations and species are also at extreme risk of extinction (Matthews et al., 2022; Rozzi et al., 2023). Indeed, some of the evolutionary patterns contributing to the island syndrome, and thus the opportunity to study speciation and adaptation on islands, have already been permanently lost following extinctions (Sayol et al., 2020). Therefore, the need to document the biology of island species is urgent. In my thesis, I have used two approaches to study island systems: i) reviewing and describing the global patterns of evolution on islands; and ii) investigating how the divergence of island populations from their mainland relatives may be associated with trait evolution consistent with the island syndrome.

Main findings

Chapter 1 (Jezierski et al., 2023) outlines the extent (in terms of both taxonomy and biological traits) of the island syndrome, and describes its supporting evidence. Frequently, the supporting evidence for certain traits (e.g. sociality) being impacted by the island syndrome is limited to one or two comparative studies, or even to anecdotal evidence alone (e.g. predator naivety). Research on the island rule (the tendency to become middle-sized on islands) is well-established, as is the evolution of flightlessness (wherein island birds tend to shift towards leg-based locomotion). Island life histories have also received broad scientific attention, albeit not in great depth. I conclude that the island syndrome requires further description and needs to be studied using large sample sizes, which are more representative of the diversity of the focal group. It is necessary to account for the existence of species that are now extinct, and to use phylogenetic comparative methods.

Chapter 2 (Jezierski 2024) makes use of a reproductive life history trait known to show patterns consistent with the island syndrome – clutch size (Covas, 2012). Using a sample of more than 40% of bird species, I find that birds evolve smaller clutch sizes on islands, consistent with what would be expected under the island syndrome (Jezierski, 2024). Overall, this result advances our knowledge of the island syndrome in three ways: i) I show that larger sample sizes and phylogenetic comparative methods can recover different patterns to studies that do not use these approaches (e.g. no evidence of a previously reported (Covas, 2012) interaction of latitude and island endemicity); ii) I show that the island syndrome in clutch size is evident across disparate ecological and phylogenetic groups of birds; and iii) I show that the pattern of clutch size evolution on

islands is consistent with the expectation, stemming from the theory of island biogeography, that the island syndrome should be stronger the smaller the inhabited island area. Although this piece of work does not identify the driver behind the reduction in clutch size on islands, it demonstrates that the island syndrome follows expected patterns at a global scale.

Chapter 3 makes use of a similar approach to Chapter 2, but focusses on the macro-ecological correlates of nest architecture in birds. Nest architecture is presented as a multivariate trait (following recent suggestions (Medina, 2019)) across all birds with readily available data. This approach identified predator diversity and body mass as the strongest predictors of nest architecture (climate and island endemicity were also significant model terms). With respect to the island syndrome, I demonstrate a 'simplification' of nests on islands – manifesting as a tendency for more basal, ground-located and simply-constructed nests. Being an island endemic has a significant impact on nest architecture evolution, even after accounting for lower predator diversity. This study investigated the potential drivers of evolution correlatively, as is frequently done in island syndrome studies (Lomolino et al., 2012; Ponti et al., 2023).

Chapter 4 fulfils the recommendation (often repeated by ornithologists, and highlighted in the literature review that forms Chapter 1) to engage in descriptive work to provide more information on island species, and presents an in-depth natural history study of a set of island populations. I investigated the insular diversification of Eurasian Wrens (*Troglodytes troglodytes*) in the British Isles. I show that these Wrens form three distinct lineages: a St Kilda clade; a Shetland/Fair Isle clade, and a British/Hebridean clade. The St Kilda and Shetland Wren subspecies show convergence in morphology, consistent with the island syndrome, despite vocal and genetic divergence. They also share patterns of genetic differentiation, although these are not obviously related to the observed phenotypic similarities. This study clarifies taxonomic relationships amongst the Wren subspecies, which have been ambiguous since their description.

Quantifying the island syndrome as an evolutionary pattern

Although many studies consider the island syndrome as an evolutionary pattern, explicitly modelling trait evolution in relation to island endemicity (Sandvig et al., 2019; Cooney et al., 2020), other works considered phylogenetic variation only in limited ways (Covas, 2012; Biddick et al., 2019). Characterising the island syndrome as a change in traits, without considering broad-scale phylogenetic history (as opposed to simple sister-species comparisons) causes issues in the interpretation of studies of the island syndrome (Jezierski et al., 2023; Whittaker et al., 2023). For example, not including phylogenetic history hinders our ability to satisfactorily identify the island syndrome as an evolutionary pattern, since (i) change along a phylogenetic tree is not shown, (ii) issues of statistical non-independence arise due to the shared origin of traits; and (iii) there is no consideration of the evolutionary dynamics of traits within clades, which may bias any inferred correlations. These methodological shortcomings are largely responsible for the criticism that groups found to evolve 'more' in island settings can bias whether a model applied to a sample of species recovers islands as significant correlates of evolution in island species (Meiri et al., 2008; Meiri et al., 2011). In this thesis, phylogenetic comparative methods correct for such clade-specific changes in trait evolution, and allow for the testing of the island syndrome at a global scale (see Chapters 2 and 3).

The evolutionary drivers of the island syndrome

The fundamental objective of this thesis was to examine the island syndrome as an evolutionary pattern. Phylogenetic comparative methods achieve that, as presented, but the results immediately beget a question – what are the evolutionary drivers of the island syndrome? Throughout this thesis, the treatment of this question has been purposefully agnostic – whilst drivers are acknowledged, they are not discussed in depth, nor are the observed evolutionary patterns attributed to any particular driver (with the exception of parts of Chapter 3).

As stated in the Introduction of this thesis, the island syndrome is thought to arise due to repeated evolution towards certain trait values, caused by the inherent similarity of all island ecosystems (MacArthur & Wilson, 1967). This similarity stems from the basic tenets of the theory of island biogeography, where island size and isolation limit the number of species on islands and alter the dynamics of their populations (e.g. by increasing population density). Paired with the overall resource limitation on islands (due to size as well as geology), this leads to biotic communities that are species depauperate and disharmonic (i.e. lacking ecological groups that should be present) (Simberloff, 1995; Whittaker et al., 2023). Such biotic communities are meant to be characterised by lower predation and inter-specific competition, and these factors, together with more benign climate and limited resources, are often cited as drivers of the island syndrome (Lomolino et al., 2012, Covas, 2012). Furthermore, explanations for the island syndrome that do not invoke adaptive change in response to island conditions have also been suggested. The most notable ones are immigrant selection (Burns & Pugnaire, 2005; Lomolino et al., 2012) (i.e. colonising islands favours certain traits, and hence they

appear more often on islands), and drift in the absence of natural selection (Lomolino, 2005; Biddick & Burns 2021). Notably, the latter still requires a lack of predation and competition, so the drivers remain the same, only the nature of the evolutionary process is meant to differ.

Whilst the purported drivers of the island syndrome were already discussed in the final chapter of *The Theory of Island Biogeography*, little empirical study has examined their contributions or mechanisms. Lomolino et al. attempted to quantify the contributions of different drivers of the island syndrome, and identified a role for predation and competition by showing stronger manifestations of the island rule on islands with fewer predators and competitors (in mammals). Ever since, this study has been cited as the main source of the 'low predation' notion, e.g. in Wright et al., 2016, Benítez-López et al., 2021 and Ponti et al., 2023. Notably, the 'low predation paradigm' has only been explored by quantifying the number of potential predators. However, islands rarely lack predators. They are often present, and might themselves be island endemic species (e.g. Hawaiian Hawk (*Buteo solitarius*) or the White-bellied Goshawk (*Accipiter haplochrous*) of New Caledonia). Although a drop in predator diversity may be inferred to result in lower predation (as fewer predator species pose a threat), the island syndrome posits greater use of available niche space by island species (Scott et al., 2003), whilst island populations are often denser than mainland ones (MacArthur and Wilson, 1967). Therefore, the island syndrome, as we understand it today, may cause species depauperate island predator communities to exert significant levels of predation, due to the higher density of predators and their potential wider diversity of chosen prey.

The above example presents just one counter-hypothesis to the currently popular notion on the drivers of the island syndrome. The current issue in driver research is that these hypotheses are rarely empirically tested, in no small part due to the inherent difficulty in testing such mechanistic links at biogeographical scales. Naturally, the proposed drivers are likely to be true, as predictions about their impact stem from well-proven theory of island biogeography (MacArthur & Wilson, 1967). However, the lack of empirical evidence, in my opinion, merits refusing the parroting of statements with weak support. Going further, understanding the drivers of the island syndrome will require better meta-analytical appraisal to quantify the current knowledge, and more in-depth quantitative studies. Correlational studies at broad geographical scales, akin to Lomolino et al, 2012, are the cornerstone of biogeographical studies, and will remain so in the study of drivers. I would suggest that as we test for drivers, we attempt to make clearer hypotheses about mechanistic links (i.e. which driver acts on which trait and in which direction), so that the observed correlations allow inference regarding the biology of island species. This thesis attempts that in Chapter 3, with the trait acted on, the kind of interaction and use of diversity of predators as a proxy being clearly defined. However, a correlation of body size with number of predator species does not achieve, in my opinion, this precision – do predators select for body size? Is it an impact on life history of which body size is a proxy? Is the expected pattern of the island rule possible given such direct impact of predators on the body size? Going further, such deeper questioning of observed patterns, paired with occasional opportunities to test drivers empirically, could be successful in showing how the island syndrome evolves. Such efforts will be particularly fruitful in taxonomic groups whose evolutionary relationships and biology are very well-understood.

Birds as a system to study the island syndrome

Theory suggests that the island syndrome should be generalisable, as the conditions causing it should be repeated across the world's islands (MacArthur & Wilson, 1967; Wright et al., 2016; Jezierski et al., 2023; Jezierski, 2024). Therefore, if the island syndrome is a general pattern, we should be able to identify the pattern across all major taxonomic groups. However, to date, such efforts have been limited due to a lack of trait and phylogenetic data (Jezierski et al., 2023; Whittaker et al., 2023). Birds offer an unmatched system with which to investigate the island syndrome, due to a recent increase in publicly available datasets spanning diverse traits (Sheard et al., 2020; Tobias et al., 2022; Sheard et al., 2024), near-complete phylogenetic data (Jetz et al., 2012), and the ready availability of distributional and ecological information (Billerman et al., 2020; Hoyo & Allen, 2020). Furthermore, birds are prime island colonisers, with some 20% of species found on islands (Tershy et al., 2015). Island birds span a diversity of ecological groups, including migratory and marine species, offering 'phylogenetic experiments' with which to identify whether the island syndrome is truly general, across even very disparate clades (Wright et al., 2016; Jezierski et al., 2023). Finally, due to the unmatched knowledge of the biology of many species, and a long record of natural history, the island syndrome can not only be described as a pattern, but also investigated with respect to drivers, particularly where they have historically changed. In this thesis, I use birds across all three empirical chapters, capitalising on the rich availability of resources to study their evolution (trait data, phylogenetic data, reference genomes), to show the island syndrome as a global evolutionary trajectory, and its possible role in divergence among islands.

Natural history is crucial to describe the pattern, and ultimately the drivers of the island syndrome

Although this thesis relied on the unmatched quantity and quality of bird natural history data to study the island syndrome (Billerman et al., 2020), significant gaps remain, as discussed in Chapters 1 and 3. These gaps stem from a lack of natural history data across species and particular traits (e.g. nesting behaviour). Continued specimen collection and recording of natural history data (Lima, 2024) is paramount for further ecological and evolutionary research (Diamond, 1987; Rocha et al., 2014). As shown in Chapter 4, continued natural history effort will not only generate additional data for comparative approaches, but will also allow for investigation of the role of the island syndrome in underpinning micro-evolutionary patterns. For example, the St Kilda Wren has been observed and described for over 300 years (this has included extensive specimen collection (Love, 2009)). In that period of time, the islands of St Kilda have undergone significant environmental change, with most significant event being the end of permanent human habitation in 1930s, resulting in the extinction of cats (Love, 2009). Thanks to generations of natural historians, it will be possible to study evolutionary trajectories in the St Kilda Wren, and to be able to disentangle drivers – changing predation pressure being one example. Future study could not only more deeply probe the observed genetic signs of divergence in the St Kilda Wren, but also try and reconstruct genetic evolution before and after the extinction of predators. Other studies that examined island systems with changing predation pressure have shown rapid responses (Blumstein & Daniel, 2005; Vanderwerf, 2012), much more convincingly making the case for predation as a driver of the island syndrome than simple correlative work.

Conclusion

The island syndrome is a global phenomenon of trait similarity among island species. The unique traits of these island species make them highly evolutionarily distinct and are responsible for their threatened status. Despite being a 'textbook' example of a biogeographical pattern, the island syndrome remains understudied, both with respect to its pattern and drivers. This thesis has comprehensively assessed the extent of our knowledge about the island syndrome in birds, both as a global pattern of similar evolutionary trajectories on islands, and as a potential driver in the divergence of island species. I demonstrate the generality of the island syndrome as an evolutionary pattern in island organisms, which suggests the syndrome is a global phenomenon of convergent evolution. At the same time, continued effort to study island species and populations will help document vanishing island diversity, aid comparative analyses, and inform efforts to understand the ways in which the island syndrome may contribute to species divergence.

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